

## RESEARCH ARTICLE

# Invasion impacts and dynamics of a European-wide introduced species

Phillip J. Haubrock<sup>1,2</sup>  | Danish A. Ahmed<sup>3</sup>  | Ross N. Cuthbert<sup>4,5</sup>  |  
 Rachel Stubbington<sup>6</sup>  | Sami Domisch<sup>7</sup>  | Jaime R. G. Marquez<sup>7</sup> | Ayah Beidas<sup>3</sup> |  
 Giuseppe Amatulli<sup>8</sup>  | Jens Kiesel<sup>7,9</sup>  | Longzhu Q. Shen<sup>7,10</sup>  | Ismael Soto<sup>2</sup>  |  
 David G. Angeler<sup>11,12</sup>  | Núria Bonada<sup>13</sup>  | Miguel Cañedo-Argüelles<sup>14</sup> |  
 Zoltán Csabai<sup>15,16</sup>  | Thibault Datry<sup>17</sup> | Elvira de Eyto<sup>18</sup>  | Alain Dohet<sup>19</sup> |  
 Emma Drohan<sup>20</sup>  | Judy England<sup>21</sup>  | Maria J. Feio<sup>22</sup>  | Marie A. E. Forio<sup>23</sup>  |  
 Peter Goethals<sup>23</sup>  | Wolfram Graf<sup>24</sup>  | Jani Heino<sup>25</sup>  | Emma J. Hudgins<sup>26</sup> |  
 Sonja C. Jähnig<sup>7,27</sup>  | Richard K. Johnson<sup>11</sup>  | Aitor Larrañaga<sup>28</sup> | Patrick Leitner<sup>24</sup>  |  
 Lionel L'Hoste<sup>19</sup> | Marie-Helene Lizee<sup>29</sup> | Anthony Maire<sup>30</sup>  | Jes J. Rasmussen<sup>31</sup>  |  
 Ralf B. Schäfer<sup>32</sup>  | Astrid Schmidt-Kloiber<sup>24</sup>  | Rudy Vannevel<sup>33</sup> | Gábor Várbbó<sup>34</sup>  |  
 Peter Wiberg-Larsen<sup>35</sup> | Peter Haase<sup>1,36</sup> 

<sup>1</sup>Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany

<sup>2</sup>University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, South Bohemian Research Center of Aquaculture and Biodiversity of Hydrocenoses, Vodňany, Czech Republic

<sup>3</sup>Center for Applied Mathematics and Bioinformatics (CAMB), Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, Hawally, Kuwait

<sup>4</sup>GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany

<sup>5</sup>School of Biological Sciences, Queen's University Belfast, Belfast, UK

<sup>6</sup>School of Science & Technology, Nottingham Trent University, Nottingham, UK

<sup>7</sup>Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Department Community and Ecosystem Ecology, Berlin, Germany

<sup>8</sup>Yale University, School of the Environment, New Haven, Connecticut, USA

<sup>9</sup>Christian-Albrechts-University Kiel, Institute for Natural Resource Conservation, Department of Hydrology and Water Resources Management, Kiel, Germany

<sup>10</sup>Carnegie Mellon University, Institute for Green Science, Pittsburgh, Pennsylvania, USA

<sup>11</sup>Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

<sup>12</sup>School of Natural Resources, University of Nebraska–Lincoln, Lincoln, Nebraska, USA

<sup>13</sup>Freshwater Ecology, Hydrology and Management, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain

<sup>14</sup>Freshwater Ecology, Hydrology and Management, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Institut de Recerca de l'Aigua (IdRA), Universitat de Barcelona (UB), Barcelona, Spain

<sup>15</sup>Department of Hydrobiology, University of Pécs, Pécs, Hungary

<sup>16</sup>Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

<sup>17</sup>INRAE, UR RiverLy, centre de Lyon-Villeurbanne, Villeurbanne, France

<sup>18</sup>Marine Institute, Newport, Ireland

<sup>19</sup>Environmental Research and Innovation (ERIN) Luxembourg Institute of Science and Technology (LIST), Belvaux, Luxembourg

<sup>20</sup>Institute of Technology, Centre for Freshwater and Environmental Studies, Dundalk, Ireland

Phillip J. Haubrock, Danish A. Ahmed and Ross N. Cuthbert contributed equally.

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<sup>21</sup>Environment Agency, Wallingford, UK

<sup>22</sup>MARE - Marine and Environmental Sciences Centre, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

<sup>23</sup>Department of Animal Sciences and Aquatic Ecology, Ghent University, Ghent, Belgium

<sup>24</sup>University of Natural Resources and Life Sciences, Institute of Hydrobiology and Aquatic Ecosystem Management, Vienna, Austria

<sup>25</sup>Finnish Environment Institute, Freshwater Centre, Oulu, Finland

<sup>26</sup>Department of Biology, Carleton University, Ottawa, Canada

<sup>27</sup>Geography Department, Faculty of Mathematics and Natural Sciences, Humboldt-Universität zu Berlin, Berlin, Germany

<sup>28</sup>Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), Leioa, Spain

<sup>29</sup>RECOVER Research Unit, National Research Institute for Agriculture, Food and Environment (INRAE), Aix-en-Provence, France

<sup>30</sup>EDF R&D, Laboratoire National d'Hydraulique et Environnement (LNHE), Chatou, France

<sup>31</sup>Section for Nature Based Solutions, Norwegian Institute for Water Research (NIVA), Oslo, Norway

<sup>32</sup>University of Koblenz Landau, Institute for Environmental Sciences, Landau, Germany

<sup>33</sup>Flanders Environment Agency (VMM), Aalst, Belgium

<sup>34</sup>Department of Tisza Research, Institute of Aquatic Ecology, Centre for Ecological Research, Debrecen, Hungary

<sup>35</sup>Department of Ecoscience - Lake Ecology, Aarhus University, Aarhus, Denmark

<sup>36</sup>University of Duisburg-Essen, Faculty of Biology, Essen, Germany

### Correspondence

Phillip J. Haubrock, Senckenberg Research Institute and Natural History Museum Frankfurt, Department of River Ecology and Conservation, Gelnhausen, Germany.  
Email: [phillip.haubrock@senckenberg.de](mailto:phillip.haubrock@senckenberg.de)

Danish A. Ahmed, Center for Applied Mathematics and Bioinformatics (CAMB), Department of Mathematics and Natural Sciences, Gulf University for Science and Technology, Hawally, Kuwait.  
Email: [ahmed.d@gust.edu.kw](mailto:ahmed.d@gust.edu.kw)

Ross N. Cuthbert, GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, Kiel, Germany.  
Email: [rossnoelcuthbert@gmail.com](mailto:rossnoelcuthbert@gmail.com)

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### Abstract

Globalization has led to the introduction of thousands of alien species worldwide. With growing impacts by invasive species, understanding the invasion process remains critical for predicting adverse effects and informing efficient management. Theoretically, invasion dynamics have been assumed to follow an “invasion curve” (S-shaped curve of available area invaded over time), but this dynamic has lacked empirical testing using large-scale data and neglects to consider invader abundances. We propose an “impact curve” describing the impacts generated by invasive species over time based on cumulative abundances. To test this curve's large-scale applicability, we used the data-rich New Zealand mud snail *Potamopyrgus antipodarum*, one of the most damaging freshwater invaders that has invaded almost all of Europe. Using long-term (1979–2020) abundance and environmental data collected across 306 European sites, we observed that *P. antipodarum* abundance generally increased through time, with slower population growth at higher latitudes and with lower runoff depth. Fifty-nine percent of these populations followed the impact curve, characterized by first occurrence, exponential growth, then long-term saturation. This behaviour is consistent with boom-bust dynamics, as saturation occurs due to a rapid decline in abundance over time. Across sites, we estimated that impact peaked approximately two decades after first detection, but the rate of progression along the invasion process was influenced by local abiotic conditions. The S-shaped impact curve may be common among many invasive species that undergo complex invasion dynamics. This provides a potentially unifying approach to advance understanding of large-scale invasion dynamics and could inform timely management actions to mitigate impacts on ecosystems and economies.

### KEYWORDS

biological invasion, long-term time series, *Potamopyrgus antipodarum*, rapid response/early detection, temporal modelling

## 1 | INTRODUCTION

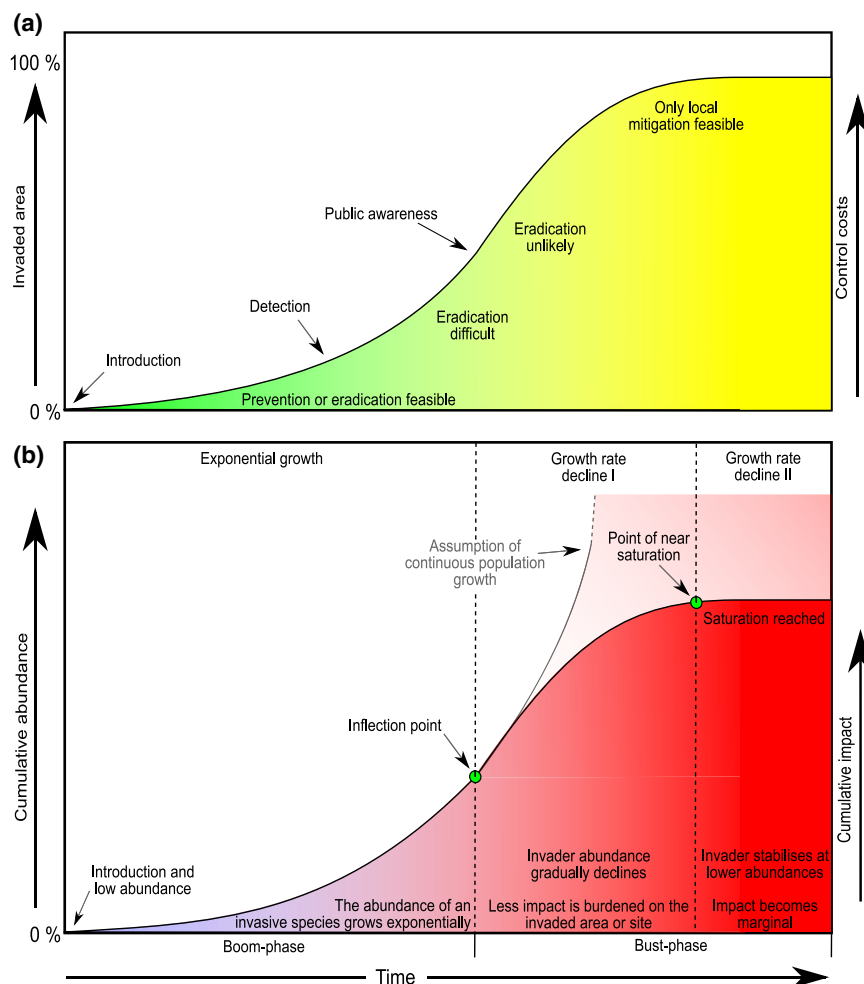
Global trade and transport have translocated thousands of species beyond their native range (Seebens et al., 2017, 2021). A subset of these species become “invasive” when they establish, spread in a non-native range, and subsequently have impacts on communities, ecosystems (Pyšek et al., 2020; Ricciardi et al., 2021), societies, and economies (Cuthbert et al., 2021; Diagne et al., 2021). A major challenge remains in identifying general patterns and processes in invasion science, with knowledge gaps hindering predictions of future invasion dynamics, their exerted impacts, and the development of efficient management responses (Courchamp et al., 2017). Although the invasion process has been conceptualized using a stage-based framework—translocation, introduction, establishment and spread (Blackburn et al., 2011; Leung et al., 2012)—the time an invader spends at each stage may be highly context-dependent (Spear et al., 2021). Thus, dependent on context, internal population dynamics and the distribution extent can be key determinants of the invasion trajectory (Bradley et al., 2019; Hui & Richardson, 2017).

Invasive species abundance-derived population dynamics describe the process after a species is introduced, successfully establishes, and consequently its population fluctuates through variations in growth rates and other dependencies

(i.e., density-dependent versus density-independent population dynamics; Hui & Richardson, 2017). Invasion dynamics, on the other hand, are extent-driven and rely on changes in the spread rate (spread dependency; Arim et al., 2006). Concomitantly, temporal changes in invasion extent have been described by the “invasion curve” (Figure 1a) (Department of Primary Industries, 2015; Lodge et al., 2006), illustrating the area occupied by invasive plant species as a proportion of the total area available. As the invaded area grows cumulatively, the invasion curve typically follows a sigmoid function (i.e., S-shaped curve), consisting of an initial lag phase (i.e., during which range expansion is slow), followed by an exponential growth phase that eventually approaches saturation (Kelly et al., 2021) (Figure 1a). In the final saturation stage, population sizes may naturally fluctuate around the asymptote (Geburzi & McCarthy, 2018). This curve, albeit largely theoretical, has been used to quantify ecological effects and related to economic costs of invasive species (Ahmed et al., 2021).

For invasive animal populations, it is often not the area occupied, but rather the local abundance of an invasive population that is a suitable proxy of potential impacts (Bradley et al., 2019; Sofaer et al., 2018). Accordingly, at large spatial scales, cumulative abundances or densities could approximate an invasive population's accumulating impacts (Hui & Richardson, 2017). Ecologically, cumulative

**FIGURE 1** The classic “invasion curve” (a) versus our “impact curve” (b). The relationship in (a) displays the implications (in economic cost of control efforts) of a generalized invasive species' population dynamics over time, after its introduction and establishment in a new environment. As the population spreads, both the area invaded (as a percentage of the total available area, which commonly reflects the invader's abundance) and its management costs increase following a S-shaped curve as adapted from Department of Primary Industries (2015) and Ahmed et al. (2021). (b) The proposed “impact curve” describes the impact exerted on an invaded area associated with the cumulative abundance of an invasive population within that area. This curve is congruent with phases shown in (a), yet considers potentially decreasing invader abundances (i.e., boom-bust dynamics) and negligible additional impact being generated (i.e., saturation phase). In an alternative scenario (pink), cumulative abundance and impacts are expected to saturate over very long time scales



abundances may represent the total negative consequences of the invasion since its inception. Against this background, we propose the use of an “impact curve” (Figure 1b) that describes the cumulative abundance and impact of invasive species over time (sensu Hansen et al., 2013; Yokomizo et al., 2009). One advantage of the impact curve is that temporal invasive species abundance data could be used to estimate and track the potential impact of an invader. Furthermore, assessment of cumulative abundance allows for empirical testing of invasion and particularly boom-bust dynamics, which are commonly associated with invasive populations (Elton, 1958; Strayer, 2020). Understanding the invasion stage and extent of invasive populations could also inform management strategies that safeguard ecosystems and economies via efficient and timely interventions.

Although available data on local population dynamics and geographic spread of introduced species are growing, the invasion curve as well as the proposed impact curve remain largely theoretical. Accordingly, empirical tests based on large spatial and temporal scales, that is, using continental and multi-annual data, remain limited (Morris et al., 2013; Reyns et al., 2018). In particular, quantification of the initial period of slow growth, which characterizes invasion curves, could critically inform management because, although successful management is challenging, smaller invasive populations (in occupied areas and/or abundance) generate less damage and can be more efficiently controlled (Strayer, 2009). Early-stage invasive species management can lead to multi-billion-dollar savings in a few decades (Ahmed et al., 2022; Cuthbert et al., 2022).

Recent compilations of large-scale monitoring datasets (Dornelas et al., 2018; Pilotto et al., 2020) enable insights into invasive species population dynamics at large spatiotemporal scales. These data provide the opportunity to test the realism of the invasion curve and elucidate how impact dynamics change over time in response to key environmental variables associated with global change (Haubrock et al., 2021; Strayer, 2009). One data-rich species is the New Zealand mud snail, *Potamopyrgus antipodarum* (Greenwood et al., 2020; Preston et al., 2022), which was introduced to the UK in 1859 via international shipping (Cejka et al., 2008; Ponder, 1988) and has since invaded freshwater ecosystems across Europe, as well as Australia, Asia, South America, and North America (Alonso & Castro-Díez, 2012). In Europe, this species is considered among the most damaging freshwater invaders (Nentwig et al., 2018). *Potamopyrgus antipodarum* populations can thrive under unfavourable conditions and alter nutrient cycles (Alonso & Castro-Díez, 2008, 2012), reduce native species abundance and fitness (Alonso & Castro-Díez, 2012; Bruce et al., 2009), and serve as vectors of pathogens and parasites (Preston et al., 2022). These impacts grow with increasing population sizes, with rapid population increases attributed to asexual reproduction, whereby 230 offspring can be produced per adult on average annually in invaded areas (Alonso & Castro-Díez, 2012). Notably, *P. antipodarum* can experience localized “boom-bust” population dynamics, characterized by rapid population increases followed by rapid declines (Moore et al., 2012). Furthermore, this species can persist despite disturbance events such as heat waves

(Mouthon & Daufresne, 2015), increasing its invasive potential. Although local-scale studies have examined both abiotic and biotic drivers of change, the limited availability of long-term data has so far precluded robust derivations of the species' population dynamics and thus potential impacts at large spatiotemporal scales.

We used *P. antipodarum* as a case study to characterize large-scale invasion dynamics and their environmental drivers. This species is a suitable test case because it can exhibit classic boom-bust dynamics applicable for invasive species (Strayer et al., 2017), tolerates a breadth of physical and chemical conditions, has a high growth rate, and uses various dispersal mechanisms (Alonso & Castro-Díez, 2012; Da Silva et al., 2019; Hall Jr et al., 2006). We hypothesized that (1) European-scale increases in *P. antipodarum* abundance are context-dependent based on environmental drivers, including local/regional climatic conditions and disturbance; and (2) cumulative abundance over time (as a proxy for impacts) follows the sigmoidal impact curve. To test these hypotheses, we used a meta-analytical approach to assess (i) how *P. antipodarum* invasions develop through time and (ii) which environmental variables explain *P. antipodarum* population trends. Furthermore, we investigate (iii) whether the species' cumulative abundance over space and time corresponds to the sigmoidal growth of the impact curve and (iv) which environmental variables can cause potential deviations from the impact curve.

## 2 | MATERIALS AND METHODS

### 2.1 | Biodiversity data

We collated available European stream benthic invertebrate data comprising 1816 time series (sites) from 22 European countries across four biogeographical regions—Atlantic, Continental, Boreal and Alpine—each comprising abundance estimates of taxonomic groups (Supplementary information 1). We extracted all time series (306 sites) that contained *P. antipodarum* observations in  $\geq 4$  years (Austria = 2; Belgium = 17; Denmark = 80; France = 8; Germany = 27; Hungary = 13; Ireland = 1; Luxembourg = 14; Netherlands = 17; Spain = 98; Sweden = 1; UK = 28 time series; Supplementary information 2 and 3) encompassing a large part of its European distribution (CABI, 2021; Da Silva et al., 2019). The resulting time series spanned on average 16.8 ( $\pm 7.4$  SD) years and contained 8.5 ( $\pm 3.7$  SD) sampling years between 1968 and 2020.

### 2.2 | Abiotic variables

We extracted mean daily air temperature and total daily precipitation data from the E-OBS gridded dataset (spatial resolution: 0.1 degrees; Cornes et al., 2018) as indicators of climatic conditions and used these data to calculate the mean annual temperature and precipitation of each site for each calendar year (Pilotto et al., 2020). We obtained site-specific runoff depth data, expressed as the monthly Q

(unit mm), from the TerraClimate dataset at 4-km spatial resolution (Abatzoglou et al., 2018). Temperature, precipitation and runoff values were extracted from the spatiotemporal datasets at the grid cell corresponding to the site location and averaged over the year in which sampling took place. We extracted the elevation of each site from the MERIT Hydro Digital Elevation model (DEM; Yamazaki et al., 2019) at 90-m spatial resolution. We used the MERIT Hydro DEM and the `r.watershed`, `r.stream.extract` and `r.stream.basins` functions in GRASS GIS to delineate the stream network, catchments, and sub-catchments (catchments between network nodes) at 90-m resolution. For each site we computed stream slope using the `r.stream.slope` function and extracted land cover from the ESA CCI Land Cover time series v2.0.7 dataset, the latter at 300-m spatial resolution (ESA, 2017). We calculated the percent cover of urban areas (%-urban) and waterbodies (%-waterbodies) within each sub-catchment in the year of sampling, using the `r.univar` function (Neteler et al., 2012).

### 2.3 | Trend identification and meta-regression modelling

To test our first hypothesis, we followed a two-step procedure that enabled analysis of datasets with different characteristics. We note that the abundance data of *P. antipodarum* were obtained using different sampling protocols among sites (e.g., equipment, duration, season), which inhibited direct comparability among time series (Supplementary information 1). However, assessment was consistent within sites (i.e., time series), with sampling occurring once annually within the same 3-month season. To address this, we first used Mann–Kendall trend tests to identify site-specific monotonic trends in *P. antipodarum* abundance, mean annual temperature and precipitation data (Kendall, 1949; Mann, 1945). When we detected temporal autocorrelation within a time series, we used auto- and cross-covariance using correlation functions (Pilotto et al., 2020; Venables & Ripley, 2002), applying the modified Mann–Kendall variance correction (Hamed & Rao, 1998). We used the Mann–Kendall test statistic ( $S$ ) and its variance to quantify the effect size of each trend (Kendall, 1949). We classified trends in *P. antipodarum* abundance using their direction and significance and used the time series midpoint to identify shifts in the trends' directionality over time as an indication of the invasions' progression.

Second, we used a meta-regression model combining the trajectories of all individual time series to describe the overall abundance trend and identify common patterns and their abiotic predictors. We used a meta-regression model implemented in the `metafor` R package, which accounts for the variance of each individual slope and treats each population as a single isolated pool (Viechtbauer & Viechtbauer, 2015). We included "dataset" as a random effect. To explore environmental predictors of variations in population trends, we included latitude, longitude, mean daily temperature and precipitation for the respective time series' period, the  $S$ -statistic of the change in mean daily temperature and precipitation, the site-specific runoff depth (expressed as the annual average runoff volume

divided by upstream catchment area), elevation, slope, %-urban, %-waterbodies, and the number of observations as a proxy of temporal coverage as predictors. Although meta-regression can handle low degrees of multicollinearity (Berlin & Antman, 1994), we ruled out the presence of multicollinearity using predictor correlations, which were  $R < 0.8$ . We considered a  $p$ -value of 0.05 for significance inference in all analyses.

### 2.4 | Testing the impact curve

To test our second hypothesis, we determined whether a sigmoidal curve  $N(t)$  accurately describes the generated impact that cumulatively grows with the changing abundance of *P. antipodarum* within time series, irrespective of the type of trend (see Supplementary information 4). For this purpose, we did not compare the fit of alternative candidate models. Each site-specific population was assumed to be an individual unit without range expansion (Hastings et al., 2005). We used a sample size of  $\geq 6$  annual observations to enable curve fitting using non-linear regression techniques, resulting in 243 time series. The sigmoidal curve was fitted for each time series independently, therefore the use of different sampling protocols did not invalidate analyses within-site dynamics. The tool `lsqcurvefit` from Matlab was used to estimate the best-fit model parameters: total population size up to the time of first sampling ( $N_0$ ), intrinsic growth rate ( $r$ ) and the carrying capacity ( $K$ , the total population size at which long-term saturation is reached). Once the sigmoidal curve was determined, we expressed the marginal abundance as a function of time  $n(t)$ , which is a bell-shaped curve (Supplementary information 4).

Using the estimated parameters ( $N_0$ ,  $r$ ,  $K$ ), we further estimated the: time that *P. antipodarum* was introduced ( $t_{\text{intro}}$ ), marginal abundance at the time of first sampling ( $n_0$ ), time elapsed to reach the inflection point ( $t_{\text{inf}}$ ) with the corresponding cumulative and peak abundances ( $N_{\text{inf}}$ ,  $n_{\text{max}}$ ), and total population ( $N_{\text{sat}}$ ) up to the time to saturation ( $t_{\text{sat}}$ ). The inflection point is where the marginal abundance has maximized, and the point of near saturation (prior to approaching  $K$ ) is where 99% of the population has accumulated (Supplementary information 4). Site-specific cumulative abundance data were identified to be well-predicted by the sigmoidal curve if: (1) the strength of the curve fitting, as quantified by the coefficient of determination was  $R^2 > 0.7$ , (2) the time of introduction was estimated to be before the time the first site was sampled  $t_{\text{intro}} < 0$  and (3) the sigmoidal curve was substantiated on a sufficiently long time scale, where the time the last site was sampled exceeded  $t_{\text{inf}}$  (or equivalently in terms of marginal abundance, the population has surpassed the boom phase and is in decline, i.e., bust) (Supplementary information 5).

Using model selection implemented in the `glmulti` function of the `glmulti` package in R (Calcagno & de Mazancourt, 2010), we included the best predictors (i.e., those in the model with the lowest corrected Akaike information criterion) from the time series and the number of observations from each individual time series (to determine if the time series duration relates to the assessed points in the sigmoidal function) as predictor variables. We then used linear mixed models with the  $R^2$

value as the response variable to identify factors linked to formation of a sigmoidal fit (i.e., the impact curve). We further included the best-fit parameters  $N_0$ ,  $n_0$ ,  $r$ ,  $K$  and the times to reach the inflection point  $t_{inf}$  and near saturation at  $t_{sat}$  as explanatory variables, to identify predictors influencing the shape of the curve. The analysis was repeated for  $r$ ,  $K$  and parameters determining the sigmoidal shape of the curve (the time to reach the inflection point  $t_{inf}$ , the point of near saturation at  $t_{sat}$ ). The procedure was also followed to estimate the time of introduction ( $t_{intro}$ ), and parameters determining boom-bust dynamics (the estimated marginal abundance  $n_0$  and the maximum value  $n_{max}$ ).

To determine if time series adhered to the sigmoidal curve at the European level, we considered all sites as a single “global” population. We averaged the abundance of all sites sampled in a given year and calculated the cumulative abundance by including values in all years up to and including the year of sampling. Because sampling protocols varied among time series and the number of sites sampled varied among years, our model provides a crude representation of European-level patterns. From this, we tested a bell-shaped curve for raw abundance, deciphering potential boom-bust dynamics. We also predicted retrospectively the time of *P. antipodarum* introduction, by assuming the marginal abundance was low, with value 1 (Figure 4, Supplementary information 4).

### 3 | RESULTS

#### 3.1 | Trend identification and meta-regression modelling

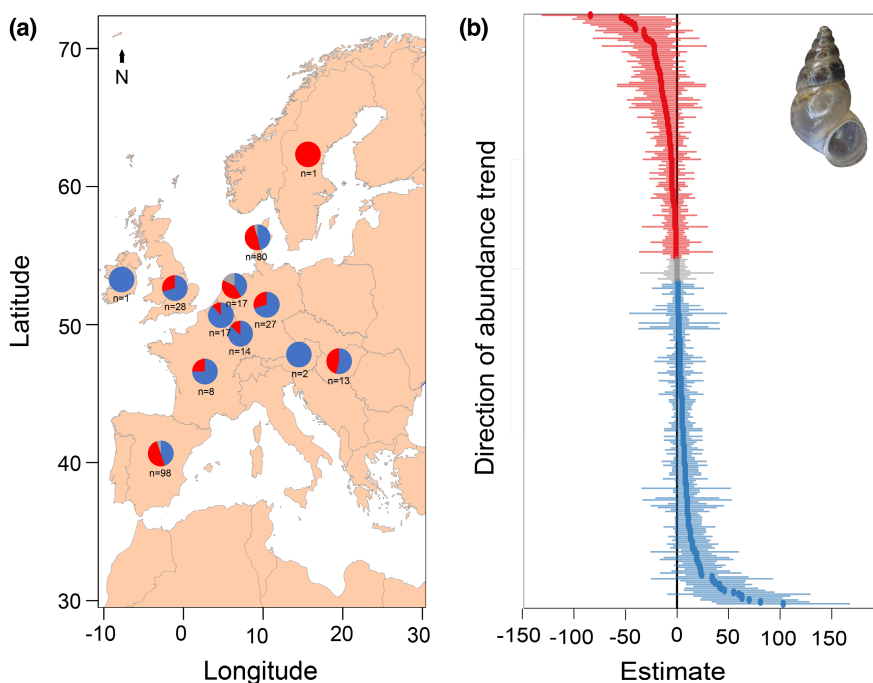
From 306 time series describing long-term temporal change in *P. antipodarum* abundance across Europe, we identified 167 positive monotonic trends including 18 which were significant, 127 negative

trends including 15 which were significant, and 12 showing no trend (Figure 2).

At the European scale, *P. antipodarum* abundance increased over time ( $k = 306$ ;  $\tau^2 = 9.5$ ;  $I^2 = 24.4\%$ ;  $H^2 = 1.3$ ;  $p \leq 0.023$ ). This abundance trend became increasingly positive (i.e., positive trends became increasingly positive and negative trends weakened), when considering the midpoint of each time series' duration (Supplementary Result 1). From all the variables considered (latitude, longitude, mean daily temperature and precipitation for the respective time series' period, the S-statistic of the change in mean daily temperature and precipitation, the site-specific runoff depth (expressed as the annual average runoff volume divided by upstream catchment area), elevation, slope, %-waterbodies and %-urban), we identified two significant predictors of the slope (i.e., rate change) of abundance: latitude and runoff depth, which were negatively and positively associated, respectively. In addition, the %-waterbodies had a positive, non-significant effect (Figure 3; Supplementary results 2 and 3).

#### 3.2 | Testing the impact curve

Using only time series with  $\geq 6$  annual observations to enable non-linear curve fitting ( $n = 243$ ), we found that 143 (59%) supported a sigmoidal curve as a model for cumulative abundances ( $R^2$  values ranging in between 0.74 and 1; Supplementary information 5). The minimum annual observations per time series ( $\geq 6$ ) exceeded the number of model parameters (3:  $N_0$ ,  $r$ ,  $K$ ), and we substantiated the model's ability to generalize across the majority of sites by successfully fitting 59% of the time series, and thus minimizing the possibility of overfitting. When we included those cases that supported a sigmoidal curve on a shorter time scale (i.e., excluding criterion 3,



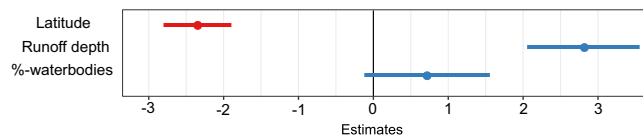
**FIGURE 2** *Potamopyrgus antipodarum* trends across Europe. (a) Contribution of increasing (blue), decreasing (red) and stable (grey) trends in *P. antipodarum* abundance across 12 European countries and over (mean  $\pm$  SD) 16.8  $\pm$  7.4 years (number of sites: Austria = 2; Belgium = 17; Denmark = 80; France = 8; Germany = 27; Hungary = 13; Ireland = 1; Luxembourg = 14; Netherlands = 17; Spain = 98; Sweden = 1; UK = 28). Pie size corresponds to numbers of time series per country. (b) Ordered S-statistics and variance for the monotonic trends of all individual *P. antipodarum* time series ( $n = 306$ ); significant trends are highlighted with darker variance intervals

see Section 2), successful fits increased to 76%. The distribution of  $R^2$  values was strongly negatively skewed, with a very strong correlation ( $R^2 > 0.95$ , see Supplementary result 4k) in 70% of the 143 time series that supported a sigmoidal growth model.

Estimated population parameters varied considerably among time series:  $N_0$  (mean  $\pm$  SD:  $2515 \pm 9223$  individuals per sample),  $r$  ( $1.24 \pm 2.03$ ),  $K$  ( $18,104 \pm 42,715$  individuals),  $t_{inf}$  ( $4.32 \pm 4.30$  years) and  $t_{sat}$  ( $14.46 \pm 11.85$  years). Furthermore, we estimated the introduction time  $t_{intro}$  of *P. antipodarum* as  $9.43 \pm 15.07$  years prior to its first detection (see Supplementary information 4 for the distributions and ranges of parameter values and goodness of fit metrics).

The  $K$ , runoff depth, and mean temperature were significant positive predictors, whereas  $N_0$  was a significant negative predictor of a good fit of the impact curve ( $R^2$ ; Figure 4). Mean precipitation, the number of observations, and runoff depth were significant negative predictors of  $r$ , thus reducing the slope of the exponential phase, while  $N_0$  significantly increased  $r$ . The  $K$  was significantly positively affected by  $N_0$ ,  $n_0$ , the number of observations and the site's slope, but negatively by temperature change, indicating that high  $N_0$ ,  $n_0$ , slope, data resolution and stable temperature increased the level of the saturation phase.

We identified two characteristic time points on the impact curve:  $t_{inf}$  and  $t_{sat}$  (Supplementary information 4). The  $t_{inf}$  was



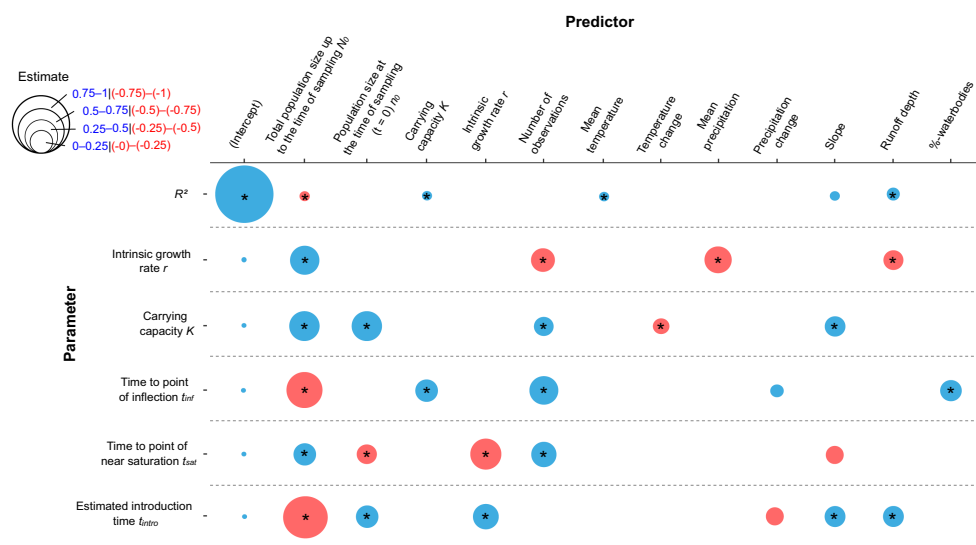
**FIGURE 3** Meta-regression model estimates of the relative effect size of each identified predictor of *Potamopyrgus antipodarum* abundance. Red and blue symbols indicate negative and positive predictors, respectively

significantly positively predicted by  $K$ , the number of observations, and %-waterbodies in the invaded site's proximity, whereas  $N_0$  was a significant negative predictor. The  $t_{sat}$  was significantly shortened by  $r$  and  $n_0$ , but significantly lengthened by  $N_0$  and the number of observations. The  $N_0$  significantly negatively predicted  $t_{intro}$ , while a high  $r$ ,  $n_0$ , slope, and runoff depth increased it. Detailed model results for these parameters that characterize the impact curve are in Supplementary result 5.

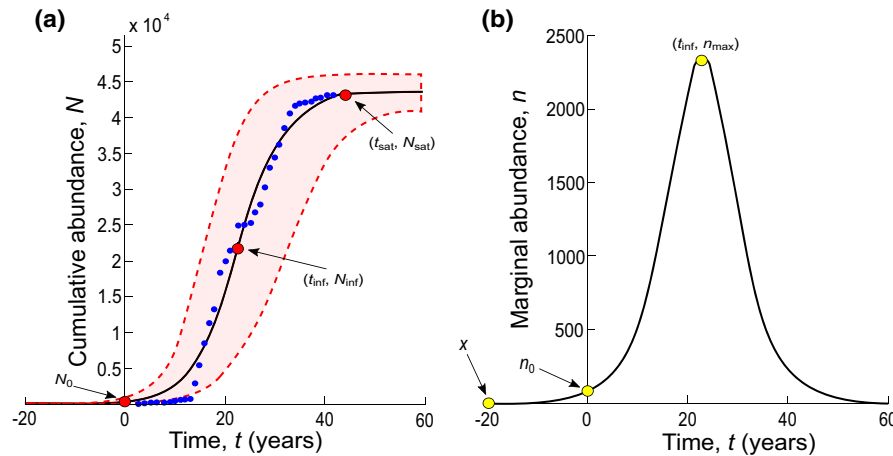
In the European-level model (Figure 5), the overall population strongly adhered to a sigmoidal fit ( $R^2 = 0.98$ ) with an estimated mean total population size at the time of sampling of  $N_0 = 325$  individuals per sample and a saturation level of  $K = 43,426$  individuals (i.e., the estimated cumulative total population in the long term). The average European-level intrinsic growth rate across the 243 sites was  $r = 0.216$  per year. In terms of marginal abundance, this sigmoidal relationship corresponded to a unimodal response, with an estimated abundance of  $n_0 = 69$  individuals at the time of sampling, followed by a peak abundance of  $n_{max} = 2340$  individuals  $t_{inf} = 22.7$  years after its first observation in our data and 42.5 years after its estimated introduction time (Figure 5). Following this, its abundance rapidly declined to near zero after approximately 60 years of its first observation.

## 4 | DISCUSSION

Population dynamics of invasive species have remained untested with empirical data beyond regional scales (Bradley et al., 2019; Elton, 1958; Sofaer et al., 2018). Our conceptualization using spatially and temporally broad data substantiates understanding of the invasion process, and thus prediction of invasive species impacts and the design of associated management responses at local



**FIGURE 4** Linear mixed model results. Overall fitting of *Potamopyrgus antipodarum* abundances using a sigmoidal curve ( $R^2$ ), as well as intrinsic growth rate ( $r$ ), carrying capacity ( $K$ ), point of inflection ( $t_{inf}$ ), point of near saturation ( $t_{sat}$ ), and the estimated introduction time  $t_{intro}$ , showing the estimate and significance ( $p < 0.05$ ) for each model and its predictors, as selected using the lowest corrected Akaike information criterion. Significant effects are shown with an asterisk. Red and blue symbols indicate negative and positive predictors, respectively



**FIGURE 5** (a) Sigmoidal curve fit for the cumulative total abundance of *Potamopyrgus antipodarum* at the European-level (all 243 sites). Abundances were averaged over the number of sites per year and accumulate in all years up to and including the year of sampling (black curve), see equation (S1) in Supplementary information 4. The estimated best-fit parameters are  $N_0 = 325$ ,  $r = 0.216$ ,  $K = 43,426$  ( $R^2 = 0.981$ ;  $RMSE = 2200$ ). Abundance data spanned the years 1979 ( $t = 0$ ) to 2020 ( $t = 41$  years) (blue points). The curve extends to time  $t = 60$ , to illustrate the point of near saturation ( $t_{sat}$ ) and the saturation level. The red points represent the point of inflection  $t_{inf} = 22.7$  years,  $N_{inf} = 21,713$  individuals and the point of near saturation  $t_{sat} = 44$  years,  $N_{sat} = 42,992$  individuals. The red-dashed curves enclose a 95% confidence region, with range of predicted model parameters  $N_0$  [98.74, 550.59],  $r$  [0.18, 0.25] and  $K$  [41,079, 45,773]. (b) Marginal abundance depicting boom-bust dynamics. Bell-shaped curve for marginal abundance given by equation (S6) in Supplementary information 4. The point  $x$  corresponds to the initial introduction, which was estimated as 19.8 years before the first monitoring datum. The estimated marginal abundance had value  $n_0 = 69$  at time  $t = 0$  when *P. antipodarum* was first observed and increased rapidly (boom) until reaching a maximum value  $n_{max} = 2340$  at  $t_{inf} = 22.7$  years (yellow points), and then subsequently declined rapidly close to zero in the long term (bust) after 60 years. See Supplementary information 4 for the mathematical expressions used to compute the characteristic time points

to regional scales. We show that the impact curve can describe invasion and impact dynamics and at a European scale across many decades. Using the New Zealand mud snail *Potamopyrgus antipodarum*—considered one of the “worst” invaders of European freshwaters (Nentwig et al., 2018)—as a case study, our model strongly supported cumulative abundance—and thus accumulating impacts—at 59% of sites. The significant increase in *P. antipodarum* abundance demonstrates that its rate of invasion of European freshwaters has increased over time, with more sites likely to be invaded in future due to increasing propagule pressure and associated secondary spread, and due to aspects of the species' ecology that promote its invasiveness (Alonso & Castro-Díez, 2008, 2012). For example, spread can be facilitated by fish internally transporting live *P. antipodarum* in their intestinal tract (Bruce et al., 2009) or individuals adhering to the exterior of birds (Coughlan et al., 2017). Importantly, our dataset only captured introductions if recently invaded sites had already been monitored for a substantial period before introduction, and thus a large share of sites were at later invasion stages (i.e., already established) or declining. Indeed, the species' first observation at a site was estimated to have occurred on average 20 years after its arrival at the European scale. Therefore, our support for the impact curve is conservative, because populations at additional sites could develop sigmoidal growth in the future, or this growth form could have been apparent with earlier sampling data. Parameterizing these invasion and impact dynamics also helps to understand the rate at which invasive species, here *P. antipodarum*, are accruing, as well as environmental variables that drive their abundance

trends and thus their impacts. That no abiotic factors, except temperature and runoff depth, altered the goodness of fit of the *P. antipodarum* impact curve suggests that this model is robust across a range of sites and land uses.

We found support for our first hypothesis that increases in *P. antipodarum* are context-dependent based on environmental drivers. Runoff depth was a significant positive predictor of population growth, potentially reflecting a preference by this species for deeper sections of larger streams, that is, the potamal zone (Alonso & Castro-Díez, 2012; Evans, 2012). Alternatively, population size could relate to a greater availability of suitable habitats in higher-order streams with moderate flow velocities. *P. antipodarum* abundance is low in non-perennial rivers and those with very low annual runoff because river drying might prevent population persistence (Múrria et al., 2008). High within-site variability in slow-to-moderate flow velocities, as well as anthropogenic alteration of in-stream conditions, such as morphology and water quality (Sousa, 1984), can facilitate rapid spread in invaded streams (Jowett & Duncan, 1990). Although upstream dispersal can be slower in faster-flowing waters (Sepulveda & Marczak, 2012), phenotypic plasticity may also promote adaptations that facilitate high rates of spread by individuals in certain environments (Haas et al., 2010; Kistner & Dybdahl, 2013). Furthermore, differences in annual runoff depth could influence invasion success by altering nutrient levels and/or competition (Jowett & Duncan, 1990), likely leading to decreasing abundance trends in some sites.

The slower increase in *P. antipodarum* abundance as latitude increased suggests that more northern European populations may



be at either an earlier invasion stage or may exhibit lower growth rates due to harsher conditions, that is, sub-zero winter temperatures. Starting as early as other time series (Jensen, 2010), our 81 high-latitude (i.e., Danish and Swedish) time series support the idea that low temperatures may prevent this species from reaching high abundances (Moffitt & James, 2012). In addition to mean temperatures, the frequency of extreme climatic events (including heat waves) is higher in southern Europe (Fischer & Schär, 2010). It is probable that *P. antipodarum* will recover more quickly from heat waves than native molluscs due to parthenogenesis that facilitates rapid reproduction (Alonso & Castro-Díez, 2012; Mouthon & Daufresne, 2015). Such disturbances create niche space in which their faster recovery causes priority effects that promote the dominance of *P. antipodarum* over native species (Yu et al., 2020). In more temperate regions, *P. antipodarum* exhibits annual population fluctuations, with population sizes peaking in the late summer and autumn, and a substantial decline in winter (Fischer & Schär, 2010; Moffitt & James, 2012). Winter declines could keep population sizes disproportionately lower at higher latitudes if colder climates intensify such reductions (Moffitt & James, 2012). Equally, contrasting population growth rates could reflect habitat preferences of the species pertaining to runoff depth, organic impact and temperature (Alonso & Castro-Díez, 2012; Evans, 2012), as well as differences in the absolute number of individuals involved in any one introduction event (i.e., initial population abundance). Indeed, populations at higher latitudes potentially have species introduction points and invasion pathways that are less conducive to *P. antipodarum* population establishment (Alonso & Castro-Díez, 2008). These trends towards greater invasion success in southern areas align with the greater marginal abundances observed at lower latitudes, reflecting faster population growth or, alternatively, later initial monitoring efforts (Supplementary results 6).

Although the rate at which the invasion progressed varied according to geographical and environmental context, overall sigmoidal growth patterns were largely comparable across time series, showing that this model is robust across a range of environmental conditions. Thus, although the observed trends could be specific to *P. antipodarum* and other invaders with comparable trait profiles (Statzner et al., 2008), our results support the second hypothesis that the impact curve adequately represents invasion and impact dynamics in the majority of studied contexts. Most *P. antipodarum* populations progressed from accelerating to decelerating phases of sigmoidal growth. A lower carrying capacity and a larger total population size up to the time of sampling shortened the time taken to reach the point of inflection (i.e., at which population growth slows). The point of near saturation (i.e., at which population growth plateaus) was reached significantly faster at higher population growth rates and larger marginal population sizes. Furthermore, our model of  $t_{inf}$  indicated that high %-waterbodies, likely due to greater occupiable area and available resources, can prolong the growth phase until the population growth rate begins to decline. Relatedly, changes in the time taken to reach these stages likely emanate from food or

habitat resource depletion. Total and marginal population sizes at the time of first sampling ( $N_0$  and  $n_0$ ) were also important predictors of carrying capacity as well as the points of introduction and near saturation, although higher abundances likely reflect detection and monitoring at later stages of invasion.

A fundamental assumption of the sigmoidal growth model underpinning the impact curve is that populations establish, grow, and eventually reach their long-term carrying capacity before their growth declines. Even if populations decline in absolute terms, this will manifest in a plateau in cumulative terms as raw abundances fall. However, in some context-specific scenarios (e.g., high predation pressure, low habitat suitability), an invading population may fail to establish stable populations (Kramer et al., 2009; Taylor & Hastings, 2005), instead experiencing more variable dynamics, with the corresponding growth function taking a more complicated form (e.g., due to Allee effects; Courchamp et al., 2008; Taylor & Hastings, 2005). The boom-bust dynamics (Doebeli et al., 2021) commonly detected for *P. antipodarum* (Greenwood et al., 2020; Moore et al., 2012) indicate that resource depletion as populations grow might cause fluctuations in densities and thus impacts within sites. However, an improvement in an invaded ecosystem's water quality and native species' competitiveness may also mediate impacts. Although up to 41% of our time series exhibited non-sigmoidal patterns, these time series could represent only part of an invasion trajectory, whereby early and late-stage data that describe exponential and decelerating parts of a sigmoidal curve, respectively, may have been missed. Indeed, when we relaxed our criterion to include sites with only early-stage observations not yet beyond the inflection point, 76% of all sites supported sigmoidal growth. Because we modelled cumulative abundances, a saturation phase in the late stages of an invasion could reflect a population that has fallen to lower absolute densities than during its rapid growth phase and shows net-positive growth (e.g., owing to local abiotic, biotic, or stochastic factors, possibly during the "post-bust" phase; sensu Strayer et al., 2017). In turn, this could minimize impacts on the invaded site or area. Such longer-term observations have been empirically reported (Moore et al., 2012), whereby a substantial *P. antipodarum* population decline was driven by decreasing water temperature and depth, as well as competitive interactions, after having been the dominant organism for four years. Such dynamics corroborate our impact curve, given that the "bust" phase can cause impacts to stabilize, as raw abundances fall drastically and cumulative impacts saturate. Previous studies have, however, found that metrics used to describe boom-bust dynamics can overestimate the severity of declines in late invasion stages (i.e., in the bust phase), necessitating improved, long-term empirical studies of such trends (Gérard et al., 2018). Here, at large spatial and temporal scales, we clearly indicated a "boom-bust" relationship with respect to impact over time, in which raw abundance peaked unimodally before declining rapidly. However, our large-scale assessment necessitated the pooling of abundances from multiple sites sampled with varying protocols in each year, and our results, therefore, represent a crude estimate of the European trend.

Our results nevertheless advance large-scale understanding of invasion dynamics, enabling prediction of future changes in invader impacts and thus informing the development of effective management actions (Cuthbert et al., 2022). Moreover, because invasion dynamics (quantified as  $R^2$  and  $r$ ) responded to runoff depth, temperature and/or precipitation, management actions may become increasingly urgent as continental temperature increases and regional rainfall declines due to climate change (Greenwood et al., 2020). In this study, the time to the point of inflection defined a critical point that ends the window of opportunity for effective management, that is, below 22.7 years, but immediate action is most effective in reducing long-term impacts (Ahmed et al., 2022). As such, this critical period for management may be conservative as it depends on the reported year of first detection in our monitoring data, which was on average 20 years after the first record in Europe. Delays to management actions likely substantially reduce their efficacy, resulting in greater monetary losses and ecological impacts (Ahmed et al., 2022).

Because detection of an invader may well occur many years after introduction, rapid management action is crucial. Control options are largely limited to non-flowing waters and include local chemical treatment, which entails collateral damage to native species (Oliver et al., 2021). As such, early control efforts (Leung et al., 2002) with species as small and unobtrusive as *P. antipodarum* in waterways typically fail. Ultimately, prevention of new introductions should be prioritized followed by measures slowing the spread of introduced populations, with approaches such as eDNA-based early detection potentially informing management action (Westfall et al., 2020). Our results thus emphasize the value of long-term biomonitoring programs (as implemented in various legislations or Long Term Ecological Research networks) to detect non-native species at early invasion stages (Thomas et al., 2020).

The saturation phase of our European-scale impact curve does not account for the high variability in invasion stages among sites, with some sites monitored at earlier invasion stages than others. Furthermore, it does not account for the likelihood of *P. antipodarum* invading new sites and newly established monitoring efforts (Pilotto et al., 2020). Accordingly, although local populations may stabilize or decline, the European-scale abundance and thus impacts of this invader are likely to continue rising (Liebhold et al., 2017), as indicated by our meta-regression. Whereas introductions typically occurred earlier in northern Europe (Supplementary information 6; Seebens et al., 2020), river site-specific invasions at northern latitudes in our data were often younger than those further south. This suggests that the observed population growth is still in an earlier phase at northern latitudes due to the species' general ecological preferences (Alonso & Castro-Díez, 2012). Air temperature, however, was not an important predictor of population growth rate in our analyses, corroborating the wide temperature tolerance of this species (Alonso & Castro-Díez, 2008) and its ability to burrow into substrate to mitigate adverse temperatures. However, our capacity to detect patterns in northern areas may have been limited by the dominance of one temperate climate class in the data (Winterbourn, 1969). Inter-population variability in temperature tolerance as well as

within-region variability in water temperatures may have also caused population growth rates to differ among sites (Dybdahl & Kane, 2005), making local temperature effects crucial while reducing the clarity of large-scale temperature effects (Vareille-Morel, 1985).

Overall, of the variables analyzed, only latitude and runoff depth were significant drivers of *P. antipodarum* abundance trends, possibly because *P. antipodarum* is eurytopic based on the variables studied. This corroborates its high capacity to invade freshwater environments with various characteristics and proliferate. While these two parameters rather represent the general ecological preferences of *P. antipodarum*, other drivers such as water chemistry were not analysed due to a lack of suitable large-scale and high-resolution data. Having determined the validity of the impact curve for *P. antipodarum*, we call for future large-scale analyses to examine whether a sigmoidal population growth model also represents other invaders and regions. Characterization of early-stage impact trajectories mediated by population characteristics could inform strategies to manage these impacts for other taxa and systems. Our findings provide an approach to test invasion dynamics of potential invaders and parameterize variables that influence the feasibility and effectiveness of management responses.

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#### CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in ["PANGAEA"] at <https://doi.pangaea.de/10.1594/PANGAEA.934976>.

#### ORCID

Phillip J. Haubrock  <https://orcid.org/0000-0003-2154-4341>  
 Danish A. Ahmed  <https://orcid.org/0000-0002-2490-1546>  
 Ross N. Cuthbert  <https://orcid.org/0000-0003-2770-254X>  
 Rachel Stubbington  <https://orcid.org/0000-0001-8475-5109>

Sami Domisch  <https://orcid.org/0000-0002-8127-9335>  
 Giuseppe Amatulli  <https://orcid.org/0000-0002-8341-2830>  
 Jens Kiesel  <https://orcid.org/0000-0002-4371-6434>  
 Longzhu Q. Shen  <https://orcid.org/0000-0001-5629-3007>  
 Ismael Soto  <https://orcid.org/0000-0002-7288-6336>  
 David G. Angeler  <https://orcid.org/0000-0003-2197-7470>  
 N ria Bonada  <https://orcid.org/0000-0002-2983-3335>  
 Zolt n Csabai  <https://orcid.org/0000-0003-1700-2574>  
 Elvira de Eyto  <https://orcid.org/0000-0003-2281-2491>  
 Emma Drohan  <https://orcid.org/0000-0002-3391-3100>  
 Judy England  <https://orcid.org/0000-0001-5247-4812>  
 Maria J. Feio  <https://orcid.org/0000-0003-0362-6802>  
 Marie A. E. Forio  <https://orcid.org/0000-0001-6675-4751>  
 Peter Goethals  <https://orcid.org/0000-0003-1168-6776>  
 Wolfram Graf  <https://orcid.org/0000-0001-6559-0644>  
 Jani Heino  <https://orcid.org/0000-0003-1235-6613>  
 Sonja C. J hnig  <https://orcid.org/0000-0002-6349-9561>  
 Richard K. Johnson  <https://orcid.org/0000-0001-7979-6563>  
 Patrick Leitner  <https://orcid.org/0000-0001-8122-4265>  
 Anthony Maire  <https://orcid.org/0000-0003-0920-773X>  
 Jes J. Rasmussen  <https://orcid.org/0000-0002-5932-3125>  
 Ralf B. Sch fer  <https://orcid.org/0000-0003-3510-1701>  
 Astrid Schmidt-Kloiber  <https://orcid.org/0000-0001-8839-5913>  
 G bor V rb r   <https://orcid.org/0000-0001-5907-3472>  
 Peter Haase  <https://orcid.org/0000-0002-9340-0438>

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