Biological invasions are a population-level rather than a species-level phenomenon

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RESEARCH ARTICLE

Biological invasions are a population-level rather than a species-level phenomenon

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Abstract

Biological invasions pose a rapidly expanding threat to the persistence, functioning and service provisioning of ecosystems globally, and to socio-economic interests. The stages of successful invasions are driven by the same mechanism that underlies adaptive changes across species in general—via natural selection on intraspecific variation in traits that influence survival and reproductive performance (i.e., fitness). Surprisingly, however, the rapid progress in the field of invasion science has resulted in a predominance of species-level approaches (such as deny lists), often irrespective of natural selection theory, local adaptation and other population-level processes that govern successful invasions. To address these issues, we analyse non-native species dynamics at the population level by employing a database of European freshwater macroinvertebrate time series, to investigate spreading speed, abundance dynamics and impact assessments among populations. Our findings reveal substantial variability in spreading speed and abundance trends within and between macroinvertebrate species across biogeographic regions, indicating that levels of invasiveness and impact

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differ markedly. Discrepancies and inconsistencies among species-level risk screenings and real population-level data were also identified, highlighting the inherent challenges in accurately assessing population-level effects through species-level assessments. In recognition of the importance of population-level assessments, we urge a shift in invasive species management frameworks, which should account for the dynamics of different populations and their environmental context. Adopting an adaptive, region-specific and population-focused approach is imperative, considering the diverse ecological contexts and varying degrees of susceptibility. Such an approach could improve and refine risk assessments while promoting mechanistic understandings of risks and impacts, thereby enabling the development of more effective conservation and management strategies.

KEYWORDS
Europe, freshwater macroinvertebrates, long-term trends, non-native species, population spread, population-level dynamics, risk assessments

1 | INTRODUCTION

Biological invasions have rapidly consolidated among the major threats of the Anthropocene, causing significant detrimental impacts to biodiversity, the functioning of ecosystem processes, and to socio-economic stability (Diagne et al., 2021; Roy et al., 2023; Shackleton et al., 2019; Simberloff, 2013; Zhang et al., 2022). Both accidental and intentional introductions of non-native species into new geographic regions, where they have no evolutionary history, can result in substantial adverse effects (Dudgeon, 2019; Leroy et al., 2023; Reid et al., 2019), including local displacement and extinction of native species through predation and competition, parasite and disease transmission, changes in ecosystem functioning, and—among other impacts—the disruption of systemic balances (Bacher et al., 2023; Lázaro-Lobo et al., 2023; Soto et al., 2024). As biological invasions continue to escalate globally, understanding what enables populations of non-native species to spread to new territories becomes crucial in devising effective strategies for the mitigation of their impacts (Heger et al., 2021; Richardson & Ricciardi, 2013).

Biological invasions can be described as a process that unfolds in four stages: transportation, introduction, establishment and spread; with potential impacts being incurred at every stage of the invasion process (Blackburn et al., 2011; Catford et al., 2009). Despite recent advancements in the understanding of biological invasions, there remain numerous inherent shortcomings pertaining to invasiveness screenings and impact assessments which are made at the species-level (Vilizzi et al., 2022). Understanding the ecology of non-native species, their dispersal dynamics (including pathways of introduction), and integrating their impacts (ecological, economic and social) are examples of the minimum standards identified by Roy et al. (2018) to assess species invasiveness. Despite their importance in e.g. the Kunming-Montreal Global Biodiversity Framework targets (Hughes & Grumbine, 2023), traditional metrics used to describe invasion dynamics, such as non-native species richness, their respective abundance, distribution and speed of spread may not offer a sufficiently standardised quantitative measure for assessing the extent of an invasion, as they are challenging to compare consistently across different contexts (e.g. regions or habitats).

In many cases, our knowledge and understanding is insufficient to precisely depict population dynamics (Simberloff et al., 2013), species dispersal and spread, and the biotic and abiotic factors influencing all stages of the invasion process in predictive models (Dominguez Almela et al., 2020, 2022). Furthermore, while there is a practical desire for global approaches to explain general principles or to create 'watch lists' to streamline risk assessments (RAs), this ultimately results in local or regional contexts being ignored. There is an urgent need for policy makers, stakeholders, and managers to transform these traditional invasion dynamics' metrics to RAs, which consider local context dependencies and include the feasibility and effectiveness of management actions (Venette et al., 2021). We argue that invasion science should follow advancements in biodiversity monitoring such as the Living Planet Index, which focus on understanding regional population trajectories to assess ecological risk (Almond et al., 2020), and therefore acknowledge that the status of species under management depends on outcomes of individual populations.

The field of invasion science has made significant strides in recent years. However, its conceptual progress remains largely disconnected from eco-evolutionary dynamics. In particular, the role of natural selection in shaping the stages of invasions (when successful and unsuccessful) is fundamentally neglected from species-level studies. Population adaptations to the demands of their local environments are driven by natural selection on traits that influence intraspecific variation in survival and reproductive success, i.e. fitness (Bolnick et al., 2003; Bolnick & Doebeli, 2003; Pincheira-Donoso et al., 2018; Schluter, 2000). These are the exact

same stages that species in general, and non-native species undergo through time (Le Roux, 2021). Therefore, understanding the underlying processes non-native populations are exposed to requires temporal data and information on numerous environmental factors that may affect non-native populations in invaded regions. Past studies, however, often relied on the compilation of annual records of non-native species or reports to infer broad spatio-temporal trends in biological invasions (Seebens et al., 2017, 2021). This historically overlooked approach (Harvey & Mazzotti, 2016; Hui & Richardson, 2017) inherently falls short of capturing the nuanced, species-specific and local-context-dependent dynamics of invasive non-native populations (Haubrock et al., 2022; Pergl et al., 2020). The variability among non-native population structure has therefore seldom been systematically examined or described, especially at larger scales (but see e.g. Bradley et al., 2019), attributable to the scarcity of long-term data (Haubrock, Carneiro, et al., 2023; Haubrock & Soto, 2023). Understanding the variability among non-native populations is, however, crucial because it can unveil specific patterns, triggers and responses that may inform targeted management strategies (Guareschi et al., 2021, 2022). While certain species-level traits determine that some species may be more likely to be invasive than others (e.g. reproductive potential, high behavioural plasticity, etc.; Hayes & Barry, 2008; Matzek, 2012), population-level changes can occur due to, for example, local conditions and external drivers within the species-level context in an invasion's timescale. Therefore, invasiveness (i.e. a non-native population's ability to spread) is fundamentally a population-level phenomenon driven by intra-population individual variability (Crystal-Ornelas & Lockwood, 2020; Milardi, Gavioli, Soana, et al., 2020), i.e. referring to a locally reproducing population with self-contained dynamics within a defined geographic area (as opposed to a meta-population encompassing multiple interconnected populations; Diekmann, 1993). Invasion dynamics of population can be subjected to selection, density, stage, sex or context dependencies, among others, and their interactions with the specific invaded habitat during all stages of the invasion process, collectively shaping the outcome of the invasion (Briski et al., 2018; Dominguez Almela et al., 2022). Consequently, a focus on invasions at the population level has important implications for both invasion ecology and ecological theory (Colautti & MacIsaac, 2004).

A more comprehensive exploration of population-specific invasion dynamics is essential for enhancing predictive modelling, refining RAs and developing effective conservation and mitigation measures tailored to the unique characteristics of each population of the invasive non-native species (Cuthbert et al., 2023; Hui & Richardson, 2017). It is, therefore, crucial to emphasise the importance of 'spread', rather than an observed 'impact', when defining a non-native population's invasiveness, because a spreading non-native species may cause impacts elsewhere, which are more difficult and costly to demonstrate (Milardi et al., 2022; Soto et al., 2024). The significance of 'spread' in invasion science lies in the representation of the dispersal of a non-native species beyond its initial introduction point (Hui & Richardson, 2017; Wilson et al., 2009). With 'spread' serving as the foundation for categorising populations as 'invasive', it becomes essential to initially perceive invasions as a context-dependent phenomenon at the population level, as no species is invasive everywhere. In other words, invasiveness is not primarily a taxonomic phenomenon, but foremost a spatio-temporal population-level phenomenon (although certain species-specific traits are strongly linked to invasiveness; Catford et al., 2019; Renault et al., 2022). Local environmental conditions, biotic resistance, bottleneck effects, rapid evolution, propagule and colonisation pressure, the existence of vectors and pathways, genetic diversity, and other factors play critical roles in determining the establishment success and subsequent spread of non-native species (i.e. invasions; Figure 1a; Aksu et al., 2021; Byers & Noonburg, 2003; Catford et al., 2009; Daly et al., 2023). Evolutionary differentiation of populations in the native or non-native ranges, for instance in response to heterogeneous anthropogenic effects on habitat (i.e. disturbances, acidification, etc.; Milardi, Gavioli, Castaldelli, et al., 2020; Milardi et al., 2022), can drive a rapid increase in dispersal in a subset of populations, which may then also be more likely to spread to other human-impacted environments and establish (Borden & Flory, 2021; Hufbauer et al., 2012). The variability in how different populations respond to these local or regional factors (Figure 1b), and the ways an invasion is perceived, may change depending on the perspective (local insular population-level versus larger regional meta-population species-level perspective; Figure 1c).

While terrestrial systems have better dealt with the population-level factors controlling true versus detectable temporal invasion dynamics (Tobin et al., 2011), this is not the case within aquatic environments. We therefore implement a comprehensive analysis of aquatic macroinvertebrate time-series and related data, to demonstrate that a shift in "unit of selection", i.e. from species- to meta−/population-level is necessary and timely in invasion science. Here, we use long-term time series of macroinvertebrate species in European fresh waters (Haase et al., 2023) to assess invasion dynamics and compare the local population spread patterns with the large-scale invasion status. First, we analysed the regional spreading speed of different non-native populations using their occurrences over time to examine whether (i) highly variable local environments make generalisations about the invasiveness of different populations of non-native species difficult. Second, we investigated the temporal variability in abundance trends of non-native species populations, hypothesising that (ii) the trajectories and dynamics of non-native species populations vary, lacking any ubiquitously applicable pattern. Thirdly, we compared population-level trends in abundances and occurrences of high-profile species to recently performed invasiveness screenings to (iii) identify plausible discrepancies by examining if the population-level perspectives based on real data will ultimately diverge from management and decision tools, which would result in ineffective use of resources. By shifting our focus to the population level, we aim to unravel the complexities of invasion dynamics and contribute to

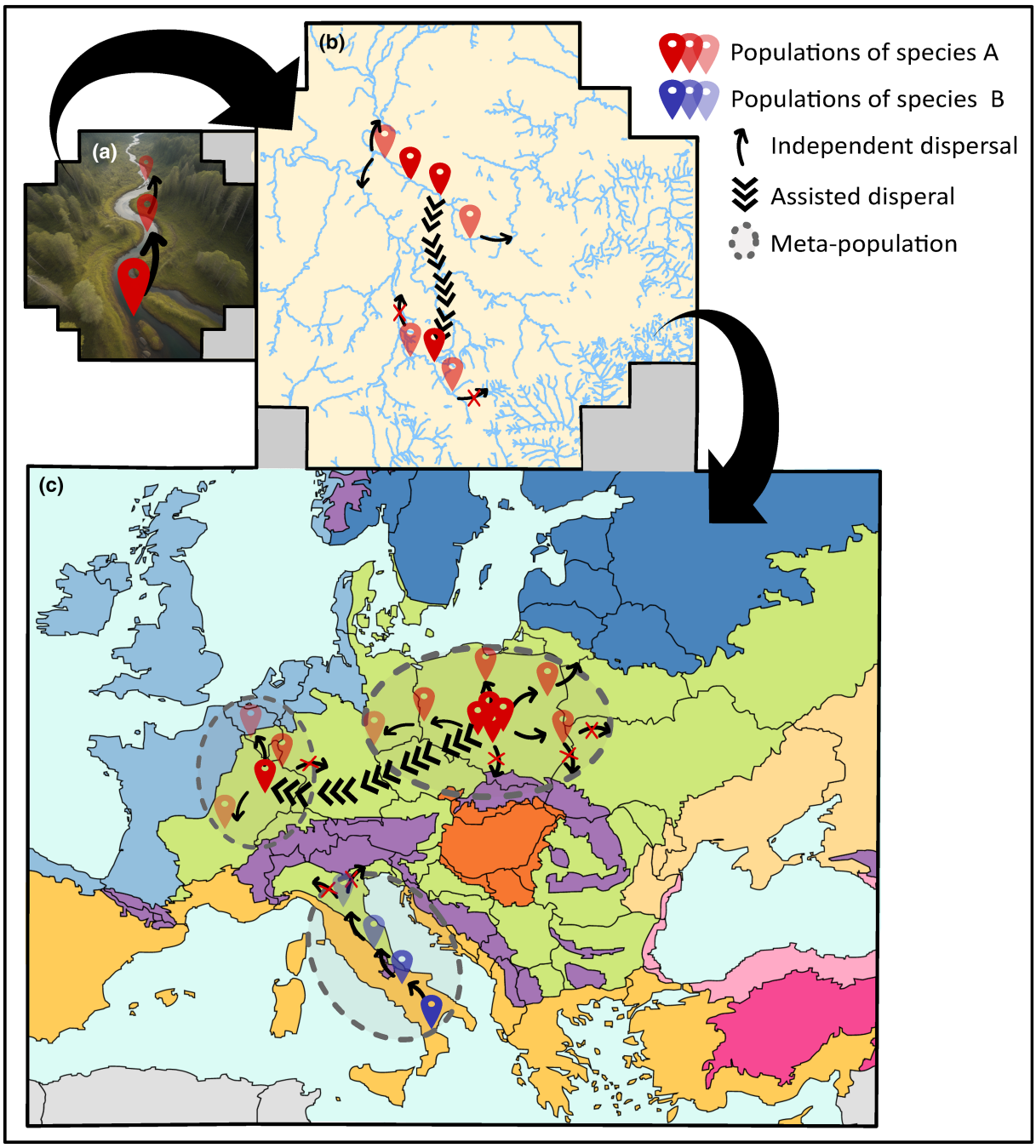

FIGURE 1 Conceptual diagram of population-level spread at different spatial scales. From site (a), regional (b), to continental meta-population level perspective (c), with independent spread (black arrows) and human-mediated dispersal (arrow heads) of populations, exemplifying with continental Europe the universal complexity of river networks and environmental heterogeneity. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

a more comprehensive understanding of how diverse non-native species interact with and impact their environments.

2 | METHODS

We identified raw abundance trends of non-native species populations within a database covering 22 European countries containing 1816 time series of freshwater macroinvertebrates, spanning the period 1968 to 2020 (Supporting Information S1). This database included time series from 1193 different rivers and streams (i.e. large rivers can contain multiple time series; Haase et al., 2023). Samples were collected using different methods and protocols across time series (Supporting Information S2), but methodology was kept consistent within each time series. We considered only time series with a minimum of eight annual sampling events—not necessarily consecutive—and that reported entries at the species level, in this database (Haase et al., 2023). We initially extracted

all time series with the occurrence of species classified as non-native. We then checked the native range of non-native species in our database consulting three open sources databases: (i) Global Invasive Species Database (GISD, iucngisd.org/gisd/, Pagad et al., 2022), (ii) the Global Biodiversity Information Facility (GBIF; gbif.org/) and (iii) the Invasive Species Compendium (CABI, cabi.org/ISC). Then, we retained time-series that included raw abundances of non-native species, continuously observed for a minimum of five consecutive sampled years ($n = 165$ time series and 20 non-native species). These included 57 time series with 10 consecutive sampling years from 12 non-native species (Supporting Information S3; Figure 2).

2.1 | Investigating spreading speed

Integrating population dynamics with a non-native species' ability to spread can provide the information needed to assess the invasiveness (i.e. capacity to spread) of a population (Clobert et al., 2009). To assess variations in the temporal trends of populations of non-native species across different regions, we focused on the six most frequent non-native species in our time series database (i.e. present in more than 10 time series), namely: the New Zealand mud snail *Potamopyrgus antipodarum*, the zebra mussel *Dreissena polymorpha*, the killer shrimp *Dikerogammarus villosus*, the amphipod *Crangonyx pseudogracilis*, the bladder snail *Physella acuta*, and the gravel snail *Lithoglyphus naticoides*. We filtered the 1816 European freshwater time series for occurrences of these six non-native species and extracted all occurrences. Additionally, we expanded our dataset by extracting occurrences of the six species from the GBIF using the *occ_download* function from the rgbif R package (Chamberlain et al., 2022). We only kept occurrences with less than 10 km of measure uncertainty to avoid problematic errors that can lead to inaccurate analyses. Our approach involved including the initial year of observation for these populations of non-native species in each time series, even for those with fewer than three sampled years. Each model (i.e. Equation 1) incorporated the count of the respectively observed non-native species' population as the response variable, with the corresponding year serving as the predictor.

To estimate the spreading speed (expressed in km year^{-1}) of each non-native species in each respective country, we then analysed changes in the number of occurrences (i.e. the number of invaded time series) over time within each invaded country, by combining occurrences from our time series dataset and GBIF. We calculated great-circle distances based on GPS coordinates between the

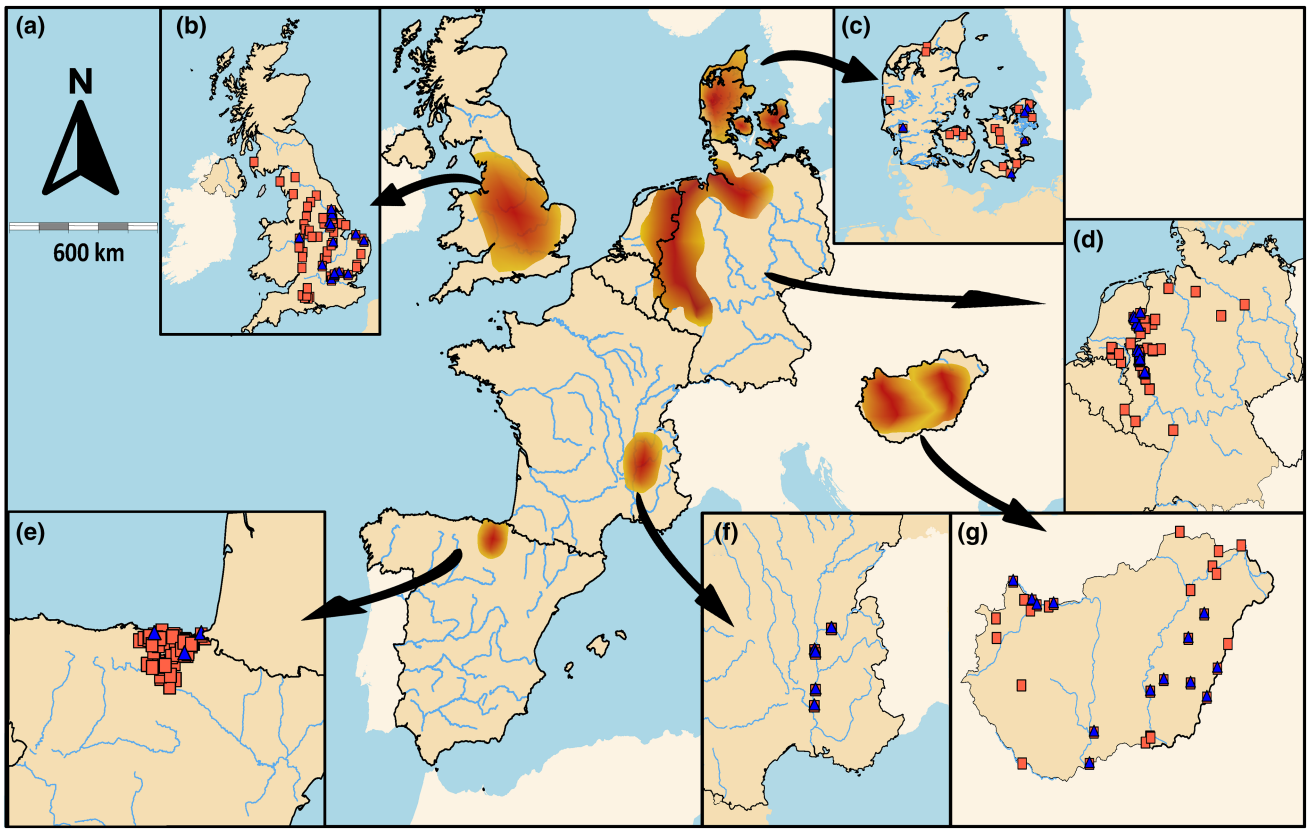

FIGURE 2 Distribution of non-native species time series with a minimum of five (orange rectangles) consecutive years of recurring abundances, highlighting particularly long time series with a minimum of 10 (blue triangles) consecutive years of recurring abundances, as identified in the database from Haase et al. (2023). (a) shows the time series selected on a European scale, (b) time series in the United Kingdom, (c) time series in Denmark, (d) time series in Luxembourg, Netherlands, Germany and Belgium, (e) time series in Spain, (f) time series in France, and (g) time series in Hungary. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

location of the first invaded site and subsequently invaded sites. An estimate for the spreading speed was computed as the mean distance in any given year over the time elapsed (since the first recorded site) and averaged over the number of occurrences. This accounts for species' spread along multiple pathways in different directions from the initial site. Note that the computation of the spreading speed does not differentiate between the natural and human-induced dispersion of populations. As a result, the estimated range expansions may be influenced by either or both of these processes. They also only capture detectable spread, and therefore likely underestimate the true distribution of the invader over time.

Assuming that the spreading speed declines gradually as a function of time, as the invaded range becomes progressively saturated, we modelled the speed using an inverse power-law function (Soto, Cuthbert, Ahmed, et al., 2023) given by:

$$v(t) = v_0\left(1+\frac{t}{\sigma}\right)^{-\alpha}, \sigma > 0, \alpha > 0, \quad (1)$$

where $v(0)=v_0$ is the initial estimated speed at $t=0$ (corresponding to the following year after the first record, because two time points are required to estimate increments in spreading speed), σ is a scaling factor (or amplitude) that determines the overall magnitude of the speed, and α is an exponent that governs how the speed changes over time in the long term, i.e., the rate of decay in the end tail. The exponent α is crucial to this analysis, whereby in the long-term the spreading speed diminishes asymptotically proportional to $1/t^{\alpha}$. When $\alpha=1$, the speed decreases inversely with time, for $0<\alpha<1$, the speed decreases with time but at a slower rate than this, and conversely, if $\alpha>1$, the speed decreases at a faster rate. The inverse power-law function (Equation 1) was fitted against the values of annual spreading speed, separately for each country and species, using the *lsqcurvefit* non-linear regression tool in Matlab and thus, the best-fit parameters (σ, α) were estimated. We accounted for the variability in the α parameter estimate by incorporating 95% confidence intervals, computed through the *nlparci* command in Matlab.

2.2 | Investigating temporal dynamics in abundance trends

We employed a series of modified Mann-Kendall trend tests to obtain the monotonic trends' *S*-statistics (i.e. slope) and the respective variance (Hamed & Rao, 1998; Pilotto et al., 2020) of the abundance of those non-native populations that were most represented in our data over a minimum of 5 or 10 consecutive years to compare the variability of non-native species trends. We then employed the *rma* function of the metafor v4.4.0 R package (Viechtbauer, 2010), using the *S*-statistics and respective variances as effect sizes and associated variances (Hamed & Rao, 1998; Pilotto et al., 2020) to calculate the heterogeneity of the trends (I^2) for each species and countries separately. I^2 is a descriptive statistic that reflects the percentage of variation across studies that is due to heterogeneity rather than randomness (Borenstein et al., 2017, 2021).

2.3 | Comparing population-level trends to species-level screenings

To infer discrepancies between species-level assessments and population-level data, we compared trends and trajectories in abundances and occurrences for the previously assessed six species (i.e. *C. pseudogracilis*, *D. polymorpha*, *D. villosus*, *L. naticoides*, *P. acuta* and *P. antipodarum*) with recently conducted invasiveness screenings performed with the Aquatic Species Invasiveness Screening Kit (AS-ISK). This tool is renowned for its reliability in evaluating non-native species and has demonstrated effectiveness in screening potential invasive aquatic organisms across various RA areas worldwide (Vilizzi et al., 2021). The screenings were conducted adhering to the "minimum standards" specified in the European Commission Regulation on the prevention and management of invasive non-native species (Roy et al., 2018). The AS-ISK screening protocol comprises 55 questions (Copp et al., 2016). The initial 49 questions focus on Basic Risk Assessment (BRA), examining the biogeographical and biological aspects of the species being assessed. The remaining six questions relate to Climate Change Assessment (CCA) and require the assessor to evaluate how future climate conditions might impact the risks associated with the introduction, establishment, dispersal and impact of the species. Each screening question requires a response, a level of confidence in the response, and a justification. After completing the screening, the species receives a BRA score and a BRA+CCA (composite) score, ranging from −20 to 70 and from −32 to 82, respectively. Scores below 1 indicate a low risk of invasiveness, while higher scores classify the species as posing a medium or high risk. The distinction between medium and high-risk levels is determined by a predefined threshold value. In this study, the threshold is based on the calibrated global BRA score of 13.25 for freshwater invertebrates (Vilizzi et al., 2021). The AS-ISK employs confidence levels associated with each question-related response, ranked as follows: 1=low, 2=medium, 3=high, and 4=very high. These confidence rankings align with those recommended by the *Intergovernmental Panel on Climate Change* (IPCC, 2005).

3 | RESULTS

The most common non-native species in our time series was *Potamopyrgus antipodarum* ($n=131$ time series; starting year: 1986; last year: 2019), followed by *Dikerogammarus villosus* ($n=30$; 1994–2019), *Crangonyx pseudogracilis* ($n=23$; 2003–2019), *Physella acuta* ($n=21$; 2000–2019), *Lithoglyphus naticoides* ($n=13$; 2005–2019) and *Dreissena polymorpha* ($n=11$; 1976–2018). All other non-native species that occurred in fewer than 10 time series were excluded. As predicted by natural selection theory, our analyses of multiple time-series from across a range of these six non-native macroinvertebrates throughout different locations across European freshwater rivers revealed considerable variation in the levels of spread and population dynamics across conspecific populations (i.e. inter-population variation in stage of adaptation).

3.1 | Investigating spread speed

On examining the spreading speed of six aquatic invasive species across Europe, we found considerable variation in the rate of spread in the long-term based on data obtained from GBIF, where α varied substantially across species and countries (Figure 3). Although the spreading speed generally decreased over time for all species in all the countries studied (Figure 4), we found that in the majority of cases (74%), α was less than 1 indicating a relatively slow rate of decline in the long-term (Figure 3). For *C. pseudogracilis*, α ranged from 0.45 in Ireland to 2.43 in the United Kingdom. *Dikerogammarus villosus* showed a narrower range for α, from a low of 0.17 in Germany to a high of 1.03 in the United Kingdom. *Dreissena polymorpha* exhibited a wide range of α values, with a minimum of 0.14 in Spain to a maximum of 1.00 in Germany, indicating spreading speed to decrease at a slower rate in the long-term among the countries studied. The α values for *L. naticoides* were comparably lower in the Netherlands (0.41), rising to a peak of 3.05 in Germany. *Physella acuta* presented α values spanning from 0.26 in the United Kingdom to 4.40 in Greece, indicating a considerably faster than linear decrease in spreading speed. Lastly, for *P. antipodarum*, α ranged from a low of 0.09 in Sweden to a high of 1.32 in Belgium. Moreover, we found considerable variance for α values, indicating substantial differences in the spreading speed of these species' population within the respective countries. Overall, the R^2 values demonstrated a sufficiently strong goodness of fit, indicating how well the inverse power-law model explained the variability in the speed data values, with 79% of the cases with an $R^2 > .5$. Some exceptions where the R^2 value was low, indicated less predictability, but were still considered. The R^2 values ranged from the lowest value of .0679 for *D. polymorpha* in Austria to the highest value of .9997 for *L. naticoides* in Hungary (Supporting Information S4).

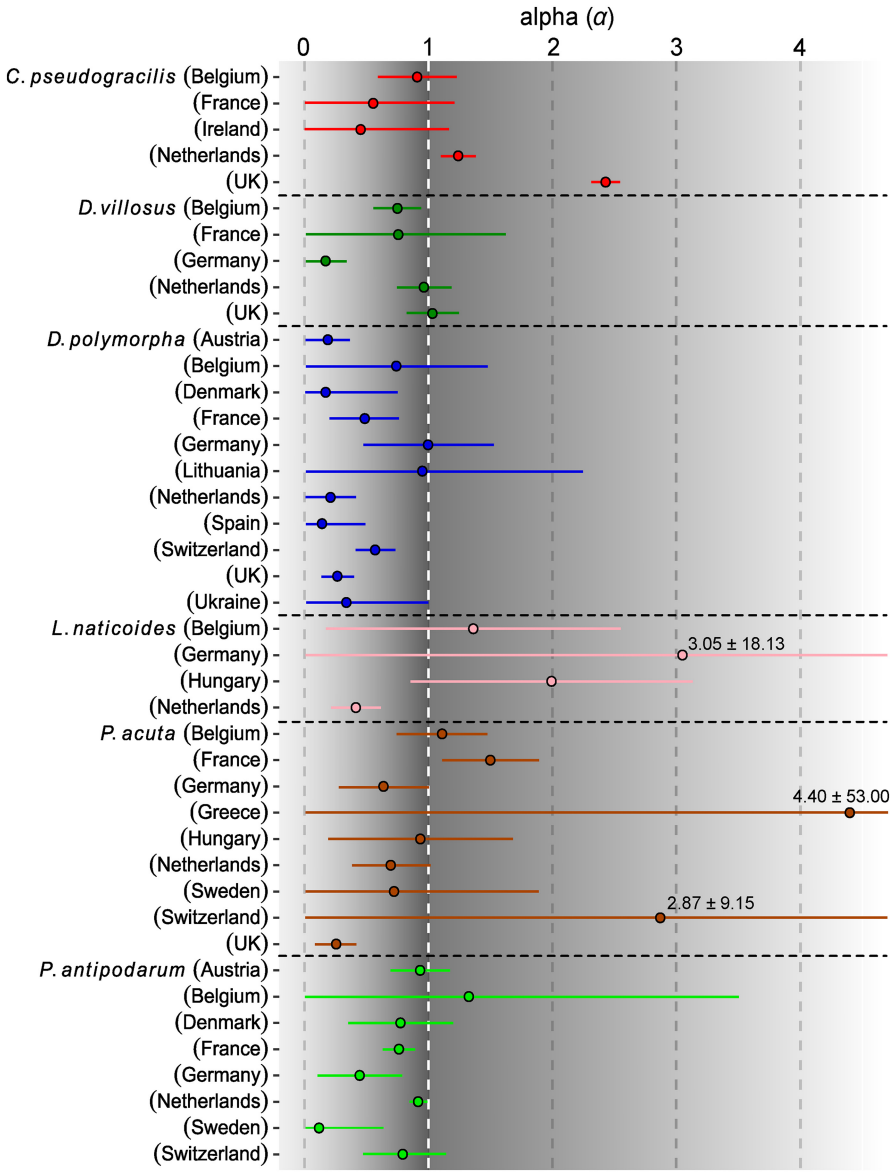

FIGURE 3 Variation in the inverse power-law exponent (α) for the investigation of long-term behaviour of spreading speed of *Crangonyx pseudogracilis*, *Dikerogammarus villosus*, *Dreissena polymorpha*, *Lithoglyphus naticoides*, *Physella acuta* and *Potamopyrgus antipodarum*, based on site location data obtained from the Global Biodiversity Information Facility for each respective country with sufficient data; $\alpha = 1$: the speed decreases in the long-term, in proportion to the inverse of time, $0 < \alpha < 1$: the speed decreases with time, but at a slower rate, $\alpha > 1$: the speed decreases more rapidly. The α values (dots) are estimated parameters obtained from the non-linear regression fit of the inverse power-law function (Equation 1) against the values of annual spreading speed. The horizontal bars represent the 95% confidence intervals, computed using the *nlparci* command in Matlab. Note that the *x*-axis is cut off for visualisation purposes. See Supporting Information S4 for a detailed breakdown and Supporting Information S5 for a country-level comparison.

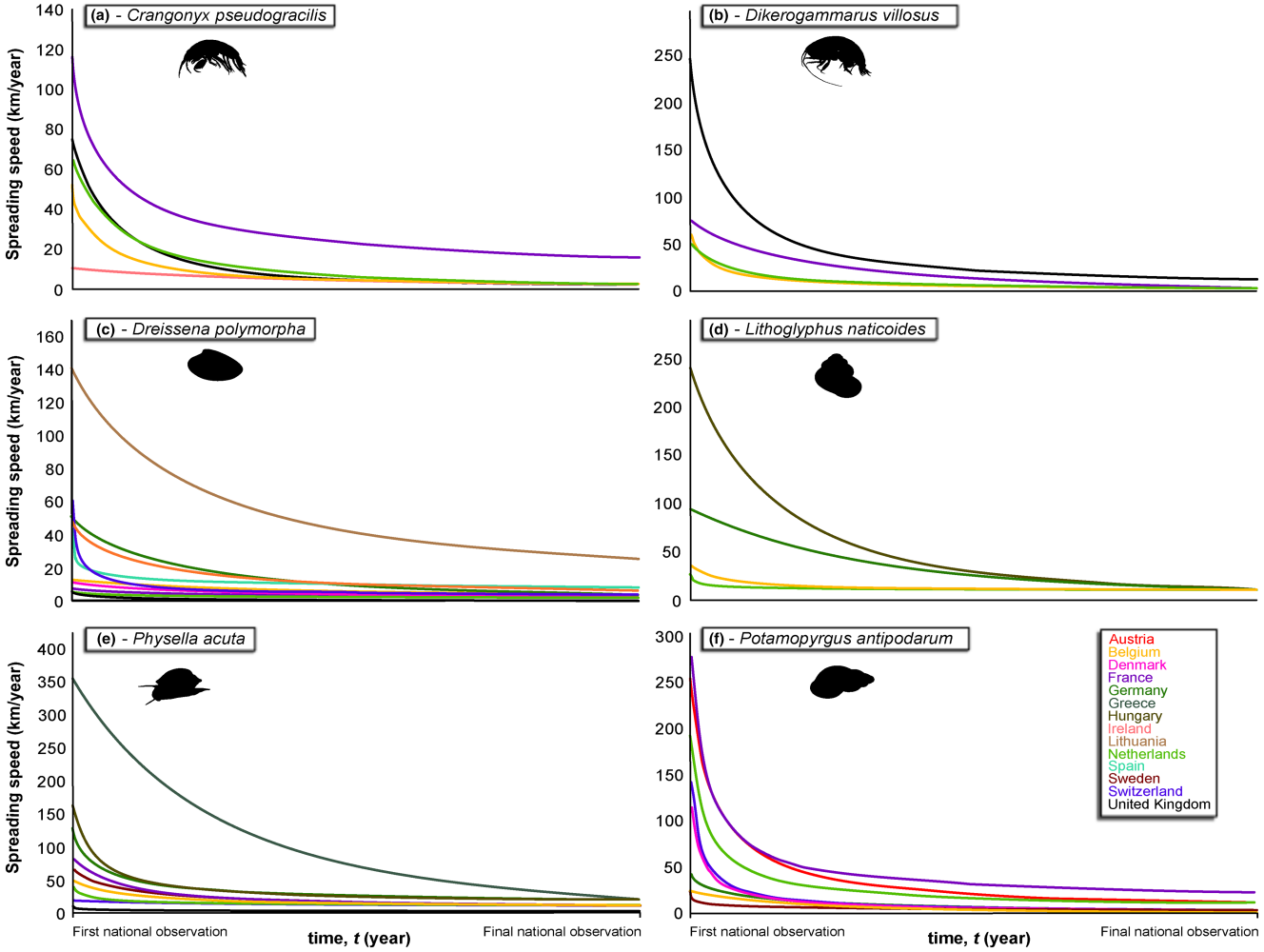

FIGURE 4 Estimated spreading speed as a function of time for six aquatic species (a: *Crangonyx pseudogracilis*; b: *Dikerogammarus villosus*; c: *Dreissena polymorpha*; d: *Lithoglyphus naticoides*; e: *Physella acuta*; f: *Potamopyrgus antipodarum*) across 14 European countries, modelled using an inverse power-law relationship based on data obtained from the *Global Biodiversity Information Facility* for 14 European countries with long data series (>10 years) (Supporting Information S4). Note the different magnitudes in speed on the vertical axis for illustration purposes.

3.2 | Investigating temporal dynamics in abundance trends

Populations of non-native macroinvertebrate species in our dataset showed variable trends in their abundance over time, ranging from relatively stable to highly fluctuating abundances, revealing significant variation across conspecific populations throughout Europe (Figure 5). Among those Mann-Kendall statistics, 12 trends were significantly positive, 8 were significantly negative, and 208 neutral (i.e. non-significant). Therefore, the vast majority of trends were not significant. From these non-significant trends, 135 were positive and 73 were negative (Figure 6). The meta-regression analysis also revealed substantial heterogeneity in the temporal trends among populations of *D. villosus* in France ($I^2 = 85.08\%$), suggesting diverse ecological influences at the population level. In contrast, *D. villosus* I^2 values for Germany and Hungary were zero, indicating no heterogeneity. *Potamopyrgus antipodarum* exhibited varying degrees of heterogeneity across countries, with high I^2 values in Spain (36.49%) and the United Kingdom (41.84%), suggesting substantial ecological diversity, while populations in Luxembourg and Hungary showed lower heterogeneity ($I^2 = 0.01\%$). *Dreissena polymorpha* in Germany ($I^2 = 44.51\%$), *L. naticoides* in Hungary ($I^2 = 46.45\%$), and *P. acuta* in Spain ($I^2 = 61.17\%$) showed moderate heterogeneity across abundance trends, while trends in the abundance of *P. acuta* in Hungary and the Netherlands were homogeneous ($I^2 = 0.01\%$). *Crangonyx pseudogracilis* in the United Kingdom displayed negligible heterogeneity ($I^2 = 0.01\%$), while in the Netherlands it exhibited a slightly higher I^2 (9.53%; Figure 6; Supporting Information S6).

3.3 | Comparing population-level trends to species-level assessments

The dataset revealed diverse trends in the abundance (Figure 5) and spread (Figure 6) of the six non-native species across Europe. Although most species displayed variable trends in terms of

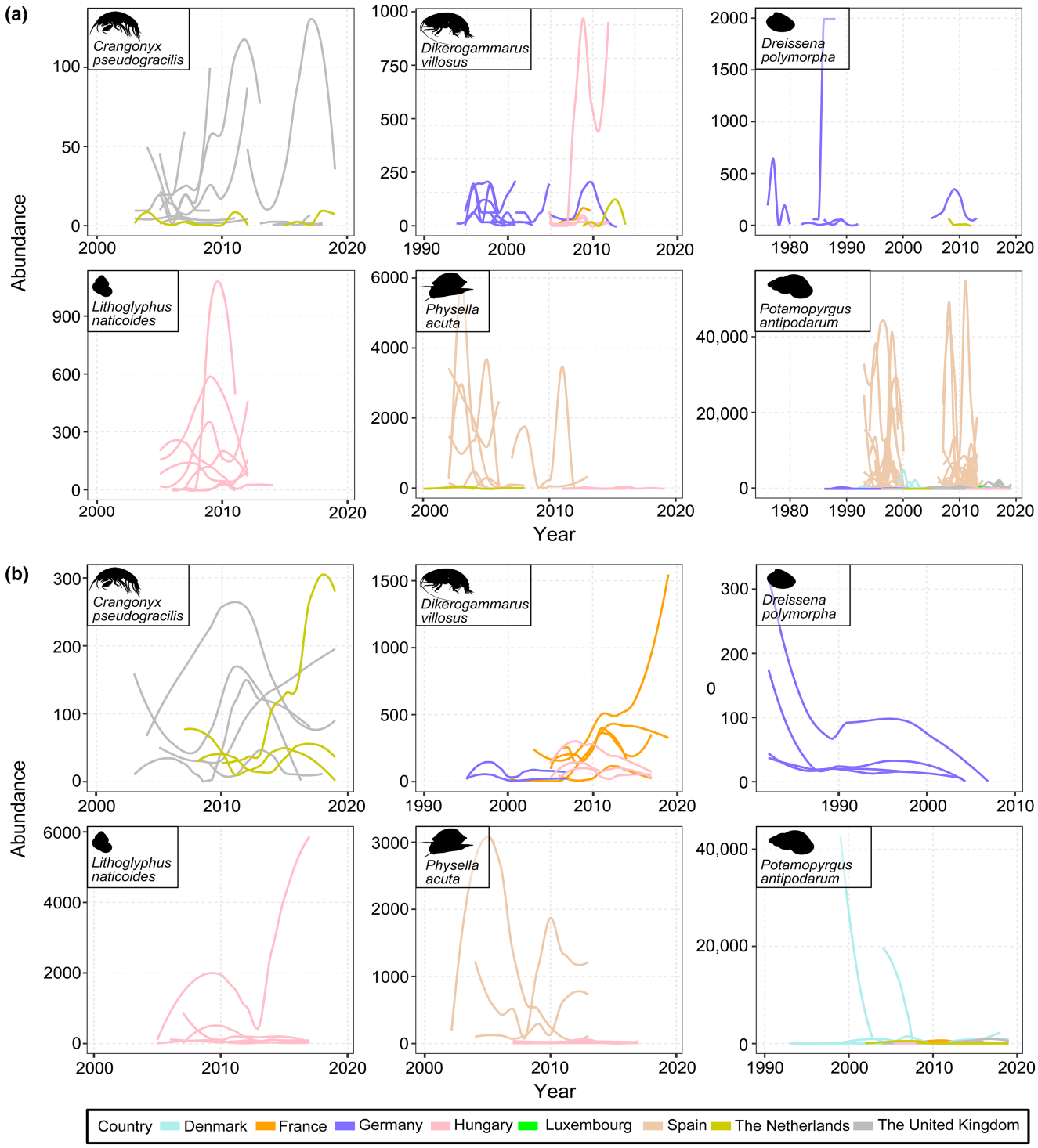

FIGURE 5 Temporal trends in abundances for six non-native macroinvertebrate species sampled for a minimum of 5 (a) or 10 (b) consecutive years in seven European countries. Trends are obtained by fitting a *loess* smoother through the data (Haase et al., 2023).

abundance, several abundance trends were non-significant at the national level (despite trending either positive or negative; Table 1). Trends in the number of invaded time series did not display the same pattern in directionality. The magnitude of risk was also observed to vary considerably across populations of these six model species, alerting to how the evolutionary differences, local conditions, or particular contexts (e.g. climate, soil, biotic interactions), among populations can translate directly into variation in management strategies through geographic space. In accordance with the calibrated global threshold value of 13.25 for freshwater invertebrates, the BRA score identified all species in all RA areas as high risk. The exception to this was *L. naticoides* in Hungary, which was categorised as medium risk (Table 1). When considering the potential impact of climate change, the BRA scores

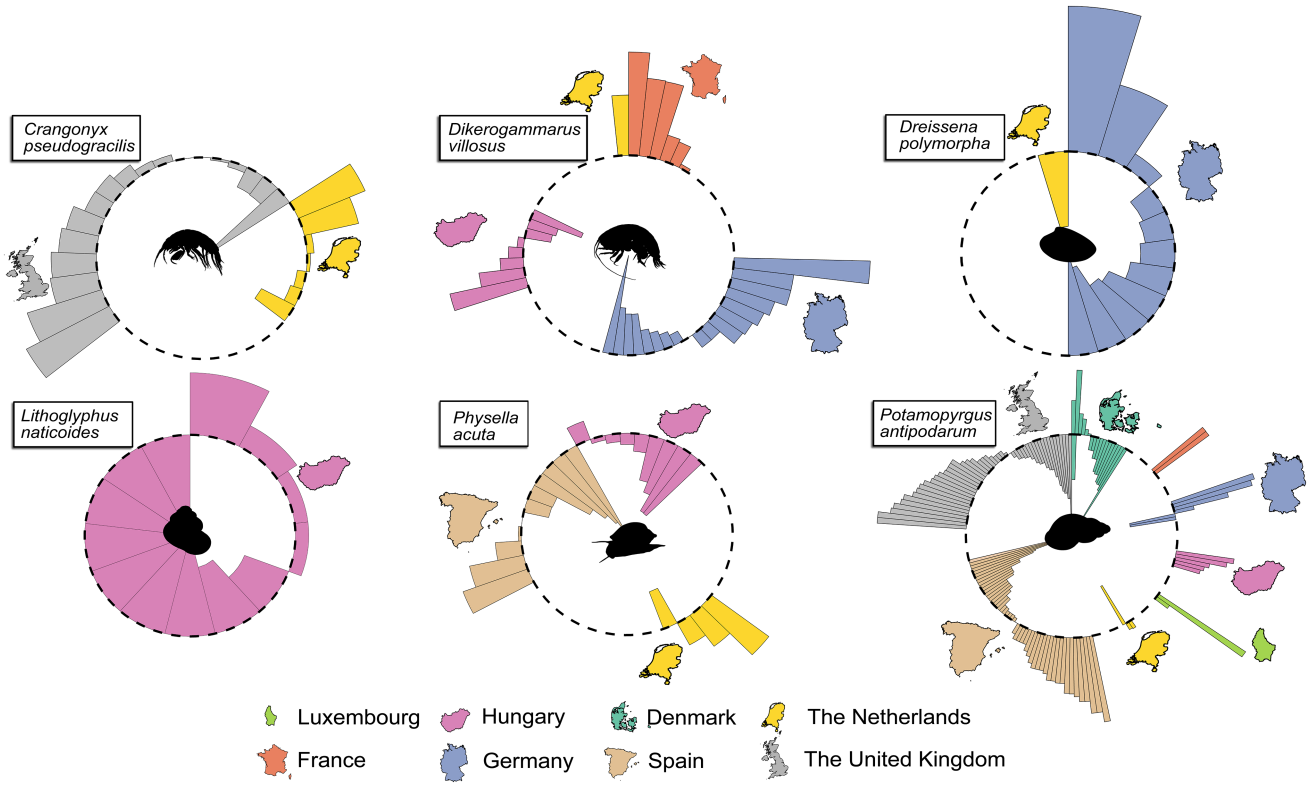

FIGURE 6 Mann-Kendall trends of six non-native species populations time series by country. Bars (each bar representing one trend and its length representing its slope) extending outward from the circle represent positive trends, whereas bars pointing inward indicate negative trends.

increased for *D. polymorpha* in Germany and the Netherlands, *L. naticoides* and *P. acuta* in Hungary, and *C. pseudogracilis* and *P. antipodarum* in the United Kingdom. This suggests a heightened risk for these species to become invasive in their respective RA areas under the projected climate change conditions (Table 1).

4 | DISCUSSION

Our results evidence that the field of invasion science would benefit from a shift at the level of units of analysis and assessment, moving from the traditional species-level to the population-level. This shift offers a comparative perspective that aligns well with the mechanistic foundations of natural selection theory, which explains adaptations in both native and non-native populations. By adopting this approach, we advocate for a more effective direction in designing management strategies for biological invasions. Such new directions are needed, as generalisation at the species level and other oversimplifications of that type hinder effective management interventions. Indeed, aside from boom-bust dynamics (Strayer et al., 2017), invasions are often generalised as an "increasing" threat, with studies frequently noting predominantly positive growth patterns (Pander et al., 2022; Seebens et al., 2017) ignoring the potential for fluctuating or decreasing trends (Niedrist et al., 2023). Our analysis, focusing on empirical long-term trends using non-native species abundances, revealed considerable variability in trends across different macroinvertebrate species, their populations, and invaded regions, underscoring the inability to generalise invasion dynamics, emphasising that each invasion is unique and contingent on a multitude of factors. These discrepancies were even larger when considering differences in the spread speed of certain species across different regions/countries.

4.1 | Investigating spreading speed

The regional disparities in spreading speed emphasise the importance of conceptualising and analysing biological invasions as a population phenomenon. This was evident from the analysis on how the spreading speed varied across species and regions, specifically in the long-term, with 74% of cases studied exhibiting a slower than linear rate of decline, and only a single species (*D. polymorpha*) consistently adhering to this particular pattern across all countries. Local populations of an invasive non-native species can exhibit remarkably different spread dynamics due to context dependencies, i.e. regional selective pressures and ecological interactions, as shown by the large variance for several species in some countries. A population's spread may be fundamentally influenced by how many individuals exist within a population's occupied area (i.e. density; Altwegg et al., 2013). High densities may trigger a non-native individual's action of leaving the established area and spreading into a new environment. Such a natural movement is constrained by the

TABLE 1 Comparison of population-level trends in the abundance and occurrence and species-level assessment. Detailed information about the Aquatic Species Invasiveness Screening Kit Screening can be found in Supporting Information S7 and S8. Trends categorised as "flat" were found to be non-significant, but the trend direction was indicated as either increasing (+) or decreasing (−).

Country	Species	First reporting	First observation within long-term data	Abundance trends (i.e. increasing or decreasing)	Number of time series invaded (i.e. increasing or decreasing)	BRA score	BRA + CCA score
Denmark	*Potamopyrgus antipodarum*	1914	1992	Decreasing ($I^2 = 56.19$)	Increase	29	29
France	*Dikerogammarus villosus*	1997	2000	Increasing ($I^2 = 85.08$)	Flat (+)	28	28
	Potamopyrgus antipodarum	1948	1992	Increasing ($I^2 = 0$)	Increase	29	29
Germany	*Dikerogammarus villosus*	1991	1994	Flat (+) ($I^2 = 0$)	Decrease	30.5	30.5
	Dreissena polymorpha	1824	1972	Increasing ($I^2 = 44.51$)	Flat (+)	39	47
	Potamopyrgus antipodarum	1887	1992	Flat (+) ($I^2 = 68.12$)	Decrease	30	30
Hungary	*Dikerogammarus villosus*	NA	2005	Flat (−) ($I^2 = 0$)	Flat (−)	41	41
	Lithoglyphus naticoides	NA	2005	Flat (−) ($I^2 = 46.44$)	Flat (−)	8	10
	Physella acuta	NA	2005	Decreasing ($I^2 = 0$)	Increase	32.5	38.5
	Potamopyrgus antipodarum	NA	2005	Increasing ($I^2 = 0$)	Flat (+)	25	25
Luxembourg	*Potamopyrgus antipodarum*	NA	2007	Increasing ($I^2 = 0$)	Increase	29	29
Spain	*Physella acuta*	NA	1993	Flat (−) ($I^2 = 61.17$)	Flat (−)	32.5	32.5
	Potamopyrgus antipodarum	1951	1993	Flat (−) ($I^2 = 36.49$)	Increase	24	24
The Netherlands	*Crangonyx pseudogracilis*	NA	2000	Flat (+) ($I^2 = 9.52$)	Increase	24	34
	Dikerogammarus villosus	1994	2004	Flat[a] (+) ($I^2 = NA$)	Flat (+)	34.5	34.5
	Dreissena polymorpha	1826	1991	Flat[a] (−) ($I^2 = NA$)	Flat (−)	29	37
	Physella acuta	1993	1983	Flat (+) ($I^2 = 0$)	Increase	32.5	32.5
	Potamopyrgus antipodarum	1913	1983	Decreasing[a] ($I^2 = NA$)	Increase	29	29
The United Kingdom	*Crangonyx pseudogracilis*	1932	1995	Flat (+) ($I^2 < 0.01$)	Increase	16.5	24.5
	Potamopyrgus antipodarum	1852	1994	Flat (−) ($I^2 = 41.84$)	Increase	29	31

Abbreviations: BRA, Basic Risk Assessment; CCA, Climate Change Assessment.

[a]The assessment is based on one time series available.

invaded habitat (e.g. a freshwater system is delimited and may have physical barriers that prevent spread), but ultimately depends on the individual's behavioural variability and genetic composition (Myles-Gonzalez et al., 2015). The subsequent establishment success can be determined by species-specific requirements and traits (e.g. species may need specific habitat quality characteristics to establish a new sustained population) but can be also driven by propagule or colonisation pressure (Briski et al., 2012). An individual spreading towards a new front (e.g. uncolonised tributary within the same river; Dominguez Almela et al., 2022) can trigger an initial exponential

growth within the population due to low numbers (until the population becomes stabilised). However, individuals at the invasion front could prioritise traits related to motility in a trade-off with reproduction, which could reduce population growth in the short-term (Friesen & Shine, 2019).

Assessing the spread rates of aquatic invasive non-native species is complicated by factors such as detection challenges, underestimation due to detection lag, biassed observational data, niche shifts following invasion process, and artificial acceleration by hydrological events, all of which can lead to inaccuracies in estimating their true spreading potential (Beck et al., 2014; Havel et al., 2015; Macêdo et al., 2021). It is therefore crucial to recognise that the spreading speed of non-native species in aquatic ecosystems has seldom been comprehensively assessed, despite its fundamental role in defining invasiveness. It is influenced by a myriad of factors, including local environmental conditions such as water temperature, salinity and habitat type; anthropogenic influences like canal and waterway construction; as well as biological interactions with native species or human-driven dispersal and species traits (Hui & Richardson, 2017; Pyšek et al., 2008). In reality, the perceived spreading speed is likely a culmination of individual population movements alongside 'pulsed' translations via primary and secondary spread in human vectors within aquatic systems.

4.2 | Investigating temporal dynamics in abundance trends

Population-level trends showed vastly different trajectories within and between species over time and space in our time series from which only 7.7% were found to be significant. The differences in trajectories and between significant and non-significant trends are likely driven by sampling errors (i.e., "random chance"; Nakagawa et al., 2017) or multiple biotic and abiotic contexts, including characteristics of founding populations, Allee effects (Drake, 2004; Taylor & Hastings, 2005), and prevailing environmental conditions, which can have effects at early and late invasion stages. These driving factors include, among others, selection during the transport, as well as the introduction stage of the invasion process, which can be particularly harsh, thereby greatly reducing the size of non-native populations available to establish (i.e. propagule and colonisation pressure; Briski, Chan, et al., 2014; Briski, Drake, et al., 2014; Briski et al., 2018). These selections produce offspring with mean trait values shifted relative to those of their original parent's population, facilitating local adaptation and possibly resulting in a greater likelihood of invasion and consequent spread and impact (Briski et al., 2018). It has been widely evidenced that species undergoing the transport phase do not automatically establish in the new area; their survival hinges upon the prevailing environmental conditions and biotic filters occurring at the local scale (Aksu et al., 2021; Emiroğlu et al., 2023).

In the establishment stage, the most crucial factors limiting the population size of non-native species are often biotic filters, although their influence intertwines with environmental conditions and species traits. An often overlooked—yet crucial—aspect is the concept of lag phase: the time elapsing between a species' introduction and its discovery, which often coincides with a demographic explosion. During the lag phase, the population remains at low abundance as it adapts to the new environment, thus creating the illusion of no or low potential threat to invaded ecosystems (Crooks, 2005; Müller-Schärer & Steinger, 2004; Soto, Ahmed, Balzani, et al., 2023). A lag phase commonly occurs between establishment and spread of non-native species, during which small populations of established non-native species acclimate to their new community (Crooks, 2005). This phase may be influenced by genetics of non-native populations, since populations introduced to new geographic regions can also vary in their genetic composition (Crooks, 2005; Emlen & Zimmer, 2019). In this sense, genetically diverse populations introduced in suitable areas (i.e. areas with high resource availability or under fluctuating resources) are more likely to become invasive (Emlen & Zimmer, 2019; Hui & Richardson, 2017; but see also the genetic paradox: Schrieber & Lachmuth, 2017). Indeed, the genetic makeup of different non-native populations of the same species—shaped through the selective effects of local environmental conditions, bottleneck effects, rapid evolution and genetic diversity—significantly influences their ability to adapt and thrive in new environments (Tsutsui et al., 2000). These effects are mirrored in certain traits, which can be crucial in determining success in a new locality (Capellini et al., 2015). For example, populations that have evolved traits like disease resistance, tolerance to varying climate conditions, or efficient resource utilisation, often have a higher chance of establishing themselves successfully in a foreign ecosystem. This success is further amplified if these traits confer a competitive advantage over native species (Geburzi & McCarthy, 2018; Leger & Espeland, 2010).

In the dispersal stage, the spread rates of non-native populations are mainly limited by invaded habitat configuration; for example, river network complexity is a key factor affecting connectivity and flow patterns in freshwater systems, which affect the spread success of the non-native population (Dominguez Almela et al., 2022; Goldberg et al., 2010; Masson et al., 2018). Other factors such as species traits and dispersal vectors also influence spread of non-native populations (Grabowska & Przybylski, 2015; Purcell & Stockwell, 2015; Rehage & Sih, 2004; Renault, 2020; Renault et al., 2018). The distinctiveness of various populations is however largely influenced by the environmental challenges faced by the individuals. Those that survive these challenges shape the unique characteristics of their population. Moreover, the variation in behaviours such as boldness and activity among non-native individuals, especially between those at the core of an invasion and those at the invasion front, can significantly alter the dispersal and impact of non-native population (Damas-Moreira et al., 2019; Myles-Gonzalez et al., 2015). Biological invasions must therefore fundamentally be seen as a population-level phenomenon and considering them as such is paramount (Hulme, 2017; Westcott & Fletcher, 2011). Instances may exist where a single individual of a non-native species can cause impactful consequences, also underscoring the significance of individual-level considerations—for

instance by predator species due to exerted predation pressures or local modification of an ecosystem (i.e. through burrowing; Haubrock et al., 2019). Simultaneously, certain populations may exhibit the potential to spread widely while maintaining low abundances, yet exert significant local impacts (Spear et al., 2021). Conversely, other populations may achieve higher abundances, be highly invasive (i.e. exert a high potential to spread) yet cause substantially less severe ecological impacts (i.e. reversible population decline rather than local extinctions) than other less-abundant species due to different impact mechanisms. These possibilities are contingent upon the characteristics of the invaded ecosystem, but non-native species abundance, biomass, occupied area, and impact may not always strictly correlate. However, while any of these four measurements may serve as a proxy for both impact and spread, abundance in particular may reflect a population's potential to spread (Booy et al., 2020) and thus, function as an indicator of a population's potential invasiveness (Soto, Ahmed, Beidas, et al., 2023; Soto et al., 2024).

Abundance trends at local scales exhibit significant variability, as demonstrated by declines in the abundance of non-native species within long-term monitoring sites for marine and freshwater environments, despite a rapid increase in reports of non-native species since the late 1970s. These declines were predominantly driven by abundance trends in non-native fish, birds and invertebrate species across three biogeographic European regions (Continental, Atlantic and the North Sea) (Haubrock, Pilotto, et al., 2023). The length of an abundance-based time series for a non-native species may, however, play a pivotal role in shaping our perception of population trajectories. Short-term observations may suggest positive, negative, or flat trends, leading to potentially misleading conclusions about the species' population dynamics. The inclusion of as many years as possible in time series is therefore crucial, as only coherent long-term data can reveal the true trajectory of dynamic non-native populations considering the background community context (Falaschi et al., 2020; Strayer et al., 2017).

4.3 | Comparing population-level trends with species-level assessments

Governments and stakeholders often fall into the trap of species-level assessments, oversimplifying the complex interplay of different populations within their respective ecosystem. This inherently flawed perspective has resulted in the compilation of species lists, like the "100 of the world's worst invasive species" (Lowe et al., 2000) or 'deny lists' for invasive species like the "Species of Union Concern" (European Union Regulation 1143/2014). While boosting awareness on the challenges associated with non-native species, selection for inclusion in these lists was often guided by arbitrary criteria (i.e. the severity of impacts on biodiversity and human activities in specific regions, as well as a species' potential to epitomise significant issues pertaining to biological invasions across diverse taxa). Moreover, while acknowledging the importance of preventive actions, the inclusion of certain species over others in e.g. deny- or blacklists is often without a factual base of criteria (impact vs. spread) or evidence-based rankings, or without information on the selected species' ability to thrive in the area of concern or part of it. These often arbitrary listings, while following a standardised and comprehensive evaluation framework, tend to overlook the dynamic nature of differing populations within ecosystems. Implementing, for instance, pre-invasion 'deny list' approaches for entire species across larger geo-political entities like the European Union or the United States could be impractical across such extensive spatial scales. This is because assessment outcomes may differ significantly among ecosystems, biogeographic regions, value systems and ultimately, also populations (Rilov et al., 2023). The diverse array of ecological contexts and the varying degrees of susceptibility among local populations necessitate a more nuanced and context-specific approach to invasive species management. A 'one-size-fits-all' strategy fails to account for the intricate interplay between species and their environments, potentially leading to misallocations of resources and regulatory efforts. As our understanding of ecological dynamics advances, it becomes imperative to shift towards adaptive, region-specific and population-focused frameworks rather than species' characteristics only, as well as the unique attributes of the ecosystems they may encounter.

The lack of consistent criteria, encompassing factors like political decisions influenced by social acceptability and socio-economic costs, can also result in inadequate management strategies, as focusing solely on the species-level disregards the variability in responses among different populations of the same species. Moreover, legislative approaches should differentiate between those species that might come in the future (even when a continental evaluation and/or a general ban are appropriate) from those that are already established and might spread. Species-level assessments may further inadvertently perpetuate the misconception that all individuals of a species behave in a consistent, uniform manner, ignoring the influence of local conditions, genetic diversity, intraspecific differences and other population-level dynamics (Bolnick et al., 2011; Pincheira-Donoso et al., 2018). Therefore, this traditional species-level view conflicts with the mechanistic foundations of natural selection theory and invasion dynamics. One exception is prevention which aims to curb the introduction of non-native species in general and employs a precautionary principle. Our data revealed a discordance between the observed population-level trends of invasive non-native species in Europe and their RAs as determined by BRA scores computed by AS-ISK (Copp et al., 2016). For example, despite *P. antipodarum* invading more areas over time, its impact, as measured by BRA scores that assess a wide variety of factors, was not considered significant. Conversely, *C. pseudogracilis* showed consistent increases in both abundance and spread, reflecting high BRA scores and signalling a high invasion risk. The medium BRA score for *L. naticoides* in Hungary, despite its population increase, indicated a more contained risk, possibly due to limited spread or impact. Furthermore, the potential impact of climate change is captured by BRA scores that predict an elevated risk for species like *D. polymorpha*, whose current abundance trends might not yet reflect this future risk. These cases

TABLE 2 Comparative analysis of species-level and population-level approaches in invasion science highlighting the strengths and limitations of each approach.

Species level	Approach	Population level
General species characteristics	Focus	Specific population dynamics
Broad-scale risk assessments, initial screening of potential invasive species without an invasion history	Applications	Sub-species levels assessments, adaptive management approaches, understanding specific invasion mechanisms, tailored interventions based on local conditions
Easier to generalise across regions, less resource-intensive, useful for broad prevention strategies, streamlined adoption across jurisdictions, generalised methodologies, clear for public engagement and communications globally	Pros	More accurate for local management, considers local environmental conditions, accounts for genetic diversity and intraspecific differences, can reveal unique invasion dynamics, can adapt to changing conditions and new information, bolsters fundamental research efforts into eco-evolutionary dynamics within species, counters supposed xenophobic perceptions towards individual species
Oversimplifies complex dynamics and interactions, may not reflect local conditions, ignores genetic diversity and intraspecific differences, may lead to misallocation of resources, management based on arbitrary species lists (e.g. knowledge gaps between global north and south)	Cons	Resource-intensive (requires more data, planning and analysis), can be complex to interpret, requires detailed local knowledge, may not be feasible for all species or regions, more difficult translation across jurisdictions, difficult for species without invasion history

exemplify the complexity of biological invasions, where increasing abundances and outgoing spread do not directly translate to high invasion risk at a national level. This underscores the importance of integrating empirical data with RA tools to accurately gauge and manage the invasion risks at the population level.

While the species-level perspective can diminish the necessity for investing in risk and impact assessments locally, a population-level approach demands significantly higher investments. Tracking invasion dynamics of single populations needs greater amounts of resources (both in terms of human effort and monetary resources) than assessing invasions at the species level. Robust population-level assessments require information on local abundances and environmental conditions to allow recording of current invasion trends or predict future population dynamics and impacts. An alternative is to propose an adaptive management approach, in which the initial management measures are based on similar invasive non-native populations (same non-native species in the same type of habitat, and similar contexts and conditions), possibly assessed by tools like the DOSI scheme (Dispersal, Origin, Status, and Impact; Soto et al., 2024). Meanwhile, the invasive non-native population trend is evaluated with and without management to assess the efficacy and feasibility of management measures. With new data, management actions are updated to improve efficacy in an adaptive cycle (Dietze et al., 2018). However, it is important to note that such resources are not always available when assessing biological invasions. In such cases, monitoring programs should focus on evaluating combinations of conditions under which populations of non-native species could become invasive (e.g., those with higher growth rates and reproductive effort; van Kleunen et al., 2010). A nuanced comparison that motivates the debate is presented in Table 2. This comparison underscores the strengths of the population-level approach relative to the species-level approach, but benefits could be potentially integrated between both among contexts.

5 | CONCLUSIONS

Variable trends of non-native species populations (i.e. in terms of local abundance and spread), even of the same species, serve as a compelling argument for population-level assessments and decision making, deviating from the traditional species-level perspective. Recognising the nuanced responses of distinct populations to the opening of current introduction pathways, environmental factors, and biotic interactions is crucial. In the future, the focus of classifications and RAs of biological invasions should transition from evaluating individual non-native species to evaluating diverse populations of non-native species. While species-level traits are important for identification of patterns, the elucidation of mechanistic pathways from transport to impacts of invasions relies on population-level analyses. Accordingly, generalising non-native species as invasive is problematic (Thomsen et al., 2011), as it overlooks the potential for intraspecific variability in invasiveness, hindering the ability to tailor effective management and conservation strategies. Assessing non-native populations allows for a more nuanced understanding of invasion dynamics, enabling the identification of specific traits or conditions that drive invasiveness in certain non-native populations. This shift in perspective is essential for advancing invasion science and evolutionary ecology, refining RAs, and developing targeted interventions that consider the diverse dynamics exhibited by populations within the broader category of non-native species.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data analysed in our manuscript and the associated R codes are included as supplementary information and can be downloaded from Zenodo at https://zenodo.org/records/11049599.

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