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Long-term trends in crayfish invasions across European rivers

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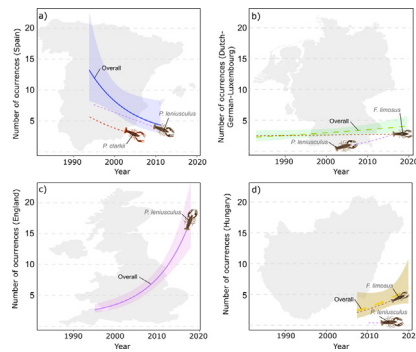
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HIGHLIGHTS

- Non-indigenous crayfish populations seem saturated in Europe, not showing a clear temporal trend.
- We identified climatic, site-, and species-specific predictors of abundance shifts.
- The range-expansion of non-indigenous crayfish was increasing in England and declining in Basque Country, northern Spain.
- The average invasion velocity of crayfish invaders ranged from 30 to 90 km/year across countries, while gradually decreasing over time.

GRAPHICAL ABSTRACT



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ABSTRACT

Europe has experienced a substantial increase in non-indigenous crayfish species (NICS) since the mid-20th century due to their extensive use in fisheries, aquaculture and, more recently, pet trade. Despite relatively long invasion histories of some NICS and negative impacts on biodiversity and ecosystem functioning, large spatio-temporal analyses of their occurrences are lacking. Here, we used a large freshwater macroinvertebrate database to evaluate what information on NICS can be obtained from widely applied biomonitoring approaches and how usable such data is for descriptions of trends in identified NICS species. We found 160 time-series containing NICS between 1983 and 2019, to infer temporal patterns and environmental drivers of species and region-specific trends. Using a combination of meta-regression and generalized linear models, we found no significant temporal trend for the abundance of any species (*Procambarus clarkii*, *Pacifastacus leniusculus* or *Faxonius limosus*) at the European scale, but identified species-specific predictors of abundances. While analysis of the spatial range expansion of NICS was positive (i.e. increasing spread) in England and negative (significant retreat) in northern Spain, no trend was detected in Hungary and the Dutch-German-Luxembourg region. The average invasion velocity varied among countries, ranging from 30 km/year in England to 90 km/year in Hungary. The average invasion velocity gradually decreased over time in the long term, with declines being fastest in the Dutch-German-Luxembourg region, and much slower in England. Considering that NICS pose a substantial threat to aquatic biodiversity across Europe, our study highlights the utility and importance of collecting high resolution (i.e. annual) biomonitoring data using a sampling protocol that is able to estimate crayfish abundance, enabling a more profound understanding of NICS impacts on biodiversity.

1. Introduction

Non-indigenous species can cause severe ecological and socioeconomic impacts (IUCN World Commission on Protected Areas et al., 2000; IPBES, 2019), inducing changes to ecological communities and their functioning (Vilà et al., 2010). There is compelling evidence that non-indigenous species are contributing to declines in native species and biodiversity in ecosystems worldwide (Ricciardi et al., 2013; Bellard et al., 2016; Renault et al., 2022), inducing environmental regime shifts (Brooks et al., 2004), and increasing risks to human well-being (Ogden et al., 2019).

In particular, non-indigenous crustaceans are among the most successful and harmful invaders globally (Holdich and Pöckl, 2007; Hänfling et al., 2011; Wacker and Harzsch, 2021). Currently, twelve crustaceans are listed among the “100 worst invasive species” in Europe (see Nentwig et al., 2018; Supplementary Table 1). Of them, six North American crayfish species – red swamp crayfish *Procambarus clarkii*, signal crayfish *Pacifastacus leniusculus*, and spiny-cheek crayfish *Faxonius limosus*, are known as “Old Non-Indigenous Crayfish Species” (Old NICS; Holdich et al., 2009). These are included in the List of Invasive Alien Species of Union concern linked to the EU Regulation 1143/2014 together with the marbled crayfish *Procambarus virginalis* and virile crayfish *F. virilis*, both belonging to the so-called “New NICS”. Recently, the rusty crayfish *F. rusticus* has also been added to the list (2022) and other crayfish species are under evaluation (EU, 2016; Tsiamis et al., 2021).

Following and driving the collapse of European crayfish species populations, Old NICS were extensively introduced to renew local fisheries, aquaculture and benefit the general public (e.g. providing aesthetic or new food source) (Lodge et al., 2012). Nowadays, these species are widely distributed on the continent (see e.g. Holdich et al., 2009; Kouba et al., 2014; Oficialdegui et al., 2019). In addition, numerous New NICS, still with restricted ranges, have appeared in European waters. Their introductions are often associated with releases of pet trade animals (e.g. *Cherax quadricarinatus*, Weiperth et al., 2020; Haubrock et al., 2021; Bláha et al., 2022). Non-indigenous crayfish species have substantial and often important consequences on local biodiversity (Lodge et al., 2000; Gherardi, 2007; Gherardi et al., 2011; Twardochleb et al., 2013; Madzivanzira et al., 2022), triggering bottom-up and top-down effects that alter ecosystem functioning by competing with species at multiple trophic levels, thus modifying the natural stability of ecosystems and interaction with native species (Angeler et al., 2001; Findlay et al., 2015; Ficetola et al., 2012; Nilsson et al., 2012; Hansen et al., 2013). North American crayfish are particularly problematic due to their propensity to locally exhibit a dominant influence in communities in their invaded ranges. This impact has been attributed to their life-history traits (early maturation, high fecundity),

wide environmental tolerance, a lack of natural predators (Larson and Olden, 2013; Pearl et al., 2013; Carvalho et al., 2022) and, among other reasons, competing native crayfish (Pilotto et al., 2008; Holdich et al., 2009), among other reasons. Thus, they have noticeable direct and indirect effects on local communities (e.g., predation and competition) and the environment (extensive burrowing abilities, altered sediment dynamics; Faller et al., 2016; Lipták et al., 2019; Sanders et al., 2021; Veselý et al., 2021). Furthermore, some NICS are vectors of the crayfish plague pathogen *Aphanomyces astaci* (Oomycetes) which is fatal to crayfish species not native to North America (Martín-Torrijos et al., 2021; Martínez-Ríos et al., 2022), and exerts significant monetary costs (Kouba et al., 2022).

Non-indigenous crayfish species present in Europe are known to differ in their biology and ecology, including ability to spread, environmental requirements, as well as invasion histories (among others; Kozák et al., 2015; Vodovsky et al., 2017; Kouba et al., 2021). However, despite localized long-term studies on NICS (Gherardi, 2007; Mathers et al., 2020), information on large-scale and long-term trends of NICS, as well as knowledge about environmental drivers or facilitating factors, is scarce (Olden et al., 2006; Almeida et al., 2014, but see Moreira et al., 2015; Souty-Grosset et al., 2016; Galib et al., 2021). Yet, while some NICS like *F. limosus* and *P. leniusculus* will likely experience range contractions from climatic changes (e.g. temperature increases; Capinha et al., 2013), several NICS such as *P. clarkii* may benefit and expand their range in certain areas (Zhang et al., 2020; Madzivanzira et al., 2021; Ruokonen and Karjalainen, 2022). An increased understanding of the biology and ecology of different crayfish species and how they respond to spatial gradients (i.e. climatic conditions) or site-specific characteristics (availability of shelter, water current velocities, etc.) will help to explain: (i) long-term trends in crayfish invasions, (ii) species or region-specific differences, and/or (iii) environmental variables that can facilitate their success and future progression, including spread. To this end, we used a large European database of time series on macroinvertebrates collected from riverine freshwater ecosystems (Haase et al., under review; Haubrock et al., 2022), and extracted abundance data of NICS in Europe. We specifically asked: (1) if large-scale biomonitoring data can effectively describe the dynamics of crayfish based on presence and abundance data; and (2) if significant spatio-temporal trends in NICS populations can be inferred from these data. We expected a high variability of trends according to the species and regions studied and consequently aimed to explain these using site-specific characteristics. Lastly, we asked if (3) the data can be used to describe the dynamics of NICS populations (i.e. the number of occurrences and the respective average invasion velocity) across invaded regions.

2. Methods

2.1. Data collection

To investigate the presence of non-indigenous crayfish species (NICS) in long-term biodiversity monitoring data and whether it can be used to analyse occurrence and abundance trends in Europe, we used a recently collated database containing 1816 macroinvertebrate community time series from 22 European countries (Haase et al., under review). Time series of macroinvertebrate species abundances were sampled with a constant effort for a minimum of eight years (not necessarily continuous). Macroinvertebrate community sampling protocols varied between time series (i.e. locations) but were consistent over time in each time series (Supplementary Table 2). From the full database, we preselected time series following the following filtering criteria: (1) repeated occurrences of at least $n \geq 3$ records within a time series; (2) at least 50 % of occurrences being continuous observations over multiple years; (3) contained the abundance of NICS. In total, we extracted 160 time series from nine countries (Fig. 1, Supplementary Table 3; Supplementary Table 4) for a total of 449 annual occurrences. These included only Old NICS (i.e. *F. limosus*, *P. leniusculus*, and *P. clarkii*), as no New NICS were identified in our data. Time series spanned a mean \pm SD of 20.1 ± 8.2 years and contained 16 ± 6.5 sampling years and on average 12.82 ± 8.4 crayfish occurrences between 1983 and 2019. From the 449 identified crayfish occurrences, 226 (50.3 %) were single occurrences, whereas 223 (49.6 %) belonged to consecutive observations over multiple years (Supplementary Fig. 1), with on average $2.2 (\pm 1.7$ SD) years without identified NICS in between. We further identify the existence of lag-times in the reporting of NICS in our data by comparing the first record of each species within each country presented in our time series with the first record for each species in each country using the Theory and Workflows for Alien and Invasive Species Tracking (sTWIST, Seebens et al., 2021) and CABI (www.cabi.org/isc; CABI, 2022).

2.2. Meta-regression modelling of European trend

We used a meta-regression approach to identify a potential overall 'European trend' in raw abundances of observed NICS and each species individually. Meta-regression allows for the synthesis of information in independent time series (Koricheva et al., 2013) and is considered more effective than comparable analyses of variance and meta-analytical approaches (Vietchbauer, 2010; Gallardo et al., 2016). We used the meta-regression approach implemented in the *rma.mv* function of the *metafor* R package (Vietchbauer, 2010), using the Mann-Kendall trend test (*S*-statistics) and its respective variance as an effect size for the models (Hamed and Rao, 1998; Maire et al., 2019; Pilotto et al., 2020). The effect sizes were extracted for each time series and combined in meta-regression models to obtain the overall effect size (i.e. trend) and confidence interval (CI). The effect size from each time series was weighted by the inverse of its variance, which is roughly proportional to sample size (Borenstein et al., 2021). We also calculated the heterogeneity (i.e. the proportion of total variance attributable to differences between time series) of each meta-regression model (I^2). We ran a meta-regression model based on the raw abundances of each individual crayfish invader within the time series in which it was detected in ≥ 3 years. In addition, two time series including *F. limosus* and three including *P. leniusculus* were removed due to insufficient variance in the abundance within the respective time series (Borenstein et al., 2021).

2.3. Analyzing trends in crayfish populations across space and time

To investigate which predictors may explain the relative abundance of NICS on time series available and of each species respectively – and thus if the population size of these species in the invaded communities changed over time – we used generalized linear models (GLMs) using the *glm.nb* function of the *MASS* R package (Ripley et al., 2013). For this, we calculated the relative abundance of each species in each community as the

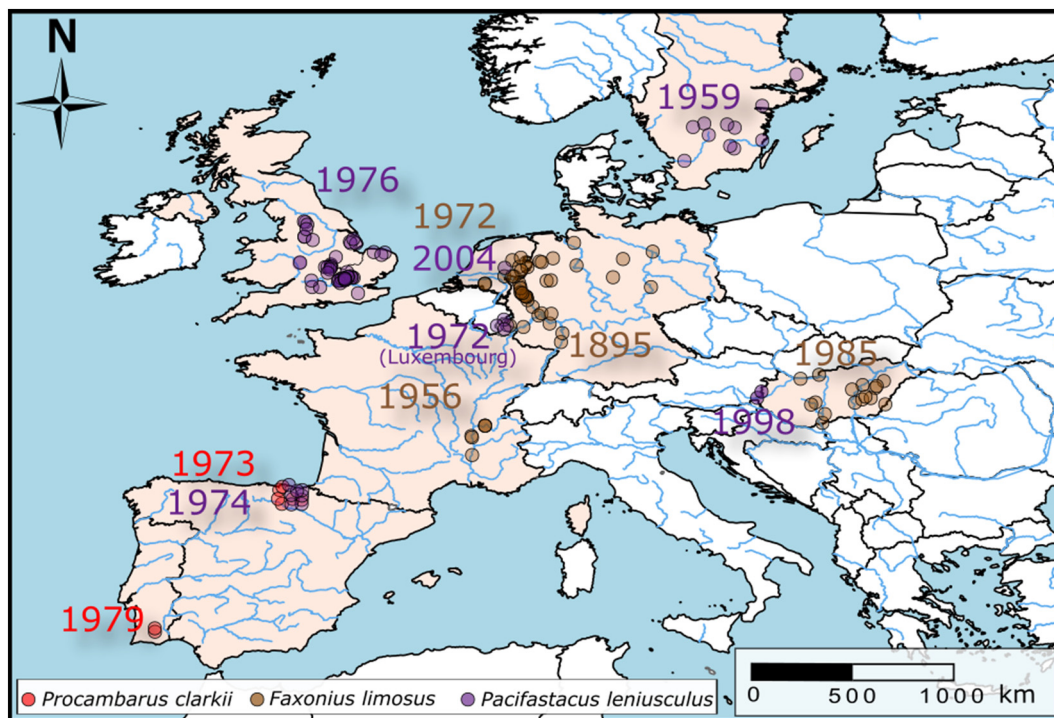


Fig. 1. Location of European time series with recorded NICS in our database. Numbers indicate the first record in each country according to the sTWIST database (Seebens et al., 2021), Machino (2000) for *P. leniusculus* in Luxembourg, and Moreira et al. (2015) for *P. clarkii* in Portugal. The countries which contain time series are highlighted in pink.

percentage of the abundance of all sampled individuals. Given that the sampling method and thus the effort may have differed between time series (but was consistent within each time series), using the relative abundances of Old NICS within each community enables the analysis of trends over time, including only those time series in which Old NICS were recorded in ≥ 3 years. We inspected the respective residual distribution of all models visually using histograms and selected a negative binomial distribution with a log-link that proved to be the most suitable distribution. Hence, each model consisted of the invader's relative abundance as the response variable and the eight variables (two climatic, five spatial, and one temporal-year) as predictor variables (see below and Supplementary Table 5). We further note that the effect of the number of time series in each year was close to zero and thus, omitted from the final model.

2.4. Extraction of predictors

We investigated the influence of two climatic variables (temperature and precipitation) and five site-specific characteristics (instream barriers, elevation, stream slope, Strahler stream order and distance to outlet) on the relative abundance of NICS (Supplementary Table 4). We extracted mean daily temperature and total daily precipitation (as a proxy for runoff and availability of water) data from a gridded European-scale observation-based dataset for each year and site (spatial resolution: 0.1° ; Cornes et al., 2018) to estimate the average temperature and precipitation of the 12 month period prior to each site's sampling event. For each site, distance to the nearest upstream barrier was extracted from the Global Reservoir and Dam Database v1.3, and elevation was determined using the MERIT Hydro digital elevation model (Yamazaki et al., 2019) using the Hydrography90m dataset that delineates stream channels at 90 m spatial resolution including a high density of headwater streams (Amatulli et al., 2022). Three site-specific variables were computed using GRASS GIS functions (Jasiewicz and Metz, 2011; GRASS Development Team, 2017): stream slope and Strahler order, using the `r.stream.slope` function (Jasiewicz and Metz, 2011); and the downstream distance to the outlet was calculated with the `r.stream.distance` function (Jasiewicz and Metz, 2011).

2.5. Analyzing regional invasion dynamics

Invasion dynamics can differ substantially between species and geographic regions (Haubrock et al., 2022; Soto et al., 2023). In order to assess temporal change in the number of NICS populations, we analyzed changes in the number of occurrences (i.e. the number of invaded sites) over time. We analyzed observations in northern Spain (in particular, the Basque Country), the Dutch-German-Luxembourg region, England, and Hungary independently, as our data clustered in these locations (see Fig. 1). For this, we included the first year of observation of an NICS within each time series, including those with <3 sampled years. Each model consisted of the number of NICS observations as response and the respective year as predictor.

To estimate the average invasion velocity (km/year) of NICS in each respective region (Spain, Dutch-German-Luxembourg, England, Hungary), we used all records of NICS within our data and computed the great-circle distances between the first invaded site and successively invaded sites in subsequent years using site GPS coordinates. The invasion velocity does not distinguish between species dispersal and anthropogenic translocation and the estimated range expansion of NICS can be the result of either or both processes. The average invasion velocity (km/year) was estimated by computing the average displacement (i.e., total displacement in a given year divided by the total no. of occurrences in that year) over time. A Pareto distribution was fitted against estimated average invasion velocity for each country/region, given by:

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

where v_0 is the initial velocity at $t = 0$ (corresponding to the following year after the year of the first record, because two time points are required to

estimate increments velocity), σ is a curve scaling parameter, and α is a curve shape parameter. Distribution parameters were determined from curve fitting using the non-linear regression tool `lsqcurvefit` in Matlab, where α determines the rate of decay in the end tail, i.e., larger α corresponds to a faster decrease in average invasion velocity over time.

3. Results

Within the 160 time series in which non-indigenous crayfish species (NICS) were recorded between 1983 and 2019, we identified three NICS: *Pacifastacus leniusculus* ($n = 85$), *Faxonius limosus* ($n = 66$) and *Procambarus clarkii* ($n = 18$). Nine time series included more than one NICS. *Faxonius limosus* was detected in the first year (1983) of a time series from Germany, then *P. clarkii* and *P. leniusculus* were first detected in northern Spain, in 1994 and 1995, respectively. There was a considerable incongruence between the first observations of NICS in our data and their respective first record in the invaded countries, ranging from 2 years in the case of *P. leniusculus* in the Netherlands to 88 years in the case of *F. limosus* in France and Germany (Supplementary Table 6). The sampling methods varied between time series. Of them, the vast majority of the occurrences were sampled using Kicknet and UK RIVPACS protocol ($N = 131$ in both cases). In addition, considering all time series from countries for which NICS populations were confirmed ($n = 160$), we found that those time series that contained abundances of NICS were collected using the same sampling procedures as those not having recorded any NICS, except for the Ekman grabs ($n = 2$), Germany MHS ($n = 5$), and Indice Biologique Global Normalisé (IBGN; $n = 299$) sampling schemes, according to which no NICS was identified (Supplementary Fig. 2). Most time series with NICS were from England ($n = 48$), Germany ($n = 32$), northern Spain ($n = 27$) and Hungary ($n = 19$), and fewer were from the Netherlands ($n = 11$), Sweden ($n = 11$), France ($n = 6$), Luxembourg ($n = 4$), and Portugal ($n = 2$; Supplementary Table 2).

3.1. Meta-regression modelling of European trends

The raw abundance (i.e., the recorded abundance during a sampling event) of each crayfish species ranged between 1 and 78 individuals of *P. clarkii* (mean \pm SD: 9.7 ± 14.2), 1–22 individuals of *F. limosus* (2.7 ± 3.7), and 1–30 individuals *P. leniusculus* (3.6 ± 4.7) per sample. Fifty-two time series (*P. clarkii*: $n = 8$; *F. limosus*: $n = 11$; *P. leniusculus*: $n = 33$) were of sufficient length ($n \geq 3$ sampled years with crayfish) for trend analysis (Supplementary Table 7). The meta-regression model identified no overall trend in raw abundance for any species (all, $p > 0.14$); comprising 25 positive and 26 negative overall relationships, of which 4 were positive and 4 negative for *P. clarkii*, 14 were positive and 16 negative for *P. leniusculus*, and 5 were positive and 6 negative for *F. limosus* (Fig. 2; Supplementary Table 8). The I^2 of each model varied between <0.01 and 34.49 % (Fig. 2).

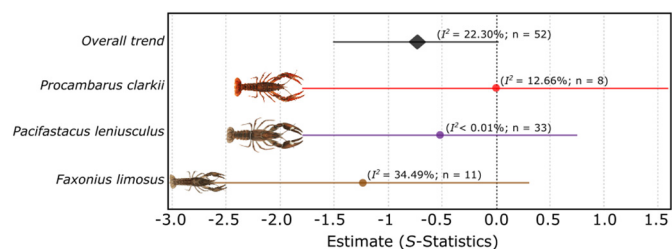


Fig. 2. Slopes (dots; mean trend estimate S -statistics and bars; CI) from the meta-regression model applied to the raw abundances for each species. The differences among time series (I^2) and number of time series included per species (n). The black diamond represents the overall trend in non-indigenous crayfish species abundance.

3.2. Trends in crayfish across space and time

Relative abundance was comparable for all NICS species, with *F. limosus*, *P. leniusculus* and *P. clarkii* contributing $0.6 \pm 1.9\%$, $0.6 \pm 1.6\%$ and $0.5 \pm 0.9\%$, of the sampled communities, respectively. Considering all 160 time series, we identified no temporal European-trend in the overall relative abundance of crayfish within the invaded macroinvertebrate communities (estimate \pm SD; 0.01 ± 0.01 ; $p > 0.45$; Fig. 3a). Precipitation, elevation, and distance to the nearest upstream barrier were negatively associated, and distance to the river's outlet was positively associated with the relative abundance of NICS when explaining differences across sites ($p < 0.01$; Supplementary Table 9). The relative abundance of each individual crayfish species remained stable over time (GLM; $p \geq 0.15$; Fig. 3b-d). For *P. clarkii*, elevation had a significant positive effect and distance to the next upstream barrier had a significant negative effect on relative abundance ($p \leq 0.05$). The relative abundance of *F. limosus* decreased with increasing temperature ($p < 0.01$; Supplementary Fig. 3). The relative abundance of *P. leniusculus* was negatively affected by both the distance to the nearest upstream barrier ($p < 0.01$) by the site's slope ($p = 0.05$), and responded positively to both Strahler order ($p < 0.01$) and distance to outlet ($p = 0.01$; see Supplementary Table 9).

3.3. Analyzing regional invasion dynamics

We identified 83 occurrences (*P. clarkii*, $n = 34$; *P. leniusculus*, $n = 49$) within the 27 northern Spain time series between 1994 and 2011. There were 103 occurrences within the 47 Dutch-German-Luxembourg time series (*P. leniusculus*, $n = 15$, *F. limosus*, $n = 88$) between 1983 and 2019,

but the largest number of occurrences were in England with 155 occurrences in 48 time series between 1996 and 2019; all *P. leniusculus*. Hungary recorded the lowest number of occurrences ($n = 30$) from 19 time series between 2008 and 2017. In northern Spain, the number of sites newly invaded by crayfish (namely *P. clarkii* and *P. leniusculus*) declined over time ($p = 0.02$), whereas in England, site numbers increased, reflecting invasion by *P. leniusculus* ($p < 0.01$; Fig. 4). Trends in Hungary and the Dutch-German-Luxembourg region were positive, albeit non-significant ($p > 0.07$; Fig. 4; Supplementary Table 10).

Crayfish average invasion velocities were well described by a Pareto distribution, with $R^2 > 0.9$ in all cases. Estimated initial velocities varied across countries, being fastest (89.9 km/year) in Hungary and slowest in England (30.2 km/year). In all cases, average invasion velocity declined gradually over time; however, the rate of long-term decline differed across countries, being fastest in Dutch-German-Luxembourg region ($\alpha = 0.94$) and slowest in England ($\alpha = 0.34$) (Fig. 5).

4. Discussion

The expansion of non-indigenous crayfish species (NICS) in Europe is a major concern due to their impacts on invaded ecosystems, which can occur across all trophic levels (Peay, 2009; Holdich et al., 2017; Patoka et al., 2018). Although the available time series covered only a minor subset of the currently known distribution of NICS in Europe (Supplementary Fig. 4), we identified a notable presence for three Old NICS in nine countries, namely from *Pacifastacus leniusculus*, *Procambarus clarkii*, and *Faxonius limosus*. However, we did not identify an overall trend in raw and relative abundances of these NICS across data available. On the other hand, we

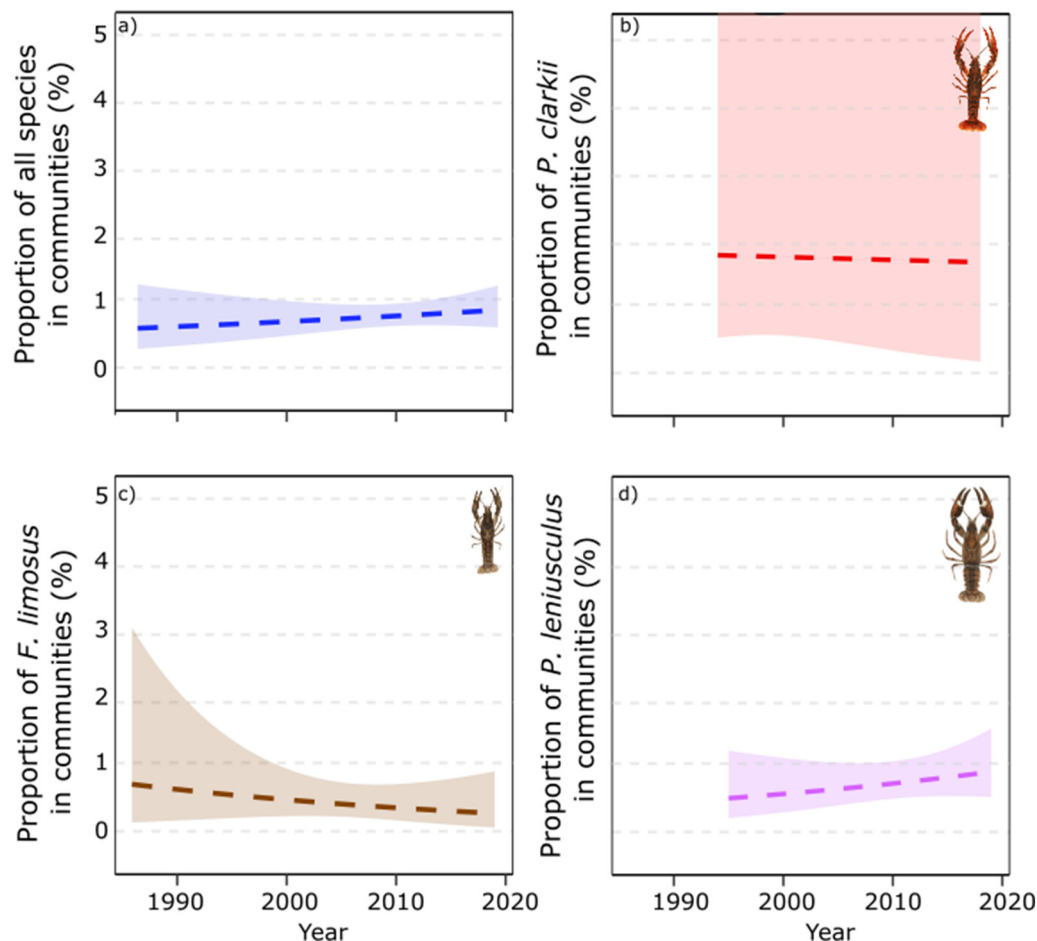


Fig. 3. Trends in the relative abundance of a) all species, b) *Procambarus clarkii*, c) *Faxonius limosus* and d) *Pacifastacus leniusculus* over time as estimated by the applied Generalized Linear Model. Dashed lines represent non-significance ($p > 0.05$).

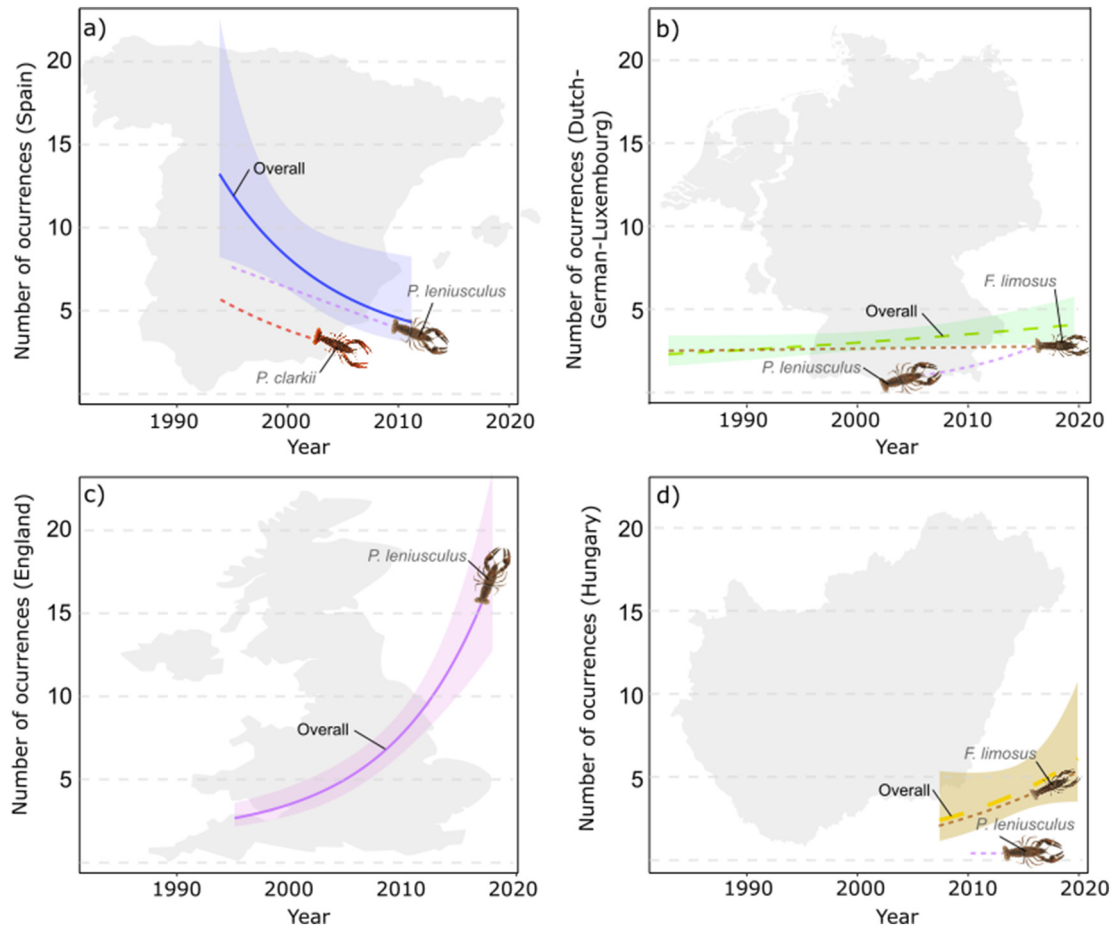


Fig. 4. Trends estimated by Generalized Linear Models in the number of occurrences of NICS in a) northern Spain, b) the Dutch-German-Luxembourg region c) England, and d) Hungary. Solid overall trend lines represent significant ($p < 0.05$) and dashed trend lines represent non-significant ($p > 0.05$) trends, respectively. When multiple species are present within a country or region, species-specific trends without confidence intervals are displayed as dotted lines. The background depicts the shape of each country studied. Silhouettes represent species-specific trends.

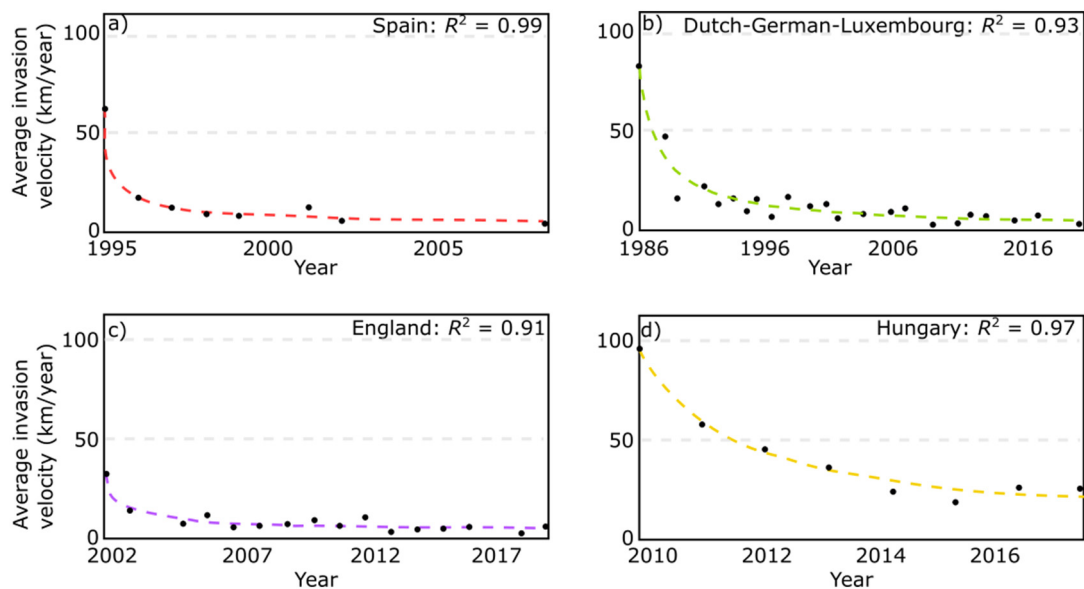


Fig. 5. Pareto distribution curve fittings against estimated average invasion velocity in (km/year) of NICS in a) northern Spain: $\sigma = 0.06$, $\alpha = 0.42$, b) the Dutch-German-Luxembourg region: $\sigma = 1.43$, $\alpha = 0.94$, c) England: $\sigma = 0.09$, $\alpha = 0.34$, and d) Hungary: $\sigma = 1.09$, $\alpha = 0.76$.

established region-specific invasion dynamics patterns, as trends in the number occurrence of NICS observations and regional average invasion velocity varied across regions. Ultimately, we found site and region-specific characteristics to affect NICS differently.

4.1. Obtaining data from biomonitoring data

A lack of sufficiently long biomonitoring data has often limited the investigation of spatio-temporal trends in invasive species, including crayfish (Brockerhoff and McLay, 2011; Almeida et al., 2014; Sor, 2017). In this study, we found time series recording NICS were mainly restricted to four European regions, including a small cluster in the Basque Country (northern Spain). Unfortunately, some regions with well-established NICS populations, e.g., Scandinavian countries, France, southern Spain, and Italy, were poorly covered in our data set (but see Sandström et al., 2014; Henttonen and Huner, 2017; Oficialdegui et al., 2020). At the same time, we found that most biomonitoring approaches (foremost RIVPACS, kicknet, and DIN 8410; see Supplementary Table 2 for explanation of the methods) applied between 1983 and 2019 contained occurrences and abundances of NICS, raising concerns why NICS were detected at some sites, but not others despite the same sampling methodology. This is in line with previous research which questioned the capability of these approaches in detecting and reporting NICS (Gallagher et al., 2006; see Supplementary Note 1).

We further found the occurrence of NICS in our time series to diverge from the respective invader's first national report, which likely originated from geographic distances between the site of first introduction in especially large countries (e.g. Spain, where the first national record was in the south-west whereas our time series is in the north; see Supplementary Material in Oficialdegui et al., 2020). Half of NICS observations were non-continuous occurrences (50.33 %), where most data gaps were due to non-reporting or non-detections (83.20 %) and only 16.80 % due to non-continuous sampling. This suggests that, in light of the resilience of invasive crayfish populations to external stressors (e.g. pollution) (Gherardi et al., 2011; Nunes et al., 2017), gaps may present false negatives (e.g., due to small population sizes not being easy to detect or site characteristics affecting the success of sampling efforts) whose filling may possibly modify identified trends (e.g. in Germany, due to scarce continuous occurrences; see Supplementary Fig. 1). We find the identified presence of NICS to likely be highly underestimated. The possibility that NICS were not identified (Maitland and Adams, 2001) indicates that Old NICS may occur in many more regions. This further suggests that NICS could cause staggering biodiversity losses that may incorrectly not be attributed to NICS. It should therefore be noted that a combination of traditional sampling using baited traps over a predetermined period and commonly utilized sampling techniques for long term biomonitoring would provide a more robust estimate of NICS abundances (Gladman et al., 2010; Larson and Olden, 2016). Considering that sampling protocols were consistent within each time series, this allowed us to effectively compare site-specific trends, although it prohibited us to directly compare raw abundances between time series.

4.2. Temporal trends in non-indigenous crayfish species

Regarding our first hypothesis, we found that data on both crayfish presence and abundance obtained from large-scale biomonitoring efforts can describe the dynamics of crayfish. In northern Spain for instance, despite having identified indications of a retreating presence of NICS – possibly indicative of a population's 'bust'-phase (see Strayer et al., 2017) – the relative abundance of NICS contributed ≤ 2.5 % of the overall community abundance, despite their capacity to reach high densities (Gherardi and Holdich, 1999; Usio et al., 2009). In contrast, the relative weight per capita of crayfish may be high compared to other macroinvertebrates (≤ 80 % of overall community biomass; Momot, 1995; Nyström et al., 2001; Neveu, 2009). The relative stability in all species raw and relative abundance therefore suggests that both distribution and presence

of NICS remained constant, underlining their wide tolerance towards diverse environmental conditions (Holdich et al., 2009; Kouba et al., 2010).

Highlighting the importance of large-scale, long-term datasets when investigating biological invasions (Seebens et al., 2017; Pyšek et al., 2020), the absence of overall and species-specific identifiable trends could also reflect the limitation of our data set, where the most recent time series begin in 2012 and all of them end in 2019 representing an artefact of the data set. In addition, NICS were not the main aim of the macro-invertebrates monitoring and thus some sampling methods could be biased against this taxonomic group (Gallagher et al., 2006). Both climatic predictors, precipitation and temperature, were associated with the relative abundance of NICS. Both precipitation and temperature tolerances affect habitat suitability for crayfish, and may thus alter their distribution and success as an invader. Crayfish are sensitive to increasing temperatures (Lowe et al., 2010; Westhoff and Rosenberger, 2016) and climate change is thus expected to result in range shifts and contractions (Capinha et al., 2012, 2013; Gallardo and Aldridge, 2013; Zhang et al., 2020). Positive and negative deviations from average precipitation can affect, for example, reproductive rates and total abundances, as well as quality of shelters or burrows (McClain, 2013; Kouba et al., 2016). Spatially, we found that the relative abundance of *P. leniusculus* and *P. clarkii* and the overall crayfish abundance increased with proximity to an upstream barrier. The distance to an upstream barrier suggests that these human alterations have substantial ecological impacts on riverine ecosystems, e.g. by decreasing native species' abundance (Gherardi, 2007) or increasing the number of crayfish introductions due to greater human access and recreational activities that often lead to the introduction of NICS (Banha and Anastácio, 2015; Beran and Petrussek, 2006; DiStefano et al., 2009), thereby functioning as "stepping stones" for range extensions (Muirhead and MacIsaac, 2005; Johnson et al., 2008; Barnett and Adams, 2021). Indeed, while dams aim to prevent further invasions by limiting the upstream movement, they increase the abundance of NICS in areas closer to these barriers (Krieg and Zenker, 2020). Yet, barriers such as dams are inefficient in limiting the upstream spread of some NICS because the species can migrate over land as reported for the three study crayfish species (Robinson et al., 2019; Krieg and Zenker, 2020; Santos et al., 2021). This confirms other studies showing the effects of impoundments to positively affect crayfish assemblages (e.g. flow regime alteration in regulated sites by dams facilitate the establishment and spread of *P. leniusculus*; Light, 2003; Barnett et al., 2022).

The relative abundance of *P. clarkii* populations in south-western Europe increased with elevation in our study – which contradicts other studies that found opposite patterns (e.g. in Catalonia; Maceda-Veiga et al., 2013). This result was probably associated by 16 out of 18 time series being in the Basque Country (northern Spain), as lower elevated sites are generally more exposed to human activities and increase of pollution and suggesting that crayfish are using higher elevation habitats as refuges from agriculture and climate change (Bland, 2017). This result contrasts with the negative effect found in the overall trend for all species led by *P. leniusculus* and *F. limosus* higher relative abundances in lower elevations although wider environmental tolerances of invasive species may occur at different elevations (Pearl et al., 2013). Despite this, distance to outlet positively predicted abundance trends in overall crayfish. This is particularly true for the abundance trend of *P. leniusculus*, which was not present in areas close to outlets and brackish water (Anastácio et al., 2015; Moreira et al., 2015; Filipe et al., 2017). The capacity of large rivers to support high crayfish population densities may differ between species and local specific conditions. *P. leniusculus* was the species with our predictors (i.e. Strahler order, slope of stream, distance to the next barrier and distance to the outlet) displaying highest explanatory power. We observed an increase in the abundance of *P. leniusculus* as to increasing stream order and distance to the outlet, while we found a decline due to increasing slope and distance to the next barrier. High discharge events can facilitate downstream dispersal of crayfish. However, *P. clarkii* might be more resistant to discharge-driven downstream dispersal, exhibiting more upstream-directed movements than other NICS such as *P. leniusculus* (Bernardo et al., 2011; Dragičević et al., 2020).

4.3. Geographic trends of non-indigenous crayfish species

Trends in the number of sites invaded by crayfish populations differed among countries, increasing in England (100 % *P. leniusculus*) and much of it decreasing in northern Spain (59 % *P. clarkii*; 41 % *P. leniusculus*), which is in line with our second hypothesis that spatio-temporal trends in NICS populations can be inferred from long term biomonitoring data. A declining trend in northern Spain is surprising, indicating that fewer sites are invaded over time, indicating that the analysis of large-scale data may mask regional or species-specific trends. These findings may be attributed to data limitations as the number of available time series was limited, but also restoration efforts in the past, natural fluctuations of crayfish populations (Charlebois and Lamberti, 1996; Ngulo and Grubbs, 2010), adaptation of native predators such as birds or fishes (Haubrock et al., 2018), as well as a natural retraction in NICS in the studied region (Hein et al., 2007; Gherardi et al., 2011; Larson et al., 2019). However, also due to the growing concern of regional governments to protect local aquatic biodiversity, several NICS control and eradication programs have been carried out in the nearby areas (Alcorlo and Diéguez-Urbeondo, 2014; Alonso et al., 2000; Vedia and Miranda, 2013).

Although crayfish have species-specific dispersal capacities e.g. upstream or overland dispersal (Bubb et al., 2004), their spread is mostly linked to human activities (i.e. angling bait, fishery production, and the pet trade). As such, an increasing trend in the occurrence of crayfish most likely reflects an increasing spatial connectivity through intensified human-mediated transport (Jussila et al., 2015). However, we only observed a significant increase in the occurrence of *P. leniusculus* in England. A steep increase in the number of occurrences in Hungary (90 % *F. limosus*; 10 % *P. leniusculus*) was not significant, likely due to a single short (9-year) time series being too limited to identify consistent patterns. However, NICS have been present in Hungary since the beginning of 20th century (Ludányi et al., 2016; Mozsár et al., 2021), making our observations a snapshot of their actual presence.

4.4. Average invasion velocity

The respective years in which the studied NICS were introduced to studied European countries (*P. clarkii*: 1973–89; *P. leniusculus*: 1959–98; *F. limosus*: 1895–1985; Seebens et al., 2021) suggest that local invasions have preceded their respective detection in our data. Despite this, we found that trends in the number of occurring populations and consequently average invasion velocity differed across regions. While regional differences in observed trends may be linked to differences in the respective non-indigenous species (e.g., their population densities and behavior), resource overlap with other crayfish species (Kuhlmann and Hazelton, 2007; Pintor et al., 2008; Chucholl, 2016), habitat characteristics (Wooster et al., 2012; Galib et al., 2022), or differences in human-mediated dispersal intensity (i.e. propagule pressure due to illegal bucket transport by fishermen; Souty-Grosset et al., 2006; Holdich et al., 2009) are the most likely explanations. Cultural and socio-economic differences lead to varying perceptions of the threat posed by NICS. This can influence governmental stances on its willingness to conduct (as well as fund) the management of NICS (Gherardi et al., 2011; Patoka et al., 2018), contributing to the widely differing averages in invasion velocity.

The increasing occurrence of *P. leniusculus* in England may be due to numerous introductions of *P. leniusculus* for crayfishing (Ackefors, 2017), being well established and widespread in England and thus the lack of new niches available to invade explain the lower average invasion velocity in England. In addition, this could be also partially explained by a low availability of time series ($n = 48$) paired with a lower degree of canalization compared to the European mainland as its smaller canals are not used for international or industrial shipping (Stubbington et al., 2008). It is furthermore possible that most of our time series largely represented populations after a possible local “boom” phase (see Sandström et al., 2014; Strayer et al., 2017; Larson et al., 2019; Perales et al., 2021). Populations within the “boom” phase likely exhibit local range expansions (Strayer et al.,

2017; Larson et al., 2019), promoting the establishment of successive populations (Strayer et al., 2017), which is emphasized in our data by the appearance of multiple isolated occurrences of NICS at sites near previously invaded sites.

Moreover, we identified average invasion velocity between 30 and 90 km/year over our time series, which represents a plausible estimate. *Pacifastacus leniusculus*, for instance, actively moves downstream (Bubb et al., 2004), while *P. clarkii* was shown to migrate upstream several kilometres in one day through water (Kerby et al., 2005; Bernardo et al., 2011). This ability to move rapidly within rivers demonstrates NICS' spreading ability, and thus, explains their invasion success (Bubb et al., 2004; Buřič et al., 2009a, 2009b). Yet, besides their high natural spread ability (Liptak et al., 2016), human-mediated transport likely remains the dominant way of their dispersal, particularly the long-distance ones (Holdich et al., 2009; Acevedo-Limón et al., 2020; Oficialdegui et al., 2020). We, therefore, find that biomonitoring data can — in line with our third hypothesis — be used to describe the dynamics of NICS populations, including the number of occurrences and the average invasion velocity across invaded regions. This information can be useful for understanding the spread and impacts of NICS and for developing strategies to manage their populations.

5. Conclusion

Our study highlights the possibility of characterizing crayfish populations and respectively their trends using standard macroinvertebrate biomonitoring methods (e.g. kick sampling). Considering the often locally high abundances of NICS, our results suggest that observed abundances as well as occurrences may be highly conservative, as they are unlikely to be observed and assessed adequately using such methods alone (Haase et al., 2004). This nevertheless underlines the need to rethink long-term biomonitoring and use much broader, more inclusive approaches (such as environmental DNA; Tréguier et al., 2014), or approaches which as a minimum include either time and cost-intensive standardizable trapping efforts that effectively catch crayfish (such as funnel traps; Larson and Olden, 2016, but see Green et al., 2018), or incorporate hand searches of possible hiding places and shelters. Secondly, we identified highly complex temporal and spatial trends, with several species-specific and region-specific drivers. In particular, we found that Europe-wide trends masked regional – or species-specific trends, emphasizing the need to investigate invasion patterns at smaller scales. Concomitantly, recognizing that overarching invasion patterns can obscure regional or species-specific dynamics remains crucial, as understanding invasions at the local and regional scale enable managers and stakeholders to prioritize efforts to reduce potential impacts and limit spread. Due to the large impacts of invasive crayfish in rivers and the increasing number of abundant invasive populations, assessing biodiversity and stream quality without a correct interpretation of this taxonomic group could lead to erroneous and misleading results. As such, trends in biodiversity and stream quality will likely be attributed to various stressors, yet neglecting the impacts of invasive species (Bellard et al., 2016). This could eventually result in wrong decisions in developing conservation strategies and resources utilized to address the wrong stressors, thus minimising the effectiveness of i.e. conservation efforts (Tockner et al., 2010).

CRedit authorship contribution statement

Ismael Soto: Methodology, Formal analysis, Data curation, Investigation, Visualization, Writing - original draft, Writing - review & editing. **Danish A. Ahmed:** Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Ayah Beidas:** Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Francisco J. Oficialdegui:** Resources, Writing - review & editing. **Elena Tricarico:** Resources, Writing - review & editing. **David G. Angeler:** Resources, Writing - review & editing. **Giuseppe Amatulli:** Resources, Writing - review & editing. **Elizabeta Briski:** Resources, Writing - review & editing.

Thibault Datry: Resources, Writing – review & editing. **Alain Dohet:** Resources, Writing – review & editing. **Sami Domisch:** Resources, Writing – review & editing. **Judy England:** Resources, Writing – review & editing. **Maria J. Feio:** Resources, Writing – review & editing. **Maxence Forcellini:** Resources, Writing – review & editing. **Richard K. Johnson:** Resources, Writing – review & editing. **J. Iwan Jones:** Resources, Writing – review & editing. **Aitor Larrañaga:** Resources, Writing – review & editing. **Lionel L'Hoste:** Resources, Writing – review & editing. **John F. Murphy:** Resources, Writing – review & editing. **Ralf B. Schäfer:** Resources, Methodology, Supervision, Writing – review & editing. **Longzhu Q. Shen:** Resources, Writing – review & editing. **Antonín Kouba:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing. **Phillip J. Haubrock:** Conceptualization, Supervision, Data curation, Methodology, Visualization, Writing - original draft, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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