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RESEARCH ARTICLE

Forecasting potential invaders to prevent future biological invasions worldwide

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Abstract

The ever-increasing and expanding globalisation of trade and transport underpins the escalating global problem of biological invasions. Developing biosecurity infrastructures is crucial to anticipate and prevent the transport and introduction of invasive alien species. Still, robust and defensible forecasts of potential invaders are rare, especially for species without known invasion history. Here, we aim to support decision-making by developing a quantitative invasion risk assessment tool based on invasion syndromes (i.e., generalising typical attributes of invasive alien species). We implemented a workflow based on 'Multiple Imputation with Chain Equation' to estimate invasion syndromes from imputed datasets of species' life-history and ecological traits and macroecological patterns. Importantly, our models disentangle the factors explaining (i) transport and introduction and (ii) establishment. We showcase our tool by modelling the invasion syndromes of 466

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amphibians and reptile species with invasion history. Then, we project these models to amphibians and reptiles worldwide (16,236 species [c.76% global coverage]) to identify species with a risk of being unintentionally transported and introduced, and risk of establishing alien populations. Our invasion syndrome models showed high predictive accuracy with a good balance between specificity and generality. Unintentionally transported and introduced species tend to be common and thrive well in human-disturbed habitats. In contrast, those with established alien populations tend to be large-sized, are habitat generalists, thrive well in human-disturbed habitats, and have large native geographic ranges. We forecast that 160 amphibians and reptiles without known invasion history could be unintentionally transported and introduced in the future. Among them, 57 species have a high risk of establishing alien populations. Our reliable, reproducible, transferable, statistically robust and scientifically defensible quantitative invasion risk assessment tool is a significant new addition to the suite of decision-support tools needed for developing a future-proof preventative biosecurity globally.

KEYWORDS

biodiversity informatics, blacklist, global biodiversity data, herpetofauna, invasive alien species, macroecology, pathways, phylogenetic imputation

1 | INTRODUCTION

The realisation of the damages and risks of alien species invasions to ecosystems and socio-economy (Bacher et al., 2018; Diagne et al., 2021; Hawkins et al., 2015) have prompted countries worldwide to develop and enforce biosecurity policies and strategies (Kunming-Montreal Global Biodiversity Framework—Convention on Biological Diversity, 2022; IPBES, 2023). Yet, decades after the initial calls for improved management of invasive alien species (Drake et al., 1989; Williamson et al., 1986), the global problem of biological invasions continues to escalate (Fenn-Moltu, Ollier, Bates, et al., 2023a; Fenn-Moltu, Ollier, Caton, et al., 2023b; Leroy et al., 2023; Pili et al., 2023; Richardson et al., 2023; Seebens et al., 2017), reflecting systemic failures in meeting biosecurity targets (IPBES, 2023; Latombe et al., 2023). Notably, a crucial biosecurity oversight is the integration of, and increasing access to, new source regions into the global flows of alien species (Hudgins et al., 2023), notwithstanding the shifting importance and the emergence of new transport and introduction pathways (Hulme, 2009; Hulme & Firn, 2015; Leroy et al., 2023; Seebens et al., 2018; Toomes et al., 2019). Thus, an integrated biosecurity plan that can anticipate and prevent future alien invaders and their invasions is needed now more than ever (Finnoff et al., 2007; Leung et al., 2002; Pyšek & Richardson, 2010). This would be the most cost-efficient route to meeting global targets (e.g., Kunming-Montreal Global Biodiversity Framework Target 6: reduce rates of introduction and establishment by at least 50% by 2030; Convention on Biological Diversity, 2022) since managing alien species' invasions becomes exponentially more difficult and expensive as species transcend the stages of the

invasion process (transport, introduction, establishment and spread; Ahmed et al., 2022; Blackburn et al., 2011; Pyšek & Richardson, 2010; Simberloff et al., 2005; Wittenberg & Cock, 2001).

A fundamental component of preventative biosecurity strategies is warning list systems (a.k.a, blacklist, alert list, watch list; Dawson et al., 2022; Essl et al., 2011; Faulkner et al., 2014; Roy et al., 2019; Roy et al., 2014). Warning lists help guide preventative biosecurity policies and strategies by identifying which alien species pose a risk of becoming invasive if introduced. Preventative biosecurity might include banning the import of listed species, intercepting them at the source region or at the border or closely monitoring them upon entry. Developing warning lists involves assessing the invasion risk of alien species before they arrive, based on their likelihood of succeeding at each stage of the invasion process, as well as their environmental and socio-economic impacts (Heger & Trepl, 2003; Hulme, 2006; Kolar & Lodge, 2001). By identifying beforehand which species have a risk of invasion if introduced, warning lists provide the much-needed science-based decision support for preventative biosecurity (Heger & Trepl, 2003; Hulme, 2006; Kolar & Lodge, 2001; Leung et al., 2002, 2005). The usefulness of warning lists is globally recognised. For example, a horizon-scanning exercise by Roy et al. (2014) in 2013 resulted in a ranked list of species likely to invade Great Britain over the following decade. And within 2 years of its publication, seven of their top-listed species were newly recorded in the country (Aldridge et al., 2014; Roy et al., 2019). But, notably, the criteria used in developing warning lists (Figure 1a) come with caveats. For instance, well-known trade and transport proxies poorly predict propagule pressure or transport risk (Pili et al., 2023; Seebens et al., 2018, 2017; Suhr et al., 2019). Meanwhile, assessing

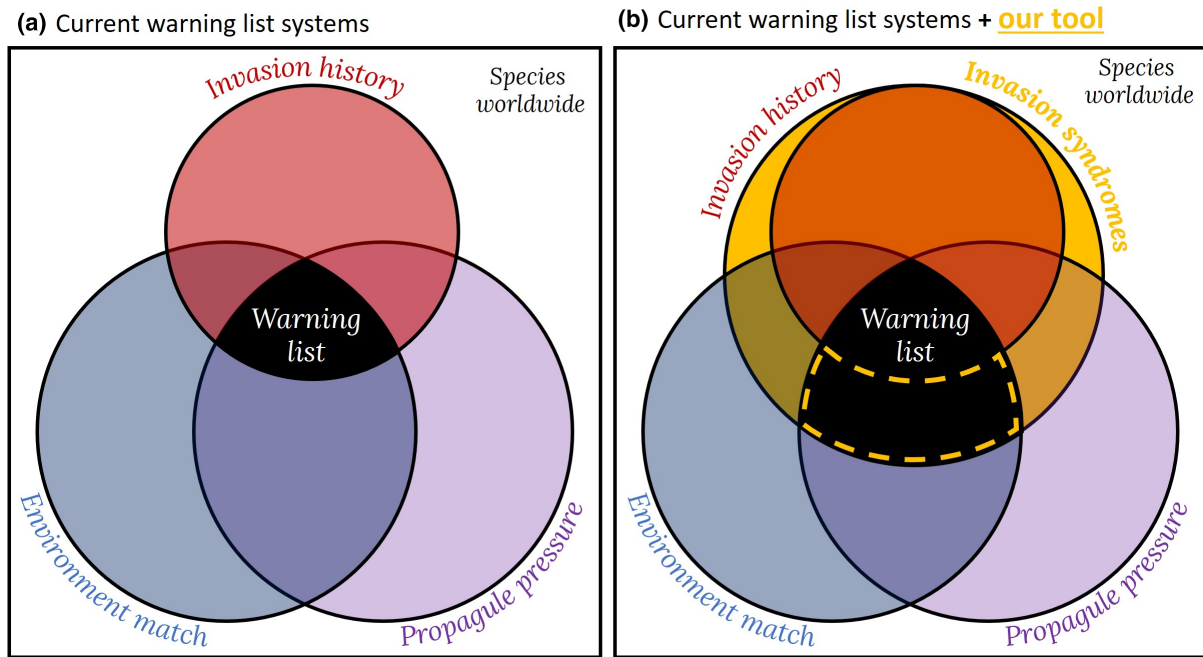


FIGURE 1 Strong and commonly used criteria in horizon-scanning exercises for developing warning lists: invasion history—does the species have a history of invasion elsewhere? propagule pressure—does the species have the opportunity to be transported and introduced into a jurisdiction? and environmental suitability—can the species survive, reproduce and establish an alien population given the environmental conditions in a jurisdiction? (a) Species that satisfy these three criteria are included in warning lists. (b) Our tool complements current horizon scanning for developing warning lists by identifying species worldwide with no prior history of invasion, but likely to have some or all attributes consistent with invasion syndromes. The Venn diagram is modified from Faulkner et al. (2014—Biological Conservation).

environmental suitability or geographic invasion risk is challenged by ecological niche shifts and environmental non-equilibrium in alien species' invasions (Pili et al., 2020). Altogether, these caveats undermine the confidence of invasion risk assessments and limit their capacity to robustly and defensibly forecast potentially invasive alien species (Bomford, 2008; Hayes & Barry, 2007; Pili et al., 2020, 2023).

Arguably, the most limiting criterion of warning lists is their reliance on invasion history—whether a given species has a history of invasion elsewhere (Figure 1a; Bomford et al., 2005; Faulkner et al., 2014; Hulme & Firn, 2015; Kulhanek et al., 2011; Ricciardi, 2003; Richardson & Thuiller, 2007). The use of invasion history arises from a deceptively simple premise: species that have a history of invasion possess intrinsic and/or inherent attributes that may also allow them to become invasive elsewhere (hereafter 'invasion syndromes'; Hayes & Barry, 2007; Novoa et al., 2020). But the logical flaw in using this criterion is that many species, despite having some or all attributes consistent with invasion syndromes, are yet to be transported, introduced, and/or establish alien populations beyond their native ranges and, therefore, have no invasion history (hereafter 'potential invaders'; Figure 1b; Bomford et al., 2005; Kulhanek et al., 2011; Ricciardi, 2003; Richardson & Thuiller, 2007; Seebens et al., 2021). Given the escalating rate of new biological invaders and invasions (Fenn-Moltu, Ollier, Bates, et al., 2023a; Fenn-Moltu, Ollier, Caton, et al., 2023b; Pili et al., 2023; Seebens et al., 2017; Toomes et al., 2019; Turner et al., 2021), relying on

information on invasion history may overlook a large proportion of current and future invasions (Figure 1b). Consequently, there is a pressing need to advance warning lists so that they can robustly and defensibly assess the invasion risk of species with no prior history of invasion. Ultimately, this is a fundamental prerequisite in forecasting and responding to the escalating global problem of alien species invasions.

In this study, we advance quantitative invasion risk assessment tools to allow invasion biologists and biosecurity authorities to identify invasion syndromes and forecast potential invaders. Following a MICE workflow (Multiple Imputation with Chained Equation; Figure 2; White et al., 2011), our tool first statistically estimates the values of missing data (i.e., imputation) in datasets of two types of predictor variables. These predictors characterise species' inherent and intrinsic attributes: (i) life-history and ecological traits (hereafter 'traits')—organismal-level intrinsic attributes depicting how typical individuals of a species allocate time and energy to reproduction, growth and survival (Ricklefs & Wikelski, 2002; Stearns, 1992), and (ii) macroecological patterns—species-level inherent attributes describing species distribution, abundance and resource use (Keith et al., 2012). Second, the trait and macroecological data are used to model invasion syndromes. Recognising that only a subset of species has had the opportunity to go through invasion stages after transportation (Blackburn et al., 2011; Chapple et al., 2012; Sinclair et al., 2019), our tool follows a two-step modelling process by

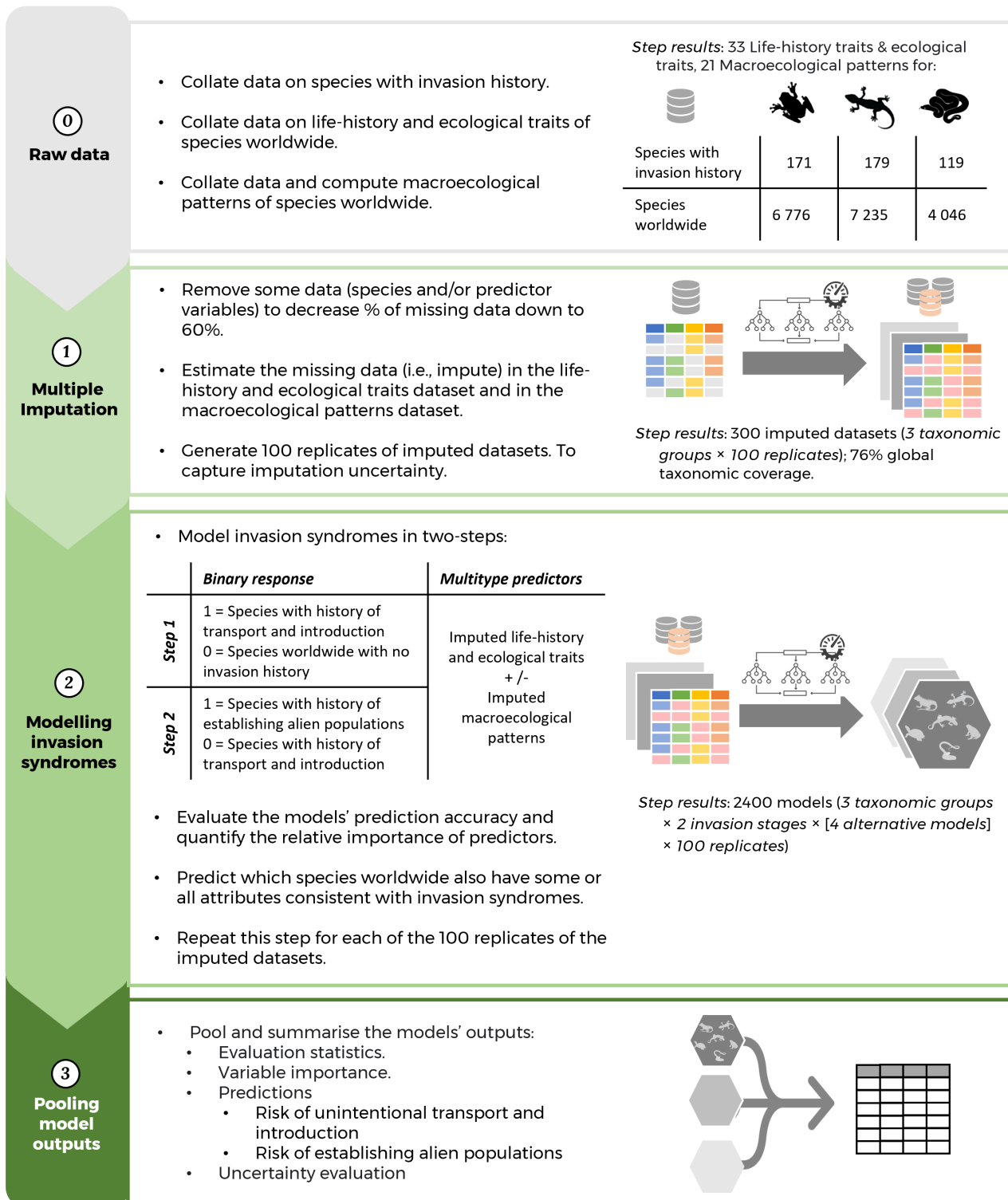


FIGURE 2 Our quantitative invasion risk assessment tool. Our tool follows a Multiple Imputation with Chain Equation Approach (MICE), comprising three steps: (1) multiple imputation—estimating the values of missing entries (i.e., imputation) in life-history and ecological traits dataset and macroecological patterns dataset. This is repeated 100 times to capture uncertainties in estimated values; (2) modelling invasion syndromes—each imputed dataset are used to fit models for identifying the attributes of successful biological invaders (i.e., invasion syndromes). Steps 1 and 2 are replicated a hundred times. (3) pooling model outputs—all models' inference on variable importance, evaluation metrics and predictions of invasion risk are pooled and summarised.

separately identifying the invasion syndromes of (1) transported and introduced alien species and, among them, (2) species that have established alien populations. The first and second steps are replicated

a hundred times to capture uncertainties brought by the imputation process. Finally, the outputs of the replicates of the invasion syndrome models are pooled and summarised. Our tool has the potential

to improve the effectiveness of warning lists because it is not limited to the subset of species with a history of invasion. Instead, it uses all information available at the organismal and species level to predict invasion risks. Because of the two-step modelling process, our tool disentangles the syndromes explaining (i) transport and introduction and (ii) establishment, and predicts separate risk assessments for each invasion stage to species worldwide. We demonstrate here our framework in addressing three guiding research questions:

Research question 1 [*invasion syndromes*]: what are the differences in the invasion syndromes of transported and introduced species compared to those with established alien populations? The invasion process involves a series of stages, with each stage filtering a taxonomically biased subset of species from advancing to subsequent stages through combinations of filters (Blackburn et al., 2011; Chapple et al., 2012; Sinclair et al., 2019). Given this, we predict that the syndromes of a typical transported and introduced species (attributes that help in overcoming entrance, survival and exit filters; Sinclair et al., 2019) are not necessarily the same as those of species that have established alien populations (attributes that help in overcoming environmental and demographic filters; Blackburn et al., 2011).

Research question 2 [*life-history and ecological traits vs. macroecological patterns*]: are macroecological patterns better than traits in predicting invasions? Studies have primarily focused on traits associated with invasion success, and they have so far found that (1) different traits are correlated with each invasion stage; (2) there are few traits strongly or significantly correlated with success in each invasion stage; and (3) there has not been a consistent trait of invasiveness across taxa, (4) nor among groups of species using different pathways (Bernery et al., 2022; Hayes & Barry, 2007; Heger & Trepl, 2003; Pysek et al., 2011; Sol et al., 2012). What has been consistent across studies is that species with large geographic range size are more likely to succeed in establishing alien populations (Cadotte et al., 2006; Duncan et al., 2001; Forsyth et al., 2004; Gallien et al., 2019; Hayes & Barry, 2007; Hui et al., 2011). Notably, commonness in the native range, habitat generalism and tolerance to human disturbance are other macroecological patterns suggested to be strong predictors of invasion success (Duncan & Williams, 2002; Gallien et al., 2019; Hayes & Barry, 2007; Jeschke & Strayer, 2006). Thus, we predict that macroecological patterns are relatively better than traits in predicting success across invasion stages.

Research question 3 [*potential invaders*]: which (and how many) species worldwide with no prior history of invasion have attributes consistent with syndromes that predispose them to be transported and introduced? And among them, which also have attributes consistent with syndromes of species that have established alien populations? Studies have shown that the rate of species establishing alien populations is continuously increasing, with no signs of saturation in the near future (Seebens et al., 2017, 2021). Moreover, the tens rule—a classical null hypothesis in invasion biology—suggests that only a tenth of species will successfully overcome the consecutive stage of the invasion process (Jeschke & Pyšek, 2018; Jeschke et al., 2012; Williamson & Brown, 1986; Williamson &

Griffiths, 1996). Thus, we expect that only a tenth of species worldwide have attributes consistent with invasion syndromes that will help them succeed in each consecutive stage of the invasion process.

We answered these questions by applying our tool to unintentionally transported and unintentionally introduced species (hereafter 'unintentionally transported and introduced species') because of this pathway's increasing importance to the current and future global flows of alien species (Kraus, 2009; Pili et al., 2019, 2023; Turner et al., 2021; Wilson et al., 2009). Such species are unintentionally transported by humans as contaminants of commodities or stowaways of transport vectors (Harrower et al., 2018; Scalera et al., 2016). Especially in jurisdictions lacking biosecurity infrastructures, unintentionally transported alien species tend to be directly introduced into novel areas (Blackburn et al., 2011; Sinclair et al., 2019). While intentionally transported and introduced species are oftentimes used by humans because of specific traits, unintentionally transported and introduced species can have traits that facilitate their undetected transportation or escape. Thus, the drivers and dynamics of the unintentional transport and introduction pathway are sufficiently unique to warrant separate studies (Bernery et al., 2022; Chapple et al., 2012; Measey et al., 2019; Mohanty & Measey, 2019; Pysek et al., 2011; Tingley et al., 2010).

Moreover, we focused on amphibians and reptiles worldwide as a case study. These taxa are quintessential examples of unintentionally transported and introduced species that are often overlooked or neglected by biosecurity agencies worldwide (Pysek et al., 2008) despite the many studies showing their concerning environmental and socio-economic impacts (Kraus, 2015; Measey et al., 2016; Soto et al., 2022). Many amphibians and reptiles are among the world's worst invasive alien species (Lowe et al., 2000) for causing massive and irreversible impacts across ecological scales (reviewed in Kraus, 2015; also see Holsbeek & Jooris, 2010; Measey et al., 2016; Savidge, 1987; von Takach et al., 2022). The global economic costs of damages wrought by and management of invasive alien amphibian and reptile invasions amount to more than US\$17.0 billion between 1986 and 2020 (Soto et al., 2022).

2 | MATERIALS AND METHODS

The glossary of key terms used throughout the paper is presented in [Box 1](#).

2.1 | Data

2.1.1 | Invasion history

We compiled a global list of amphibians and reptiles that have been unintentionally transported and introduced. Among these, we also identified those that have successfully established alien populations. These data sources include online databases, published scientific literature and reports (species list and references are provided in

BOX 1 Glossary of key terms.

Warning list—list of alien species that are currently not occurring in a jurisdiction, but with a risk of invasion if introduced.

Invasion history—whether a given species has a history of invasion elsewhere.

Invasion syndromes—the set of inherent and intrinsic attributes that predispose a species to being transported, introduced, and/or establishing alien populations.

Life-history and ecological traits—organismal-level intrinsic attributes depicting how typical individuals of a species allocate time and energy to reproduction, growth and survival.

Macroecological patterns—species-level inherent attributes describing species distribution, abundance, and resource use.

Unintentionally transported and introduced species—any species that has contaminated a commodity (i.e., contaminant) or entered a transport vector (i.e., stowaway) destined to be moved into locations beyond the species' native or current invaded range.

Established alien species—alien species that survived, reproduced and maintained self-sustaining populations in sites where they were introduced.

Imputation—a process of statistically estimating the value of missing data points to allow for complete data analysis.

Imputed dataset—a dataset whose missing values have been estimated via imputation.

Potential invaders—species with no invasion history but have syndromes of transported and introduced alien species (transport and introduction risk score ≥ 30).

High-invasion risk species—potential invaders that also have syndromes of species that have established alien populations (establishment risk score ≥ 30).

Table S1 in Supporting Information S1). We defined 'unintentionally transported and introduced species' as any species that has contaminated a commodity (i.e., contaminant) or entered a transport vector (i.e., stowaway) destined to be moved into locations beyond its native or invaded range (Harrower et al., 2018; Scalera et al., 2016; Sinclair et al., 2019). Therefore, we excluded species that are only known to have been intentionally transported and introduced (e.g., pet trade, aquaculture and aesthetic improvement) from our analysis. Notably, we included in our analysis species, such as the cane toad (*Rhinella marina*), that were initially intentionally transported and introduced but later used unintentional transport and introduction pathways in their spread (secondary long-distance dispersal events; Pili et al., 2019, 2023). Meanwhile, we defined 'established species' as

those that survived, reproduced and maintained self-sustaining populations in sites where they were introduced (Blackburn et al., 2011).

About 488 species (171 frogs [Order Anura], nine salamanders [Order Urodela], 179 lizards [Suborder Sauria], 119 snakes [Suborder Serpentes] and five turtles [Order Testudines]) of amphibians and reptiles have a history of being unintentionally transported and introduced, among which 129 species (39 frogs, two salamanders, 68 lizards, 17 snakes and three turtles) have established alien populations. Due to a low number of representative species, we only analysed frogs, snakes and lizards to avoid compromising the robustness of our statistical analysis. In subsequent analysis, we separately analysed the invasion syndromes of frogs, snakes and lizards.

2.1.2 | Life-history and ecological traits

We retrieved 15 traits of 5836 frog species worldwide from AmphiBIO (V1; Oliveira et al., 2017). We retrieved 17 traits of 7235 lizard species and five traits of 4046 snake species worldwide by harmonising multiple published datasets (Feldman et al., 2015, 2016; Meiri, 2018; Meiri, Avila, et al., 2020a; Meiri, Feldman, et al., 2020b; Slavenko et al., 2022; Zimin et al., 2022). These traits describe the species' activity time, diet, fecundity, microhabitat preference, mode of reproduction, size and substrate preference (see Tables S2.1–3 in Supporting Information S2).

2.1.3 | Macroecological patterns

We retrieved or quantified 21 variables describing species' macroecological patterns. These variables relate to geographic range size, commonness, habitat generalism and tolerance to human disturbance (Tables S2.1–3 in Supporting Information S2). Although presumed to be independent, these three macroecological patterns are triangularly correlated, and one is not necessarily a good predictor of another (see Supporting Information S4; Rabinowitz, 1981; Yu & Dobson, 2000). We retrieved the native geographic range of species from online databases (International Union for the Conservation of Nature Red List v. 2022-2 and the Global Assessment of Reptile Distributions v. 1.7; Gumbs et al., 2020; IUCN, 2022; Roll et al., 2017) or estimated them based on 10-km-radius buffers of species' occurrence records (GBIF.org, 2023a, 2023b). We estimated species' commonness using a metric of the species' relative abundance, measured by summing the raw, cleaned and thinned species' occurrence records in its native geographic range (Enquist et al., 2019). We estimated species' habitat generalism using metrics that describe the diversity of habitats within the species' native geographic range (International Union for Conservation of Nature (IUCN) habitat classification scheme v.3.1; Jung et al., 2020). We estimated the species' tolerance to human disturbance by summarising the human pressures index scores across the species' native geographic range (Venter et al., 2016). Moreover, we also quantified the accessibility of

transport vectors for the species based on the number of airports and seaports, as well as the amount of trade outflows and outgoing passengers from these ports, across the species' native geographic range (The World Bank, 2020a, 2020b). See [Supporting Information S3](#) for more details on how we quantified macroecological patterns.

2.1.4 | Data harmonisation

We harmonised invasion history, traits and macroecological patterns data (hereafter 'harmonised dataset'; following best practice recommendations of Grenié et al., 2022) using standardised and updated taxonomies for global amphibians (Amphibians of the World v.6.2; Frost, 2023; accessed on 1 July 2023 using the 'AmphiNom' package v.1.0 in R; Liedtke, 2018) and reptiles (accessed on 1 March 2023 using the 'taxize' package v.0.9.99 in R; Chamberlain & Szöcs, 2013; Uetz et al., 2022). For species that had been grouped into one species after data harmonisation (e.g., cases of recent taxonomic revision), we took the median (continuous variables) or mode (categorical data) of multiple trait entries.

2.1.5 | Exploratory data analysis

We quality-checked the data by exploring the distribution of each variable, inspecting outliers and analysing the correlation structure among variables (see [Figures S4.1–6](#) in [Supporting Information S4](#)). We also assessed the proportion of species with data for each variable through a missing data exploratory analysis (using the 'naniar' package v.0.6.1 in R; Tierney & Cook, 2023; see [Tables S2.1–3](#) in [Supporting Information S2](#)).

2.2 | Multiple imputation with chained equation

Overview. Data missing not at random have the potential to bias statistical analyses (Little & Rubin, 2019), and this is the case for biodiversity data (Hortal et al., 2015; Penone et al., 2014). To minimise biases brought by missing data and, in turn, optimise confidence in statistical inference and predictions, we modelled the invasion syndromes of alien amphibians and reptiles under a Multiple Imputation using the Chained Equation approach (MICE; Little & Rubin, 2019; White et al., 2011). Our MICE approach involves three steps ([Figure 2](#)): (1) *multiple imputation*—we estimated the values of the missing data (i.e., imputed) in the harmonised dataset using a random forest approach. We separately imputed the dataset of traits and the dataset of macroecological patterns. Each variable was imputed using the rest of the variables in the dataset as predictors; but for traits, we additionally used phylogenetic information (i.e., phylogenetic imputation; Penone et al., 2014). We repeated this multiple times to capture the variability of the imputation process, resulting in 100 imputed datasets. (2) *modelling invasion syndromes*—each

imputed dataset was used to fit a random forest model of invasion syndromes. We employed a two-step modelling process, whereby we first fitted random forest models of the invasion syndrome of unintentionally transported and introduced alien species and then a separate set of models for the invasion syndrome of species that have established alien populations. For each invasion syndrome model, the predictive performance and variable importance were measured. We also projected each invasion syndrome model to data on amphibian and reptile species worldwide to forecast species with some or all attributes consistent with the syndrome of unintentionally transported and introduced species (i.e., potential invaders) and among those species that have established alien populations. Finally (3), *pooling model outputs*—We pooled and summarised the output of invasion syndrome models and their predictions. The advantage of MICE over other imputation approaches is that it provides information on variability/uncertainty in inferences and predictions brought by the data imputation process.

2.2.1 | Multiple imputation

Selection of variables

Because of varying degrees of data missingness across variables (4%–94%; see also [Tables S2.1–3](#) in [Supporting Information S2](#)), we opted to first reduce the harmonised dataset by selecting the most ecologically relevant variable(s) among highly correlated sets of variables. We then gradually removed species (rows), traits and macroecological patterns (columns) with too many missing values until we arrived at a subset with a maximum of 60% missing values (hereafter 'working dataset'; see [Tables S1](#) in [Supporting Information S1](#)). The working dataset retained 5, 10 and 3 traits for frogs, lizards and snakes, respectively, whereas all macroecological patterns were retained. Moreover, the working dataset retained 5817, 6516 and 3525 species of frogs, lizards and snakes (~76% global coverage for amphibians and reptiles, or ~85% coverage for these taxonomic subgroups). Notably, only 157 species of frogs (out of 171), 173 species of lizards (out of 179) and 108 species of snakes (out of 119) with a history of unintentional transport and introduction were retained (see [Table S1](#) in [Supporting Information S1](#)).

Random forest imputation

We separately imputed traits and macroecological patterns using a random forest multiple imputation approach (using the *miceRanger* package in R v.1.5.1; Wilson, 2021). Here, each variable is imputed using the information on all other variables. Life-history and ecological traits are often shaped by evolutionary history (Diniz-Filho et al., 2012, 2015; Guénard et al., 2013), and thus, accounting for phylogenetic information can potentially increase the accuracy of imputation (Penone et al., 2014; Swenson, 2014). Here, we accounted for phylogenetic information when imputing trait data. We retrieved the phylogenetic trees of amphibians and reptiles worldwide from TimeTree (v.5, retrieved 2023-04-15;

Kumar et al., 2022) and used these to quantify 100 phylogenetic eigenvectors using a Phylogenetic Eigenvector Mapping approach (See [Supporting Information S6](#) for more details; Diniz-Filho et al., 2015; Guénard et al., 2013). This series of phylogenetic eigenvectors holds information on the phylogenetic distances among species and clades, as well as the overall topology of the tree (Diniz-Filho et al., 1998, 2012). We used these Phylogenetic eigenvectors as additional imputation predictors of traits (*sensu* Phylogenetic Imputation; Penone et al., 2014). Although supposedly captured by phylogenetic eigenvectors, we also included family taxonomic information as an additional predictor. Contrarily, we did not use phylogenetic information to impute macroecological patterns because of insufficient evidence to soundly assume that macroecological patterns of global amphibians and reptiles are strongly shaped by evolutionary history.

In imputation, random forest models were fitted with a maximum of five iterations, as this level reached optimal correlation convergence and optimal values of central measures, dispersion and accuracy. Moreover, we configured the random forest models to implement a predictive 'mean matching' approach in selecting which values were imputed from model predictions. This selection approach is most useful when variables to be imputed are multimodal, skewed or integers, which is the case for all included traits. We iterated this imputation procedure to produce 100 imputed datasets of traits and macroecological patterns.

Imputation accuracy

We measured the accuracy of the random forest imputation models by computing their out-of-box accuracy (R-squared for numeric variables and classification accuracy rate otherwise) for each variable and at the final iteration. About 90% of variables showed high out-of-box accuracy rates of >0.75 (see [Figures S7.1–7.3](#), [Supporting Information S7](#)).

2.2.2 | Modelling invasion syndromes

To compare invasion syndromes for successfully transported and introduced species and for successfully established species (research question 1), we fitted random forest models (different from the random forest models used in the imputation process) with traits and macroecological patterns (Breiman, 2001; Malley et al., 2012; implemented in 'ranger' package v. 0.15.1 in R; Wright & Ziegler, 2017). We employed a two-step modelling approach. We first modelled the traits and macroecological patterns of unintentionally transported and introduced species contrasted against those of species worldwide. Here, we assumed that all species worldwide have had the opportunity to be unintentionally transported, as it has been shown that alien species intercepted in a given region originated from all across the world, irrespective of the magnitude of international trade (Fenn-Moltu, Ollier, Bates, et al., 2023a; Fenn-Moltu, Ollier, Caton, et al., 2023b; Pili et al., 2023; Turner et al., 2021). We subsequently modelled the traits and macroecological patterns of species

that have established alien populations (only those that had initially or secondarily been unintentionally transported and introduced) contrasted against all species known to have been unintentionally transported and introduced. This two-step approach allowed us to disentangle the syndromes of each invasion stage and separately predict the species' risk of succeeding in each invasion stage. Notably, each invasion syndrome model was replicated 100 times, wherein each replicate model is fitted with one of the 100 imputed datasets.

To assess the relative importance of traits and macroecological patterns in explaining invasion syndromes (research question 2), we refitted invasion syndrome models, but this time with only trait data, only macroecological patterns data, and an optimal subset of traits and macroecological patterns (for the latter, we conducted a stepwise variable selection to select variables contributing the most amount of information to the model; Coelho et al., 2019). This allowed us to investigate whether models fitted with (1) a combination of all traits and macroecological patterns, (2) traits only, (3) macroecological patterns only or (4) an optimal subset of both types of variables were better in predicting invaders (See details in [Tables S2.1–3](#) in [Supporting Information S2](#)).

In total, we fitted 2400 invasion syndrome models (three taxonomic groups × two invasion stages × four alternative models × 100 replicates corresponding to each imputed dataset).

Model fine-tuning and evaluation

To balance model complexity and generality, we fine-tuned each invasion syndrome model by optimising the number of variables to split in each node (*mtry* argument of *ranger()* function). Here, we implemented a *k*-fold cross-validation approach in evaluating model accuracy—we first randomly partitioned the working dataset into five (i.e., *k*-folds), each partition having an approximately equal sample size. We then fitted five invasion syndrome models using four of five (i.e., *k*-1) partitions of the working dataset for training and the remaining partition for testing. We addressed class imbalance by down-sampling (Chen et al., 2004). For example, in modelling invasion syndromes of unintentionally transported and introduced species, we randomly down-sampled species worldwide to equal the number of unintentionally transported and introduced species. We iteratively fitted the five invasion syndrome models by incrementally increasing the number of variables to split in each node from 1 to the total number of predictor variables while leaving the other parameters to their default values. We evaluated accuracy by summarising the five invasion syndrome models' out-of-box accuracy rate, mean absolute error (MAE), area under the receiver operating characteristic curve (AUC), Boyce Index, precision, recall and F1 score (see [Table S8.1](#) in [Supporting Information S8](#) for definitions and interpretation of evaluation metrics). Well-performing models would have high scores for the Boyce Index, AUC, precision and F1 score, and low scores for recall, MAE and out-of-box. We identified the optimal *mtry* as the one that resulted in an invasion syndrome model with the highest Boyce Index.

Variable importance

We measured the importance of each variable based on the accuracy lost from variable permutation (i.e., measuring how randomly shuffling a variable's values reduces model accuracy), averaged across all trees.

Prediction

To forecast potential future invaders (research question 3), we used the invasion syndrome models fitted with the optimal set of variables to predict the probability of unintentional transport and introduction and the probability of establishment of amphibians and reptiles worldwide. We also binarised the probabilities (1 = has some or all attributes consistent with invasion syndrome; 0 = has very few or no attributes consistent with invasion syndrome) using a threshold where positive observations are just as likely to be wrong as negative observations ('sens=spec' criteria of the optimal. thresholds() function of PresenceAbsence package v.1.1 in R; Freeman & Moisen, 2008). Furthermore, we quantified for uncertainty caused by prediction extrapolation and flagged species which have at least one variable with a value beyond the minimum or maximum limits of that used to train the invasion syndrome models (using MESS() function of modEvA package v.3.11 in R; Barbosa et al., 2024).

2.2.3 | Pooling model outputs

We pooled and summarised the outputs of the 100 replicates of invasion syndrome models. We calculated the mean and standard deviation of evaluation metrics, each variable's importance statistic, and each species' predicted probability of unintentional transport and introduction and probability of establishment. The standard deviation of these outputs represents the uncertainty brought by the multiple imputation process. We also computed a 'transport and introduction risk score' and 'establishment risk score' by summing species' binarised predicted probability of unintentional transport and introduction and binarised predicted probability of establishment, respectively, across 100 model replicates. These risk scores thus range from 0 to 100 and can be intuitively interpreted as the confidence level of whether the species have some or all attributes consistent with invasion syndromes and, thus, a predisposition to succeed in the respective invasion stages.

We inspected the traits and macroecological patterns of the predicted species for plausibility, starting with those predicted by the most number of invasion syndrome model replicates (risk scores). We performed a basic scan online, searching for scientific publications and unpublished reports that stated or inferred that a predicted species had been transported or introduced. We used the search query 'species' scientific name' AND 'introduced' OR 'transported' in Google on 21 January 2024. We inspected the first five pages. We found that species predicted by less than 30 of 100 invasion syndrome model replicates are unlikely to be unintentionally transported, introduced and establish alien

populations (e.g., species are endangered or restricted to close canopy forests).

We classified species into three classes: (1) potential invaders—species with no invasion history but with a transport and introduction risk score of 30; (2) high-invasion risk species—potential invaders with an establishment risk score of 30; (3) uncertain risk—all other species that do not fall into the first two groups.

2.3 | R codes

The R script of our quantitative invasion risk assessment tool workflow can be accessed in Zenodo at <https://zenodo.org/doi/10.5281/zenodo.11533251> and in GitHub at <https://github.com/armanpili/ForecastingInvaders>.

3 | RESULTS

3.1 | Differences in the invasion syndromes of transported and introduced species and established alien species

Among traits, measures of body size (e.g., snout-to-vent length for frogs and lizards, total length for lizards and mass for lizards and snakes) and reproductive output (e.g., clutch size for lizards and clutch number for frogs) were the most important variables in predicting both invasion stages (Figure 3). Notably, these traits were relatively more important in predicting species with established alien populations than those unintentionally transported and introduced. Other traits with notable, albeit weak, importance in predicting unintentionally transported and introduced species were diurnal and crepuscular activity times for frogs and lizards, and diet, microhabitat, and saxicolous and arboreal substrates for lizards.

Macroecological patterns are important variables in predicting both invasion stages and are relatively more important than traits (Figure 3). This is especially the case for unintentionally transported and introduced species, where commonness, followed by tolerance to humans (maximum human footprint index), and then distributional overlap with ports with high outgoing passengers and outflows of commodities were consistently the most important variables across taxonomic groups. Meanwhile, for species with established alien populations, human tolerance (maximum, median or minimum human footprint index), habitat selectivity (proportional similarity of occupied vs available habitats), habitat diversity (normalised Levin's index of habitat diversity) and native geographic range size were the most important variables, albeit with varying ranking, across taxonomic groups. Nonetheless, commonness was also a highly important variable for frogs and snakes with established alien populations. Notably, the ranking of relative variable importance did not differ among alternative invasion syndrome models (see Figures S8.1–8.3 in Supporting Information S8).



FIGURE 3 Relative importance of life-history and ecological traits and macroecological patterns (y-axis) on the invasion syndrome models of unintentionally transported and introduced species (blue) and species that have established alien populations (yellow). For life-history and ecological traits, we indicated 'f', 'l' or 's' in parenthesis if the variables were used to fit invasion syndrome models of frogs, lizards or snakes, respectively. Variable importance was summarised from invasion syndrome models fitted with all life-history and ecological traits and macroecological patterns and was max-min standardised to scale from 0 to 1; points indicate the mean, and error bars indicate one standard deviation summarised from 100 model replicates.

3.2 | Relative importance of macroecological patterns and traits in predicting invasions

Across taxonomic groups and invasion stages, and considering different evaluation metrics, invasion syndrome models fitted only with macroecological patterns (yellow points in Figure 4) often performed substantially better than those fitted only with traits (blue

points in Figure 4). This is indicated by the higher scores for the Boyce Index, AUC, precision and F1 score, as well as lower scores for recall, MAE and out-of-box error. Meanwhile, invasion syndrome models fitted with all or an optimal subset of traits and macroecological patterns performed slightly better than those fitted only with macroecological patterns. This indicates that traits complement macroecological patterns in increasing the predictive performance

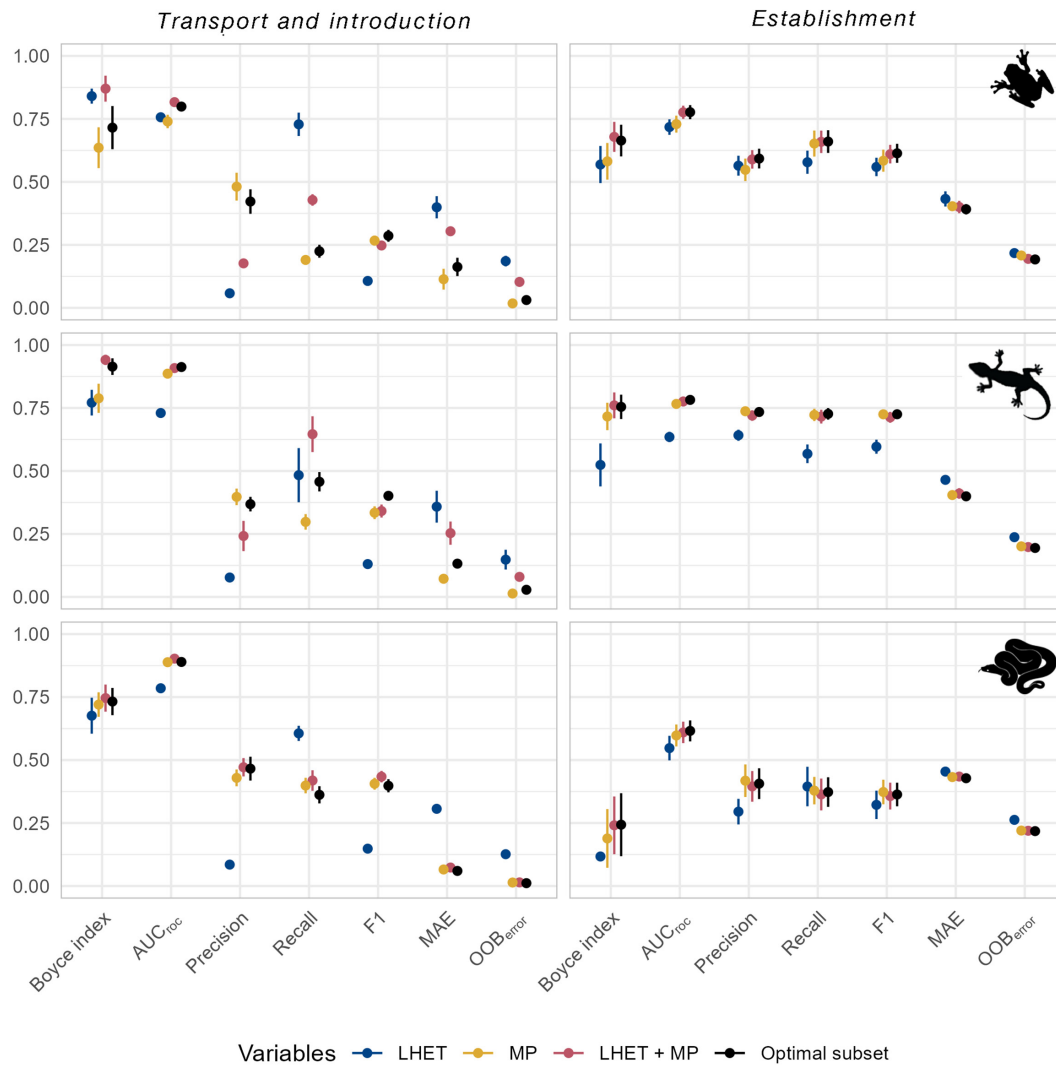


FIGURE 4 Relative performance of alternative invasion syndrome models in predicting unintentionally transported and introduced amphibian and reptile species and, among them, species with established alien populations. Alternative invasion syndrome models were fitted with life-history and ecological traits only ('LHET'), macroecological patterns only ('MP'), both traits and macroecological patterns ('LHET + MP'), and an optimal subset of traits and macroecological patterns ('optimal subset'). Predictive performance was measured based on seven evaluation metrics (x -axis): Boyce Index, area under the receiver operating characteristic curve (AUC_{roc}), precision, recall, F1 score, mean absolute error (MAE) and out-of-box error rate (OOB_{error}). Points indicate the mean and error bars indicate the standard deviation summarised from the outputs of 100 invasion syndrome model replicates.

of invasion syndrome models. Notably, aligning with the principle of parsimony, the invasion syndrome models fitted with an optimal subset of traits and macroecological patterns were more balanced (more plausible level of specificity and generality, as indicated by balanced precision, recall, F1 and out-of-box error statistics; see [Table S8.1](#) in [Supporting Information S8](#) for definitions and interpretation of evaluation metrics) than those fitted with all traits and macroecological patterns. Inspecting the predictions of invasion syndrome models fitted with an optimal subset of variables, all frogs, lizards and snakes with a history of unintentional transport and introduction were correctly predicted (based on binarized probabilities) by at least 87 of 100 model replicates. Meanwhile, 84.7%, 96.5% and 100% of frogs, lizards and snakes, respectively, with a history of unintentional transport and introduction were correctly predicted by

all 100 model replicates. These invasion syndrome models were as accurate for lizards and snakes, but less so for frogs, in retrospectively predicting species that established alien populations: 55.6%, 97.6% and 100% of frogs, lizards and snakes were correctly predicted by all 100 model replicates.

3.3 | Forecasting potential invaders

A total of 80 frogs, 73 lizards and 7 snakes worldwide (160 species in total) with no invasion history were forecasted to have attributes consistent with invasion syndromes of unintentionally transported and introduced species ('potential invaders'; [Figure 5](#)). Among them, 9 frogs, 45 lizards and 3 snakes (57 species in total) have attributes

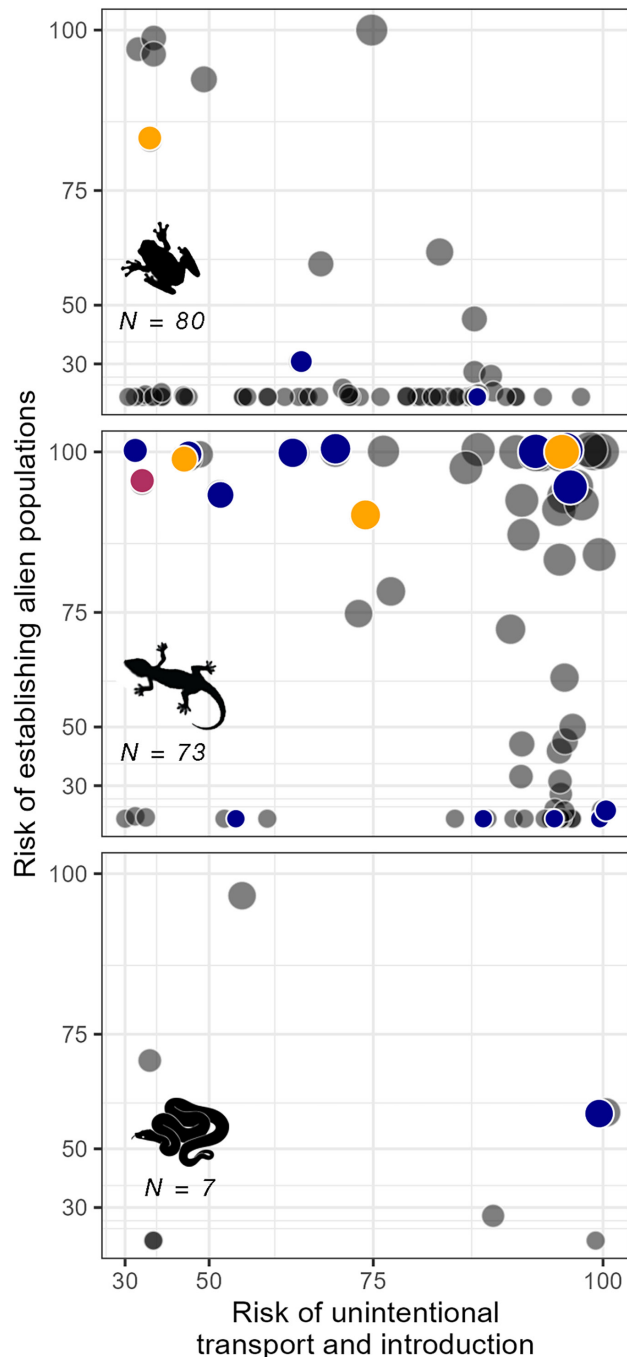


FIGURE 5 Amphibian and reptile species with no invasion history, but with concerning risk of unintentional transport and introduction (x-axis) and establishing alien populations (y-axis). Amphibian and reptile species with >30 risk score for unintentional transport and introduction are 'potential invaders'; among them, species with >30 risk score for establishing alien populations are 'high-invasion risk species'. Risk scores were based on the number of invasion syndrome model replicates (out of 100) that identified the species as having some or all attributes consistent with invasion syndromes. The size of the dots increases with the risk score for both invasion stages. The red point is *Tenuidactylus caspius* whose first introduced population was reported in September 2023, just days after the conclusion of our analysis. The orange points are species that have native exotic populations or populations with reduced genetic diversity due to suspected recent human-mediated dispersal (Lizards: *Agama picticauda*, *Plestiodon fasciatus*, *Hemidactylus robustus*, *Scleroporos grammicus*; Frogs: *Rhaebo blomeri*). Blue points are species regulated by CITES (Frogs: *Agalychnus callidryas*, *Euphylyctes hexadactylus*; Lizards: *Chamaeleo dilepis*, *C. gracilis*, *C. zeylanicus*, *Ctenosaura hemilopha*, *Phrynosoma blainvillii*, *Strophurus spinigerus*, *Tiliqua rugosa*, *Varanus albigularis*, *V. bengalensis*, *V. exanthematicus*, *V. gouldi*, *V. varius*; Snakes: *Eunectes murinus*). See also [Tables S1](#) in [Supporting Information S1](#) for predictions for amphibians and reptiles worldwide.

have attributes consistent with syndromes of species that have been unintentionally transported and introduced ([Table S1](#) in [Supporting Information S1](#)).

The tens rule states that 10% of species worldwide could be successfully transported; of these, 10% could successfully be introduced; and of these, 10% could successfully established. Thus, for our analysis, the null expectation is that 1% of species worldwide could be transported and introduced, and among which, 10% could established. Combining our models' forecasts and list of species with invasion history, the proportion of species predicted to succeed on each consecutive invasion stage is higher than expected based on the tens rule: the models predict 3.4% (257 of 7565 species) of frogs, 3.5% (257 of 7310 species) of lizards and 3.2% (128 of 4038 species) of snakes worldwide could be unintentionally transported and introduced based on their invasion syndromes (null expectation = 1%). Among these, 20.3% (51 of 251 species) of frogs, 44.8% (113 of 252 species) of lizards and 15.9% (20 of 126 species) of snakes could successfully establish alien populations based on their invasion syndromes (null expectation = 10%).

consistent with invasion syndromes of a typical species that has established alien populations ('high-invasion risk species'; [Figure 5](#); see also [Table S1](#) in [Supporting Information S1](#) for the predicted invasion risk of all species).

We also inspected our model forecasts on species that have been unintentionally transported and introduced but have not established alien populations. Among them, three frogs have attributes consistent with invasion syndromes of species that have established alien populations. Meanwhile, among species that have a history of establishing alien populations but are not known to be unintentionally transported and introduced, our models forecasted six frogs (out of 22), five lizards (out of 51) and two snakes (out of 17) also

4 | DISCUSSION

Responding to the escalating global problem of biological invasions requires an integrated biosecurity infrastructure with a future-proof preventative strategy (Ahmed et al., 2022; Finnoff et al., 2007; IPBES, 2023; Leung et al., 2002; Pili et al., 2023; Pyšek & Richardson, 2010). Here, we showcase a quantitative tool for assessing the invasion risk of species worldwide. Our tool allowed us to successfully forecast 160 species of frogs, lizards and snakes with no prior history of invasion that have a risk of being unintentionally

transported and introduced, and among them, 57 species have a high risk of establishing alien populations. We find that a typical unintentionally transported and introduced species tends to be more common, can thrive well in human-disturbed habitats and has more access to transport vectors within its native geographic range. Among these species, those that have so far successfully established tend to be larger in body size, are habitat generalists, also thrive well in human-disturbed habitats and have large geographic range sizes. Overall, macroecological patterns were more important than life history and ecological traits in explaining successful transport and introductions, and successful establishment of alien populations. Notably, the most accurate models were those fitted with an optimal subset of traits and macroecological patterns.

4.1 | What factors determine whether a species will be an invader or not?

Understanding which attributes determine species' invasion potential is a classic and still largely unanswered research objective in invasion science (Drake et al., 1989; Richardson, 2011; Richardson & Pyšek, 2008; Williamson et al., 1986). Our findings show that traits are relatively weak predictors for unintentional transport and introduction. Counter to the presumption that unintentionally transported and introduced alien species would have relatively small body sizes, which would allow them to easily contaminate or hitchhike on goods and vehicles unnoticed (Chapple et al., 2011; García-Díaz et al., 2019; Kraus, 2009; Toomes et al., 2019), we found that these species range in body size from small to large. It is also for this same reason that our findings do not align with previous analyses on introduced alien amphibians and reptiles (Allen et al., 2017; see Supporting Information S9 for a table of studies on alien amphibian and reptile invasion success); however, these previous studies did not distinguish the traits of alien species that have been intentionally vs. unintentionally transported and introduced, which may have confounded their analysis (Pyšek et al., 2011). It is important to note that we fitted the models with species' adult body sizes, which was the only widely available variable describing species' body size. Juveniles and sub-adults, which are smaller in body size, would be in the most dispersive life stages (Sinsch, 2014) and, thus, would likely hitchhike on transport vectors or contaminate commodities. Although age and size have a logarithmic relationship (Von Bertalanffy growth curves; Fabens, 1965) and, thus, a correlation between juvenile and adult body sizes, it is still interesting to investigate whether intercepted individuals are more likely to be juveniles or sub-adults and whether juvenile body size would be a stronger and more important predictor of unintentional transport and introduction. Another interesting trait, albeit with weak importance to the model, was that arboreal (i.e., living in trees) and saxicolous (i.e., living among rocks) species are more likely to be unintentionally transported and introduced. Species with such a propensity to climb on objects can end up living, coincidentally find themselves in, and/or depositing their eggs on artificial habitats, such as commodities, storage materials or vehicles

destined to be transported. Overall, our findings show no generalisable life-history and ecological trait among frogs, lizards and snakes that contaminate commodities and hitchhike on transport vectors.

Measures of body size were the most important variable for establishment, at least for frogs and snakes. Differences in the body size distribution (see Figures S5.1–6 in Supporting Information S5) show that established species tend to have relatively larger body sizes than those that failed to establish (or have not yet established). Given that large body size is indicative of a slow life strategy, our findings coincide with the inference of Sol et al. (2012) in invading birds that species with a slow life strategy would be more successful in establishing alien populations, particularly when starting from a small founding population size, such as is the case of unintentionally transported and introduced species (Pili et al., 2023; Wilson et al., 2009). Species with slow life strategies prioritise future over current reproductive returns: they grow relatively slower, but have large adult body sizes, and survive longer (Blackburn et al., 2009). Altogether, this allows them to distribute their reproductive effort across multiple breeding events (i.e., bet-hedging; Stearns, 2000), temporally spreading out reproductive failure due to demographic and environmental stochasticity (Duncan et al., 2014; Melbourne & Hastings, 2009). Notably, this inference on slow life strategies of established alien species is counter to the findings of previous studies on alien amphibian and reptile establishment and spread (Allen et al., 2013, 2017); but then again, their analysis did not disentangle differences brought by varying pathways of transport and introduction (Pyšek et al., 2011). As shown here, only a few life-history and ecological traits strongly determine whether a species could become invasive.

In our search for alternative or complementary predictors, we uncovered the potential of species macroecological patterns in assessing species' invasion risk. Species' macroecological patterns—particularly geographic range size, commonness and habitat generalism—have been central to extinction risk assessments (e.g., IUCN red list assessments; IUCN Standards and Petitions Committee, 2022; Rabinowitz, 1981; Yu & Dobson, 2000). In another light, we have shown how macroecological patterns can also play a foremost role in assessing species' invasion risk. Our findings are consistent with previous studies in showing that species with large native geographic ranges are more likely to be transported and introduced (García-Díaz et al., 2019; Tingley et al., 2010) and succeed in establishing alien populations (Allen et al., 2013; Cadotte et al., 2006; Duncan et al., 2001; Forsyth et al., 2004; Hayes & Barry, 2007; Hui et al., 2011). Notably, geographic range size has been used chiefly as a surrogate for more ecologically direct measures of invasion potential (Dukes & Mooney, 1999; Peterson et al., 2011; Williamson & Griffiths, 1996). Here, we provide empirical evidence on the long-standing presumptions of how macroecological patterns—particularly commonness, habitat generalism, human tolerance and access to transport vectors—determine invasion risk. We find that unintentionally transported and introduced species tend to be more common, more tolerant to human disturbance, and are distributed in areas with higher total

trade outflows and outgoing passengers across ports. This makes sense since being locally and/or widely abundant while having access to plenty of transport vectors would together increase the chances that individuals of these species will be unintentionally transported and introduced (Hulme et al., 2008). Meanwhile, habitat generalism, tolerance to human disturbance and large native geographic range size were the strongest macroecological predictors of establishment success. Such species would have better prospects of finding suitable conditions in sites where they are introduced, which are often in human-modified habitats (Dukes & Mooney, 1999; Hufbauer et al., 2012; Stringham et al., 2018; Williamson & Griffiths, 1996), ultimately aiding in their population establishment. In the same way that it has played a major role in conservation science, the foremost novelty of our study and our tool is in showing how a diverse range of variables describing species' macroecological patterns hold much promise in advancing invasion science by allowing us to understand the determinants of invasion success better, to forecast potential invaders and high-invasion risk species and, thereby, to inform preventative biosecurity robustly.

4.2 | How can knowledge of invasion syndromes be used to develop effective management strategies?

Our quantitative risk assessment tool identified 160 frogs, lizards and snakes as species with high potential to be unintentionally introduced. We additionally identified 13 species that already established alien populations elsewhere but have not yet been recorded to use unintentional transport and introduction pathways yet show the potential to do so (e.g., stratified long-distance spread and bridgehead invasions; Bertelsmeier et al., 2021; Capinha et al., 2023; Pili et al., 2019; Roura-Pascual et al., 2004). Some of the forecasted potential invaders are also using intentional transport pathways, such as the pet trade (Figure 5; Frogs: *Agalychnis callidryas*, *Euphylyctes hexadactylus*; Lizards: *Chamaeleo dilepis*, *C. gracilis*, *C. zeylanicus*, *Ctenosaura hemilopha*, *Phrynosoma blainvillii*, *Strophurus spinigerus*, *Tiliqua rugosa*, *Varanus albigularis*, *V. bengalensis*, *V. exanthematicus*, *V. gouldi*, *V. varius*; Snakes: *Eunectes murinus*; CITES Secretariat and UNEP-WCMC, 2023). More interestingly, some of the forecasted potential invaders have or may have already been introduced outside their native ranges. For example, an introduced population of the Caspian Bent-toed Gecko *Tenuidactylus caspius* was observed in Georgia in August 2023 (Figure 5; reported by K. Prondzynska in iNaturalist on 2023-08-29, around the time our analysis was concluded). Meanwhile, molecular biogeography studies found reduced genetic diversity in some populations of the Heyden's gecko *Hemidactylus robustus* and the Mesquite lizard *Sceloporus grammicus*, suggesting possible human-mediated transport in recent history (Figure 5; Arévalo et al., 1991; Šmíd et al., 2013). These unpublished reports and scientific inferences independently validate the statistical robustness of our tool's forecasts and, together with our findings,

highlight the urgency in addressing unintentional transport and introduction pathways to put a stop to the global problem of biological invasions.

Our tool's forecast of potential invaders can directly guide preventative biosecurity of nations worldwide. For instance, national horizon-scanning exercises for developing warning lists can include our tool's forecasted potential invaders alongside the list of species with invasion history (Figure 1b) to assess which species have a high risk of being unintentionally transported and introduced and establish alien populations in their jurisdictions. Such warning lists identify which alien species should be prioritised by preventative biosecurity strategies (e.g., sanitation policies, inspections and quarantine) and which species should be banned from import if not monitored. Given recent studies showing unintentionally transported species can come from anywhere in the world (Fenn-Moltu, Ollier, Bates, et al., 2023a; Fenn-Moltu, Ollier, Caton, et al., 2023b; Pili et al., 2023), nations should anticipate the forecasted potential invaders to arrive past their borders, especially for the vast majority of countries that lack preventative biosecurity infrastructures (Latombe et al., 2023). But should all the forecasted potential invaders be prevented from entry? For instance, as shown here, only 57 of the 160 forecasted potential amphibian and reptile invaders have some or all attributes consistent with syndromes across all invasion stages. Should we also be concerned about the forecasted potential invaders with no or few attributes consistent with syndromes predisposing them to establish alien populations? We stress the importance of the higher complexity required in predicting establishment success, which warrants predictors beyond intrinsic and inherent species attributes (Catford et al., 2022; Robeck et al., 2024). A comprehensive assessment of establishment risk should account for propagule pressure, suitability to environmental conditions and biotic community, among others (Bomford et al., 2008; Cassey et al., 2018; Catford et al., 2022; Hayes & Barry, 2007; Herborg et al., 2007; Wittenberg & Cock, 2001). Ultimately, the most fool-proof approach would be to uphold the Precautionary Principle (Kumschick et al., 2023) and expect the worst outcomes from the arrival of the forecasted potential invaders.

4.3 | Progress in quantitative invasion risk assessment

Our quantitative invasion risk assessment tool is a significant advancement and addition to the existing arsenal of biosecurity decision-support tools—the majority of which are qualitative or semi-quantitative. The key qualities that make our tool appealing and complementary to existing warning lists are its reproducibility, transferability, statistical robustness and scientific defensibility. The underlying code to run our tool is readily accessible online (<https://github.com/ArmanPili/ForecastingInvaders>) and adequately documented and maintained, following best practices for reproducible computational research (Jenkins et al., 2023). As the framework builds on widely accessible traits and macroecological

patterns, it is easily transferable to other taxonomic groups beyond frogs, lizards and snakes (Fournier et al., 2019). As we have shown here, invasion syndrome models fitted only with macroecological patterns may be sufficient, as they resulted in high predictive accuracy (Figure 4). Macroecological patterns of different taxonomic groups are widely available from and/or quantifiable using open-source biodiversity databases (i.e., occurrence records, shapefiles of geographic range sizes, and biogeographic regions). This highlights the integral role of big open biodiversity data, including data on invasion histories, in tackling global biodiversity issues (Kelling et al., 2015; Pagad et al., 2018; Seebens et al., 2017; Wüest et al., 2020). Meanwhile, traits for fitting invasion syndrome models would vary among taxonomic groups, and we thus advise to separately train models for different taxonomic groups rather than forecasting across them. For instance, although body size is a strong indicator of establishment success among unintentionally transported and introduced frogs, snakes (as shown here) and birds (Sol et al., 2012), this is not true for lizards (as shown here) and likely other taxonomic groups. Similarly, the model framework could also extend to other invasion pathways, for example to intentionally transported and introduced alien species (e.g., exotic pet trade) to investigate factors that determine drivers and dynamics of these intentional introductions (Bernery et al., 2022; Measey et al., 2019; Mohanty & Measey, 2019; Pysek et al., 2011). Finally, our tool's MICE backbone is a significant advancement in quantitative biosecurity and, more broadly, macroecology. This backbone implements cutting-edge statistical approaches in every step (Diniz-Filho et al., 1998, 2015; Guénard et al., 2013), allowing us to circumvent and account for uncertainties brought by the highly biased and inherently limiting missing data in life-history trait databases (Diniz-Filho et al., 2015; Lall, 2016; Penone et al., 2014; Taugourdeau et al., 2014), and ultimately to forecast potential invaders among species worldwide.

Of course, our tool comes with caveats. In applying our tool to other taxonomic groups, the most important limiting requirement would be data on invasion history, which is hampered by delays in reporting, if not underreporting due to alien species' low detectability and invasion lags or due to low monitoring effort (Robeck et al., 2024). As was the case here, insufficient data on invasion history prevented us from modelling the invasion syndromes of other amphibian and reptile groups, such as salamanders, crocodiles and turtles. However, future studies can test or optimise the cross-taxonomic predictive power of invasion syndrome models fitted only with macroecological patterns; these models performed better than models fitted with traits only, and macroecological patterns are easily quantifiable variables comparable across the tree of life. Finally, many of the predictor variables are expected to change in the future—taxonomic changes are common, new species are being described (e.g., Uetz et al., 2022), new alien species are regularly reported (Pagad et al., 2018; Seebens et al., 2017), species distribution data are increasingly made available (Kelling et al., 2015; Wüest et al., 2020), new airports and shipping ports open up, globalisation increases and shifts global trade dynamics (Seebens et al., 2018),

among many. Thus, for predictions to stay abreast of changes in input data, our tool must be regularly re-run.

5 | CONCLUSION

'An ounce of prevention is better than a pound of cure'—is the most crucial guiding principle of global biosecurity (Ahmed et al., 2022; Hulme, 2021; Leung et al., 2002) and continues in relevance (Convention on Biological Diversity, 2022; IPBES, 2023). Crucial to preventing biological invasions are warning lists, which identify what arriving alien species to watch out for, prevent from entry or closely monitor because they run the risk of becoming invasive. We showcase here a reliable, reproducible, transferable, statistically robust, and scientifically defensible quantitative invasion risk assessment tool that allows invasion scientists and biosecurity authorities to identify invasion syndromes and forecast potential invaders. By integrating our tool to horizon-scanning exercises for developing warning lists, risk assessments are no longer limited to species with invasion history but a much broader range of species worldwide with some or all attributes consistent with invasion syndromes. Our tool is a significant new addition to the suite of decision-support tools needed for developing future-proof preventative biosecurity strategies against the escalating global problem of biological invasions.

AUTHOR CONTRIBUTIONS

Arman N. Pili: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing. **Boris Leroy:** Methodology; writing – original draft; writing – review and editing. **John G. Measey:** Data curation; writing – original draft; writing – review and editing. **Jules E. Farquhar:** Methodology; writing – original draft; writing – review and editing. **Adam Toomes:** Data curation; methodology; writing – original draft; writing – review and editing. **Phillip Cassey:** Data curation; methodology; writing – original draft; writing – review and editing. **Sebastian Chekunov:** Data curation; methodology; writing – original draft; writing – review and editing. **Matthias Grenié:** Writing – original draft; writing – review and editing. **Dylan van Winkel:** Data curation; writing – original draft; writing – review and editing. **Lisa Maria:** Data curation; writing – original draft; writing – review and editing. **Mae Lowe L. Diesmos:** Writing – original draft; writing – review and editing. **Arvin C. Diesmos:** Writing – original draft; writing – review and editing. **Damaris Zurell:** Writing – original draft; writing – review and editing. **Franck Courchamp:** Conceptualization; writing – original draft; writing – review and editing. **David G. Chapple:** Conceptualization; data curation; funding acquisition; methodology; project administration; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The R script of our quantitative invasion risk assessment tool workflow can be accessed in Zenodo at <https://zenodo.org/doi/10.5281/zenodo.11533251> and in GitHub at <https://github.com/armanpili/ForecastingInvaders>. The data that support the findings of this study are openly available in FigShare at <https://doi.org/10.26180/24080646>.

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DATA SOURCES

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