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Tracking a killer shrimp: *Dikerogammarus villosus* invasion dynamics across Europe

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Abstract

Aim: Invasive alien species are a growing problem worldwide due to their ecological, economic and human health impacts. The "killer shrimp" *Dikerogammarus villosus* is a notorious invasive alien amphipod from the Ponto-Caspian region that has invaded many fresh and brackish waters across Europe. Understandings of large-scale population dynamics of highly impactful invaders such as *D. villosus* are lacking, inhibiting predictions of impact and efficient timing of management strategies. Hence, our aim was to assess trends and dynamics of *D. villosus* as well as its impacts in freshwater rivers and streams.

Location: Europe.

Methods: We analysed 96 European time series between 1994 and 2019 and identified trends in the relative abundance (i.e. dominance %) of *D. villosus* in invaded time series, as well as a set of site-specific characteristics to identify drivers and determinants of population changes and invasion dynamics using meta-regression modelling. We also looked at the spread over space and time to estimate the invasion speed (km/year) of *D. villosus* in Europe. We investigated the impact of *D. villosus* abundance on recipient community metrics (i.e. abundance, taxa richness, temporal turnover, Shannon diversity and Pielou evenness) using generalized linear models.

Results: Population trends varied across the time series. Nevertheless, community dominance of *D. villosus* increased over time across all time series. The frequency of occurrences (used as a proxy for invader spread) was well described by a Pareto distribution, whereby we estimated a lag phase (i.e. the time between introduction and spatial expansion) of approximately 28 years, followed by a gradual increase before new occurrences declined rapidly in the long term. *D. villosus* population change was associated with decreased taxa richness, community turnover and Shannon diversity.

Main Conclusion: Our results show that *D. villosus* is well-established in European waters and its abundance significantly alters ecological communities. However, the multidecadal lag phase prior to observed spatial expansion suggests that initial introductions by *D. villosus* are cryptic, thus signalling the need for more effective early detection methods.

KEYWORDS

biological invasion, crustacean, freshwater ecosystem, invasive alien species, long-term monitoring, time-series

1 | INTRODUCTION

Humans have translocated thousands of invasive alien species beyond their native ranges (Seebens et al., 2021). Their establishment and spread have been recognized as a leading cause of biodiversity loss and a growing socio-economic burden worldwide (Bellard et al., 2016; Diagne et al., 2021). It is therefore imperative to understand and predict large-scale invasion patterns, identify future invaders (i.e. introduced species that become invasive; Fournier et al., 2019; Pyšek et al., 2020) and assess their impacts (Essl et al., 2020). With the ongoing global increase in invasion rates (Seebens et al., 2021) and a growing threat to ecosystems and economies (Pyšek et al., 2020), there is an urgent need to characterize population dynamics at large scales to inform effective detection, management actions and monitoring (Cuthbert, Kotronaki, Carlton, et al., 2022; Seebens et al., 2021).

The form of population dynamics may differ among invaders, invasion pathways, biogeographical regions, abiotic or biotic gradients and spatio-temporal scales (Arim et al., 2006; Haubrock et al., 2020). Characterization of population dynamics of invasive alien species at a broad spatio-temporal scale has been limited by insufficient long-term data. However, advances in availability in long-term biodiversity monitoring (Dornelas et al., 2018; Mirtl et al., 2018) and data analysis approaches for biodiversity time series (Bowler et al., 2017; Dornelas et al., 2014; Pilotto et al., 2020) have been made. These and other initiatives have collated large datasets for diverse taxonomic groups and examined biodiversity and ecosystem function trends at regional and global scales (Seebens et al., 2019, 2020). Large-scale, community-level data can also be used to examine distribution and abundance patterns of invasive alien species, as well as their potential effects on ecological communities over time (Dornelas et al., 2014; Haubrock et al., 2020).

Invaders may take considerable time before becoming established, detected and disruptive (Crooks, 2005; Spear et al., 2021), and such time lags are very difficult to predict (Coutts et al., 2018). Furthermore, the invaders may not remain disruptive or could become less so, owing to population declines (e.g. reflecting boom-and-bust cycles and/or community adjustment; Strayer et al., 2017). Finally, the type and magnitude of ecological impacts an invader causes are dependent, in part, on its abundance (Sofaer et al., 2018; Yokomizo et al., 2009), and thus can change through time according to the invader's population dynamics. Given that the long-term population dynamics of even widespread conspicuous invaders are often poorly characterized (Strayer et al., 2006), this gap challenges our ability to (i) predict in which situations the invader's impacts on invaded ecosystems will be maximal and (ii) decide if/when management should intervene. However, species having well-documented invasion histories within large contiguous regions offer temporally highly resolved data whose collation and analysis could reveal essential information to guide risk assessment and management prioritization.

One such species is the "killer shrimp" *Dikerogammarus villosus*, an invasive alien freshwater amphipod listed among the "100 worst" invaders in Europe (Nentwig et al., 2018). The confirmed native range of *D. villosus* is the northern margins of the Ponto-Caspian region (i.e. Black Sea, Caspian Sea and Azov Sea; Dedyu, 1980; Mordukhai-Boltovskoi, 1960). This voracious predator has spread rapidly through European inland waterways and the Baltic Sea, aided by canalization and anthropogenic vectors (Cuthbert et al., 2020; De Ventura et al., 2017), and also poses an invasion risk to the North American Great Lakes (Kramer et al., 2017). Facilitated by the known influence of streams on the spread of *D. villosus*, it has substantial impacts on biodiversity in invaded regions, causing marked declines in native macroinvertebrates via predation and competition (Dick et al., 2002; Dick & Platvoet, 2000). It also potentially impacts egg and embryonic stages of large, ecologically important crustaceans, fish and amphibians (Roje et al., 2021; Taylor & Dunn, 2017; Warren

et al., 2021), causing disruptions across multiple trophic levels (i.e. trophic cascades; Van Riel, Van der Velde, & Bij de Vaate, 2006). Its displacement of native species (MacNeil et al., 2011; MacNeil & Platvoet, 2013) also facilitates the establishment of other invasive alien species (Bollache et al., 2004; Leuven et al., 2009). Notably, it is the only invasive amphipod with documented monetary costs (Kouba et al., 2021). Yet, information on this invader's effects on native species assemblages over time is still scarce.

Dikerogammarus villosus invasion success has been promoted by its suitability for transport by anthropogenic vectors (e.g. ships; Anderson et al., 2014), wide thermal and salinity tolerances (Cuthbert et al., 2020), aggressive competitive behaviours (Kobak et al., 2016), effective anti-predator strategies (Rolla, Consuegra, & de Leaniz, 2020) and high growth rates and fecundity (Holdich & Pöckl, 2007; Pöckl, 2009), as one female can carry nearly 200 eggs (Pöckl, 2009). Accordingly, this invader's potential to successfully establish after introduction – from even a single gravid female – into a novel environment is substantial (Devin et al., 2004; Lockwood et al., 2005). Reflecting its impacts on recipient ecosystems (e.g. extirpation of native species and changes in biotic indices; Kouba et al., 2021; MacNeil et al., 2013), *D. villosus* has been the focus of various management actions, although measures for management post-establishment are undeveloped, and prevention of initial introduction has been advocated (Bradbeer et al., 2020; Wood et al., 2021). Moreover, understanding the population dynamics of this species remains limited at large spatial scales regarding temporal and climatic gradients (e.g. time since invasion; variability in temperature and precipitation), hindering quantification of impact and population trends that could inform management strategies. For example, earlier invasions, such as those detected in Hungary (Bij de Vaate et al., 2002: in 1926; Huber et al., 2015 in 1970; Figure 1), might already be regressing from their peak abundance to a stable, intermediate level or exhibiting "boom-bust" dynamics (Rolla, Consuegra, Hall, & Garcia de Leaniz, 2020; Strayer et al., 2017) and therefore be expanding to new areas more slowly than populations with a more recent invasion history (Seebens et al., 2018). More recent invasions may be at an early stage of spread, potentially preceding future exponential population increases. In addition, invasion success and exerted impacts are intertwined with anthropogenic stressors such as hydromorphological alterations and dam construction, which can influence spread rates (Colautti et al., 2006; MacNeil & Platvoet, 2013).

To characterize the population dynamics of *D. villosus* across time series, we collated European riverine macroinvertebrate biomonitoring data containing this species. We hypothesized that the (i) dominance of *D. villosus* populations is increasing within time series, whereas the number of new occurrences is declining in the long-term, indicating a deceleration in the invasion; (ii) recent invasions exhibit more rapid population growth, whereas populations originating from earlier invasions are stable or declining; (iii) population dynamics of *D. villosus* are mediated by site-specific climatic and spatial characteristics, with populations affected by warming and the presence of anthropogenic barriers such as dams. Lastly, we

hypothesized (iv) changes in recipient communities to be associated with *D. villosus* population dynamics.

2 | METHODS

2.1 | Data compilation

To investigate the population dynamics of *D. villosus* and the response of recipient communities across Europe, we considered 1816 time series (Peter Haase, unpublished data) reporting the abundance of macroinvertebrate taxa in streams and rivers across 22 European countries. Macroinvertebrates were sampled using different methods and protocols (see Table S1) among time series, but were consistent within each time series. Each time series comprised macroinvertebrate assemblages collected at a single site in multiple years. We initially selected all 132 time series with *D. villosus* populations and then excluded 36 time series that contained ≤2 sampled years, retaining 96 time series (Figure 1), of which most are from large European rivers (e.g. Danube or Rhine) across six European countries (i.e. Austria, France, Germany, Hungary, Netherlands and Switzerland). For time series in which samples were not collected in all years, we coded missing years as "not available" (NA). Time series spanned a mean ± SD of 10.1 ± 3.4 years and contained 7.7 ± 3.6 sampling years between 1994 and 2019.

2.2 | Trend identification and meta-regression modelling

To synthesize and describe the directionality and the trends in the number of sampled *D. villosus* individuals, we used a meta-regression modelling approach, which synthesizes the slopes of individual regressions (as in our case from different time series). For this, we used the "rma.mv" function of the R package *metafor* (Viechtbauer, 2010), using the time-series Mann–Kendall trend test (*S*-statistics) and respective variance as the effect size. The Mann–Kendall trend test is a non-parametric test to evaluate a monotonic increase or decrease in trends. In particular, we used the trends calculated by modified Mann–Kendall trend tests with variance correction to account for temporal auto-correlation (Hamed & Rao, 1998; Maire et al., 2019). To correct the spatial autocorrelation between time series, we used a random effect model, specifying the geographic coordinates as a random effect according to a Gaussian correlation structure (Cressie, 1993; Maire et al., 2019). This approach uses a regression model and enables comparability of time series by analysing the individual time series abundance trends (i.e. its slope) rather than the raw abundances. These models account for the variance of each individual temporal trend and treat each population as an individual spatial unit associated with scale and sampling protocol (Viechtbauer et al., 2015). Lastly, based on two data clusters, we classified the time series according to their first year of sampling into two groups and visually inspect if there are differences in population growth among groups. For this, we selected 2003 as a middle point between earlier (i.e. the first year of the time series before 2003) and later (i.e. the first year of the time series after 2003) invasions.

Although raw abundances are not comparable directly across time series due to differences in sampling methods, we approximated the temporal trend in *D. villosus* relative abundance (%) by averaging abundance records across all samples from a given year, as a proxy of dominance of the species to avoid introducing a bias from the comparison of different sampling methods. We considered only those years in which at least 15 assemblages were sampled and thus omitted 1994, 2018 and 2019 (5–7 sampled assemblages). Once removed, the mean number of assemblages sampled was 27.3 ± 6.8,
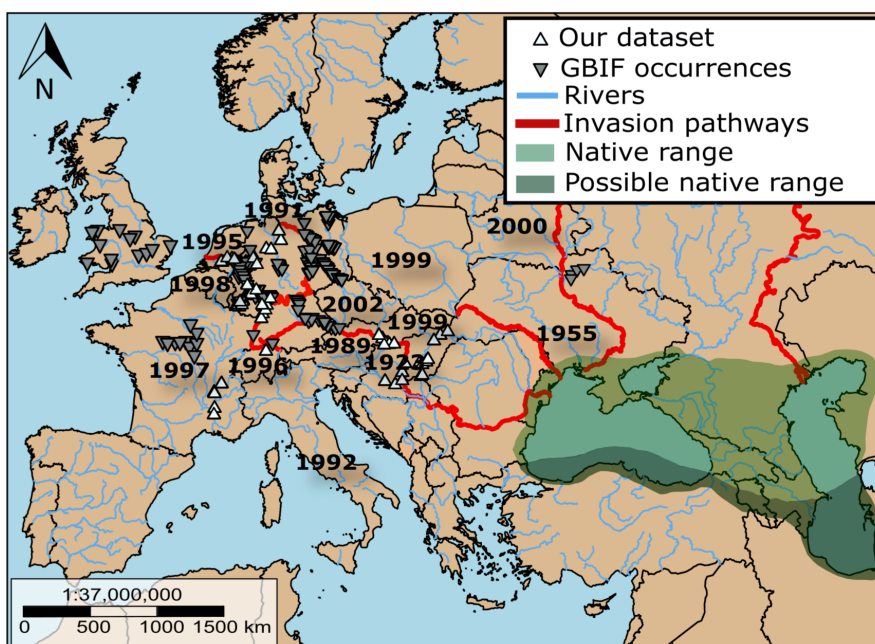
FIGURE 1 Map summarizing the native and invaded range of *Dikerogammarus villosus* in Europe, showing populations reported by the Global Biodiversity Information Facility (GBIF, 2021; grey triangles) and our time series (white triangles). Years within countries indicate the year of the first introduction according to the sTWIST database of first records (Seebens et al., 2018). The invasion pathways by which *D. villosus* has spread (i.e. Rhine, Danube, Volga and Dnieper rivers) are inferred from Bij de Vaate et al. (2002).

and maximum 42 in the year 2007. We tested a linear model for the dominance of *D. villosus* over time using least squares regression and thus estimated the proportion of abundance (%) at the time the assemblage was sampled.

2.3 | Effects of site-specific characteristics on *D. villosus*

To investigate the spatial and climatic drivers of *D. villosus* trends, we used site-specific characteristics of each time series. Climatic regions (i.e. Köppen-Geiger climate zone) were extracted from Beck et al. (2018). Biogeographical regions were defined following the European Environment Agency classification map and estimated visually using the site-specific coordinates (EEA, 2021). We further classified the type of ecosystem of each time series based on Strahler order (i.e. stream <8 or large rivers ≥8) to evaluate differences in the degree of invasions between both. We obtained site-specific runoff data, expressed as the annual Q (mm), from the TerraClimate dataset at 4-km spatial resolution (Abatzoglou et al., 2018). We extracted the elevation of each site from the MERIT Hydro digital elevation model (Yamazaki et al., 2019) at 90-m spatial resolution and used the Hydrography90m (Amatulli et al., 2022) stream network, catchments and sub-catchments (catchments between network nodes) as underlying spatial units. For each site, we computed the stream slope using the r.stream.slope function. We extracted land cover data from the European Space Agency Climate Change Initiative (ESA CCI) Land Cover time series v2.0.7 dataset, at 300-m spatial resolution (ESA, 2017), as the percentage cover of a given land cover category within the sub-catchment. We used the Global Reservoir and Dam Database (GRanD) v1.3 to identify dams along the river network. We then measured the distance to the nearest dam to investigate the effect of instream barriers. We extracted mean daily temperature and total daily precipitation data from a gridded European scale observation-based dataset (spatial resolution: 0.1°; Cornes et al., 2018) and calculated the average annual temperature and precipitation for each sampled assemblage in each sampling year (Pilotto et al., 2020), as well as their respective *S*-statistics (i.e. the Mann–Kendall trend test statistic, see above), as indicators of climatic changes. Precipitation in particular can be used as a proxy for river discharge (Higashino & Stefan, 2019) and was included as it affects the availability of water and nutrients as well as the habitat suitability for many species (Gallardo et al., 2012; Shi et al., 2010). We then calculated the mean maximum and minimum temperature and precipitation and each respective *S*-statistic. *Dikerogammarus villosus* slopes (to investigate factors determining *D. villosus'* rate of change over time) and relative abundances (as a proxy of *D. villosus'* dominance in invaded ecosystems over time) were analysed as a function of these spatial, temporal, and site-specific characteristics, to identify significant drivers of temporal trends (see Table S2). We used generalized linear models (GLMs) via the *MASS* R package (Ripley et al., 2013). We used a Gaussian distribution for continuous data and quasibinomial distribution (to account for high variance of

the dataset) for proportion data (i.e. relative abundances) after visually inspecting their respective residual distributions for normality through histograms.

To identify the best model, we first tested for collinearity among the numerical variables using the variance inflation factor (VIF) for continuous predictors using the "corvif" function (Zuur et al., 2009). We selected VIF>5 as the threshold, and those variables with high VIF values for each model were assessed for their ecological relevance based on expert knowledge (Table S3; Dorman et al., 2013; Zuur et al., 2009). Regarding the four categorical variables (country, biogeographical region, Köppen-Geiger classification and ecosystem type), we used chi-square tests to investigate the collinearity, and retained only the biogeographical region (Table S4). We considered each model and the respective predictors, using expert-based opinion to determine if the inclusion predictors would make sense from an ecological perspective (Table S5). Hence, the model consisted of a single response variable (i.e. the Mann–Kendall trend test slopes of *D. villosus* abundances or the relative proportion of *D. villosus*) and site-specific characteristics (see above; Table S2). Following the alphabetical order, the Alpine region was used as a reference factor (i.e. as intercept), and therefore, we do not infer any results about this region.

2.4 | Modelling occurrence frequency and invasion speed

We combined the first occurrence of *D. villosus* in each time series in our data with those occurrences (as coordinates and year of records) in the Global Biodiversity Information Facility database (GBIF, 2021). Eight GBIF occurrences were removed due to insufficient information (e.g. no recorded year), resulting in 400 records.

We excluded those sample years from the dataset of 400 records that reported relatively high occurrence frequencies, that is, any number of occurrences that was greater than $Q_3 + 3 \times IQR$, where Q_3 is the upper quartile and IQR is the interquartile range of the dataset. A single outlier was found with 120 occurrences in the year 2009, and thus, it was removed. We modelled the remaining 280 occurrences to represent invader spread, using a logistic distribution and a two-tailed Pareto distribution. A key difference between these distributions is the decay rate at the end tails: the logistic distribution decays exponentially fast (thin tails), and for the Pareto distribution, the decay is much slower according to an inverse power law (fat tails; Nolan, 2020). Moreover, Pareto distributions with distinct parameters were considered (i.e. two-tailed) for the early and late phases of the invasion. Both distributions were fitted against the occurrence data using the non-linear regression tool *lsqcurvefit* in Matlab. The better-fitting model was determined based on lower number of parameters and higher R^2 value (see Note S2). Further, we estimated the frequency of occurrences f_0 at the time of first sampling ($t = 0$) the time of introduction t_{intro}, and the duration of the lag phase t_{lag} that is, the period before *D. villosus* was observed in additional assemblages, evaluated at 10% of the largest recorded occurrence frequency f^*.

As a complementary analysis, we computed the distance between the locations of every sampled site from the first invaded site using site location data (GPS coordinates recorded as latitude and longitude) over the years 1994–2021. An estimate for the invasion speed (km/year) was obtained by computing the mean distance (i.e. total distance averaged over the number of occurrences per year) over time and modelled using a linear equation (Bagnara et al., 2022). We also calculated the differences between the first record of *D. villosus* in our data and sTWIST database (the most comprehensive source of first records of alien species, integrating several databases and merging them into a single database; Seebens et al., 2018).

2.5 | Impacts of *D. villosus* on community metrics

To assess the effect of *D. villosus* abundance on recipient communities (proxied by the *S*-statistic of *D. villosus* trends), we computed five common metrics for each community and year within each time series: total abundance (i.e. individuals), taxon richness (i.e. the total number of taxa), temporal turnover (i.e. the proportion of species either gained or lost over time relative to the total number of species observed; Carvalho et al., 2012), the Shannon diversity index (Shannon & Weaver, 1949) and Pielou's evenness (Pielou, 1966). The metrics were calculated considering all species in the community except *D. villosus*, potentially including both native and other non-native species. For evenness, we followed the formula: $H/\ln(S)$ (where H is the Shannon Index and S is the taxon richness of a community). Metrics were calculated using the "diversity" function in the R package *vegan* (Oksanen et al., 2013) and the "turnover" function in the R package *codyn* (Hallett et al., 2016). In analysing these metrics as response variables in meta-regression models, we included the middle point of each time series (see above) in addition to the rate change of *D. villosus* to infer the effects of temporal variability in changing temporal trends (i.e. slopes) over time and evaluate the change of sampled individuals of *D. villosus* individuals to test its associated effect on community metrics.

All models used restricted maximum likelihood estimation (REML). We also quantified the proportion of variance in the model not attributed to sampling error by using the I^2 statistic. In addition, we evaluated the results of the meta-regression by a graphical representation (i.e. forest plots) using the "forest" function of the R package *metafor* (Figure S2; Viechtbauer, 2010). To inspect potential biases that may alter the results, we checked the symmetry of the data using funnel plots and statistically evaluated this symmetry using the Egger's test (Egger et al., 1997; see Figure S3; Table S6).

All analyses were carried out in R v.4.1.3. (R Core Team, 2022). The reproducible R script is available with the manuscript and lists all R packages that were used.

3 | RESULTS

3.1 | Trends of *D. villosus* across Europe

Across the sampling sites in Europe included in this study, the abundance trend of *D. villosus* increased in 49 locations, decreased in 44 locations and has not changed in 3 locations (Figure 2a). Our analysis therefore suggests that the total number of *D. villosus* individuals in the study region experienced no overall significant change in its rising trajectory between 1994 and 2019s (*S*-statistics = 4.74; CI: −9.32, 18.82, $p = .50$; Table 1; Figure 2a), albeit expressing low heterogeneity ($I^2 = 3.62\%$). In addition, we did not find differences in the population growth between earlier (for which $t = 0$ was before 2003) and later time series (i.e. $t = 0$ after 2003; Figure S1).

Averaged across all time series, the overall proportion of *D. villosus* was well described by a linear model ($r = .45$), suggesting a steep rise in relative abundance over time. An average of 8.66% of *D. villosus* was recorded per sampled assemblage at the first time point. On average across all time series, the rate of increase in relative abundance (i.e. dominance) increased by 0.31% per year for each sampled assemblage (Figure 2b). In addition, our first records for *D. villosus* were on average

(a)

(b)
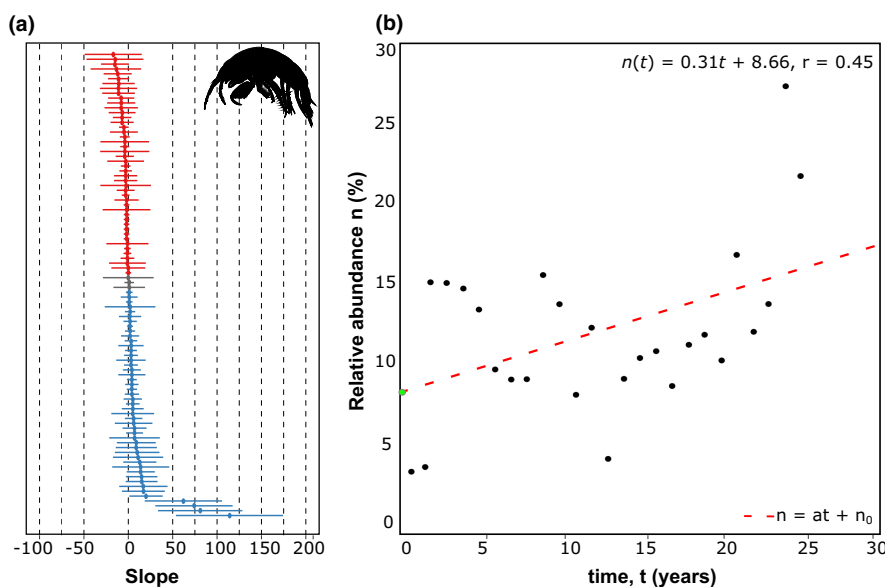
FIGURE 2 Changes in trends (slopes) of *Dikerogammarus villosus* in individual time series (*S*-statistics ± confidence intervals): red represents negative trends, blue positive trends, and grey indicates no significant change over time (a). Relative abundance of *D. villosus* in sampled sites at the European level. Proportions were averaged over the number of sampled assemblages each year from 1995 ($t = 0$) to 2017 ($t = 22$; black dots) (b).

10.8 years later than those referenced in the sTWIST database. This difference was reduced to 2.8 years after excluding time series from Austria and Switzerland ($n = 2$), for which the difference between both databases was 14 years (Seebens et al., 2018).

3.2 | Effect of site-specific characteristics on *D. villosus* trend

We did not identify a change in individuals of *D. villosus* sampled over time, despite a positive tendency (i.e. change in the *S*-statistics; GLM: 0.59 ± 0.45; $p = .19$; Figure 3a; Table S7). The rate of change in the trend of *D. villosus* increased significantly across the Mediterranean biogeographic region ($p < .05$). The average minimum temperature and the rate change of the maximum temperature had positive effects on the rate of change of *D. villosus* individuals ($p < .05$), while the distance to the next barrier had negative effects ($p < .05$; Figure 3b; Table S7). Regarding the relative abundance of *D. villosus* over time, we identified a significant increase ($p < .05$; Figure 3c; Table S7). This increase was shown in all biogeographic regions (relative to Alpine), as well as with increasing distance to the next barrier and the elevation of the stream ($p < .01$; Figure 3d; Table S7). The relative abundance decreased in streams relative to large rivers ($p < .01$; Figure 3d; Table S7).

3.3 | Modelling occurrence frequency and invasion speed at the European level

The mean $\pm$ SD for the number of *D. villosus* occurrences was 13.33 ± 19.07, with the maximum recorded occurrence frequency

$f^* = 78$ in the year 2008 ($t^* = 14$). The occurrence frequency of *D. villosus* was best described by a two-tailed Pareto distribution ($R^2 = .90$ for $t \leq t^*$ and $R^2 = .98$ for $t \geq t^*$ see Figure 4a), which fits better than the logistic distribution ($R^2 = .86$; see Note S2). Moreover, the Pareto distribution depends on fewer parameters. On considering an occurrence frequency of 1 (i.e. first invaded site), we predicted the time of introduction $t_{intro} = -20.67$ years prior to the first sampling event. The estimated number of occurrences at the time of first sampling was $f_0 = 3.37$. The duration of the lag phase was 27.64 years after t_{intro}. Beyond t^*, occurrence frequency rapidly declined, reaching low levels 45–50 years after t_{intro}, indicating low levels of spread for *D. villosus*.

We estimated the invasion speed of *D. villosus* at the time of first sampling as 80.27 km/year, with deceleration at a rate of 2.83 km/year^2, eventually reaching minimum speed at time $t = 28.34$ years (see Figure 4b). The estimation of null speed corresponds to a cessation in the frequency of occurrences at approximately the same time (49.03 years after t_{intro}, Figure 4a).

3.4 | Impact of *D. villosus* on community metrics trends

We did not find a significant trend over time for community metrics (Table 1). The rate of change in the number of *D. villosus* individuals sampled over time (i.e. its slope) had a significant negative effect on trends in taxon richness, temporal turnover and Shannon diversity (Figure 5; Table 1). We did not find a significant effect of the number of sampled *D. villosus* individuals on total community abundance and Pielou's evenness trends (Table 1; Figure 5).

TABLE 1 Meta-regression results according to time and *Dikerogammarus villosus* abundance for the following response variables: *D. villosus* abundance (a), community abundance (b), richness (c), turnover (d), diversity (e) and evenness (f) of recipient community.

Response variable	Predictor	Estimate	Standard error	*p*-Value	Confidence interval (lower)	Confidence interval (upper)
(a) *D. villosus* abundance $I^2 = 3.62\%$	Intercept	4.74	7.18	.50	−9.32	18.82
(b) Abundance $I^2 = 21.86\%$	Intercept	−15.70	196.46	.93	−400.76	369.34
	Middle point of time series	0.13	0.13	.32	−0.13	0.39
	Change in *D. villosus* abundance	0.14	0.08	.10	−0.03	0.31
(c) Richness $I^2 = 68.96\%$	Intercept	−327.49	237.33	.16	−792.66	137.67
	Middle point of time series	0.11	0.20	.57	−0.28	0.52
	Change in *D. villosus* abundance	−0.24	0.09	.01	−0.43	−0.05
(d) Turnover $I^2 = 4.55\%$	Intercept	47.70	187.37	.75	−319.53	414.94
	Middle point of time series	−0.03	0.09	.75	−0.21	0.15
	Change in *D. villosus* abundance	−0.17	0.08	.03	−0.32	−0.01
(e) Diversity Shannon $I^2 = 21.80\%$	Intercept	74.45	188.24	.69	−294.50	443.41
	Middle point of time series	<0.01	0.15	.95	−0.30	0.32
	Change in *D. villosus* abundance	−0.22	0.08	.01	−0.39	−0.04
(f) Evenness Pielou $I^2 = 14.42\%$	Intercept	148.23	190.31	.43	−224.78	521.25
	Middle point of time series	−0.03	0.12	.78	−0.27	0.20
	Change in *D. villosus* abundance	−0.15	0.08	.08	−0.33	0.02
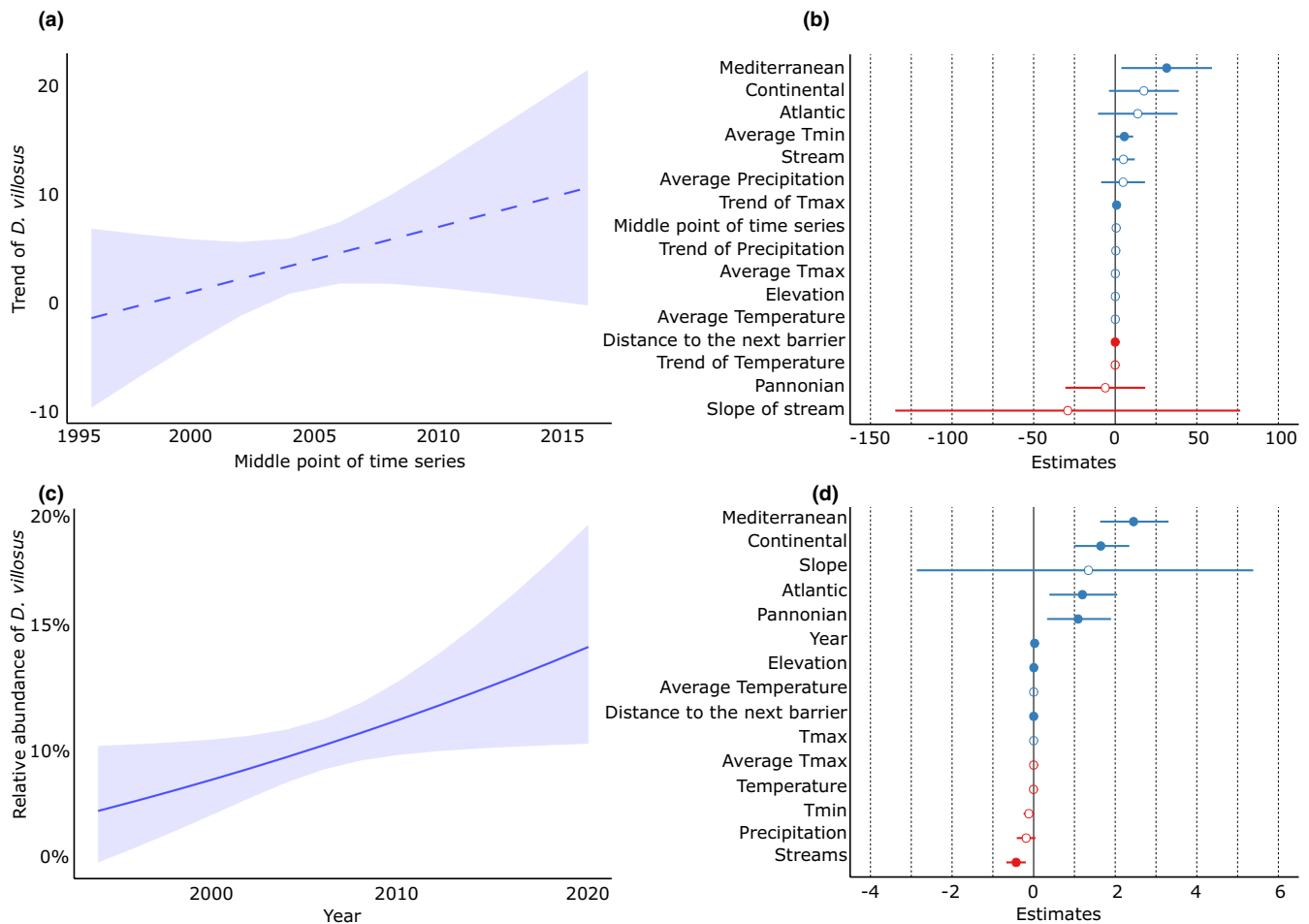
FIGURE 3 Trend of *Dikerogammarus villosus* abundance over time ± standard error (SE, blue shaded area) (a). Effect ± SE of the predictors included in the *D. villosus* model (b). Relative abundance of *D. villosus* over time ± standard error (SE, blue shaded area) (c). Effect ± SE of the predictors included in the model (d). Solid trend lines are significant and dashed lines not significant. Blue dot: positive effect; red dot: negative effect; filled dots: significant effects; empty dots: non-significant effects.

4 | DISCUSSION

4.1 | Overview

We characterized the population dynamics of one of the most notorious invasive alien species in Europe, *D. villosus*, and its effects on freshwater macroinvertebrate community metrics across available European time series. Contrary to our first hypothesis, we detected no significant trend in the number of *D. villosus* individuals sampled, although its dominance in invaded ecosystems increased over time. Contrary to our second hypothesis, the growth of earlier and more recently invading populations was comparable. Supporting our third hypothesis, *D. villosus* populations were influenced by site-specific climatic and spatial characteristics. Finally, supporting our fourth hypothesis, *D. villosus* was negatively associated with trends in macroinvertebrate community taxon richness, temporal turnover and Shannon diversity. These results highlight the need towards proactive management actions to contain *D. villosus* as well as to better understand the potential synergistic effects of stressors (Ricciardi et al., 2021).

Contrary to our first hypothesis, our meta-regression models identified no trend in the *D. villosus* population across time series. This lack of identifiable patterns could (i) reflect the complex population dynamics of invasive alien species at large spatial scales, (ii) climatic variability across European countries and biogeographical regions or (iii) genetic differentiation across invaded sites, ultimately leading to differing trends (Arim et al., 2006; Haubrock et al., 2022). For example, in France, all temporal trends (i.e. *S*-Statistics) were positive, whereas most trends were negative in Hungary. The sustained dominance of *D. villosus* in recipient ecosystems increased over time, which could reflect its ability to rapidly reach high population densities in combination with its capacity to predate, eliminate and replace native and alien species (Dick & Platvoet, 2000; Nentwig et al., 2018; Warren et al., 2021). In addition, the difference between the first record of *D. villosus* in sTWIST and our database was ~10.8 years. Yet, after excluding Switzerland and Austria—which had a difference of ~14 years between both databases likely due to the scarce time series from that country (*n* = 2)—the difference among both databases shrank to ~2.8 years only, underlining the accuracy of our data.
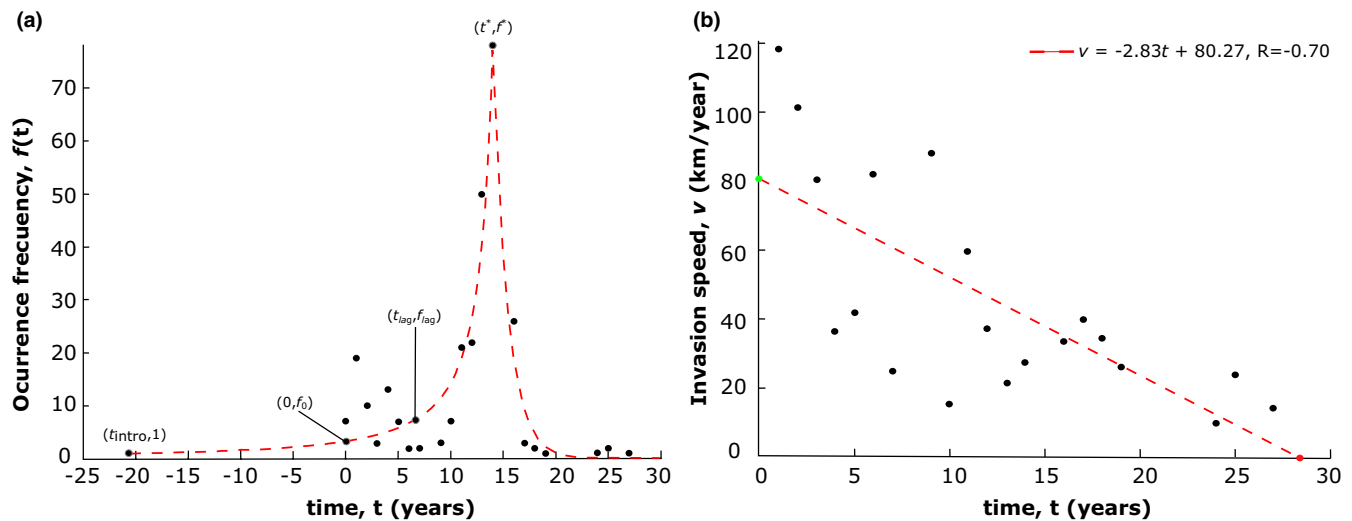
FIGURE 4 Occurrence frequency of *D. villosus* between 1994 ($t = 0$) and 2021 ($t = 27$) (circle markers) (a). Pareto distributions were fitted with $R^2 = .90$ for $t \leq t^*$, RMSE = 6.7 and $R^2 = .98$ for $t > t^*$, RMSE = 3.6, where the maximum occurrence frequency $f^* = 78$ was recorded at $t^* = 14$ years. Estimated model parameters for the left-hand tail are $s_1 = 1.81$, $\mu_1 = 1.45$, which were used to predict the: time of introduction $t_{intro} = -20.67$ years, number of occurrences at the time of first sampling ($t = 0$) $f_0 = 3.37$, duration of the lag phase $t_{lag} = 27.64$ years (after t_{intro}) with occurrence frequency $f_{lag} = 7.8$ (fixed at 10% of f^*). Model parameters for the right-hand tail are $s_2 = 1.08 \times 10^4$, $\mu_2 = 7.51 \times 10^3$, see Note S2 for mathematical details related to the Pareto distributions, and how these key points were determined from estimated model parameters. Linear model $v = -2.83t + 80.27$ fitted using least squares regression against estimated values of annual invasion speed with R $= -0.70$. The estimated speed at the time the first site was sampled is $v_0 = 80.27$ km/year, and acceleration $v_1 = -2.83$ km/year^2 (b).

In addition, contrary to our fourth hypothesis, we observed no difference in the growth rates of earlier and more recently invading populations, suggesting that the time since invasion does not influence *D. villosus* population dynamics. In addition, time series representing earlier and more recent invasions originated from different biogeographical regions: earlier ones were mostly from Atlantic and Continental regions, and more recent ones from Pannonian and Alpine regions.

4.2 | Occurrence frequency and invasion speed of *D. villosus*

We estimated that the introduction of *D. villosus* occurred on average 21 years before the first sampling event suggesting current monitoring of European streams is insufficient for early detection of invasive alien species. Following their introduction, such species often have low abundance during an initial establishment phase before increasing or becoming detected (Crooks et al., 1999), although lag phases are rarely measured in freshwater systems (but see Karatayev et al., 2011). Here, after a considerably long lag phase of 28 years from the time of introduction, *D. villosus* then only took another seven years to reach peak abundance. A lengthy lag period could reflect non-mutually exclusive phenomena including, *inter alia*, limits on the organism's reproductive rate in the early phase of exponential growth (e.g. Allee effects); (ii) multiple failed introductions prior to colonization success; (iii) genotypic selection of locally adapted organisms; and (iv) sudden population growth triggered by disturbance, environmental stochasticity or interspecific interactions (Crooks et al., 1999;

Crooks, 2005; Sakai et al., 2001; Spear et al., 2021). Although reporting efforts may be increased over time, this lag phase may explain the rapid decrease in new occurrences 35 years after an assemblage was first invaded (Ricciardi, 2013; Rouget et al., 2016). Nevertheless, records extracted from GBIF have to be taken with caution, as the taxonomic validity cannot always be ensured, simultaneously suggesting that many observations may be missing (Nekola et al., 2019; Shirey et al., 2019). Predicting future trends in the abundance of *D. villosus* is hampered by context dependencies, which may cause sudden shifts in population dynamics at different temporal scales, for example reflecting boom-bust dynamics (Strayer et al., 2017).

4.3 | The influence of site-specific characteristics on *D. villosus*

Understanding how site-specific characteristics influence invasive populations can enable the identification of factors facilitating and limiting their spread. Supporting our third hypothesis, *D. villosus* populations were influenced by site-specific abiotic characteristics, in particular, elevation, distance to the next barrier and climatic variables (average minimum temperature and the trend of maximum temperature). Focusing first on the rate of change of *D. villosus* trends, the distance to the next barrier had a negative effect on *D. villosus* populations. The reservoirs created by the construction of barriers such as dams are a hotspot for the introduction of invasive alien species, due to, for example, recreational fishing activity (Anderson et al., 2014), with *D. villosus* able to survive for up to three and a half days out of water attached to ropes and other equipment
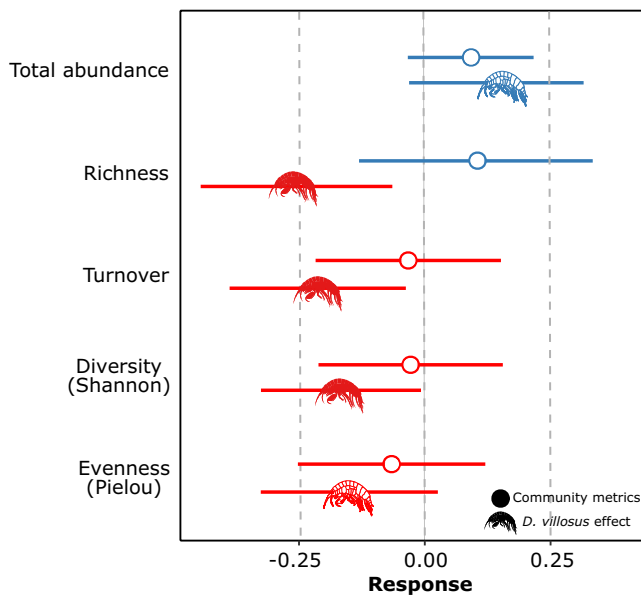
FIGURE 5 Effect of general temporal trend (circles) and the number of sampled individuals of *Dikerogammarus villosus* (*D. villosus* shape) on the rate at which trends in community metrics (total abundance, richness, temporal turnover, Shannon diversity and Pielou's evenness) changed across all time series. Empty dots represent no significant effects ± standard error (bars). Hollow shapes represent no significant effects of *D. villosus*, while the filled shapes represent significant effects. Red represents negative effects of *D. villosus* and negative trends in community metrics, while blue represents positive effects and positive trends of community metrics.

(Bacela-Spychalska et al., 2013). Furthermore, dams can be used as refuges and "stepping stones" for further spread, but also limit the spread upstream. Therefore, invasive alien species can accumulate near these barriers (Rahel, 2013). For invasive alien species, climatic variables – in particular temperature – can be the most important environmental variables determining the survival, reproduction and establishment in recipient ecosystems (Müller & Baur, 2011). Temperature is also well-known for its influence on life cycle characteristics such as fecundity in *D. villosus* (Pöckl et al., 2003). In congruence with Kobak et al. (2017), *D. villosus* preferred warm water and exhibited a stronger tendency to select extreme temperatures.

The dominance of *D. villosus* increased over time. This increase can be explained by propagule/colonization pressures, such as by the species exploiting increasing anthropogenic invasion corridors such as canals (MacIsaac et al., 2001; Lockwood et al., 2005). Reduced abiotic and biotic resistance resulting from degradation of ecosystems directly or indirectly by humans could also promote invasion (Hufbauer et al., 2012). The more rapid increase in *D. villosus* population growth at higher elevations nevertheless contradicts other studies that show lower elevation as high bioclimatic suitability for *D. villosus* (Gallardo et al., 2012), but suggests the species is invading higher elevated regions as a potential response to the ongoing climate change (Pauchard et al., 2016). Lastly, the dominance of *D.*

villosus was lower in streams in comparison to the major European rivers. This result may be partially explained by fast water flow or lower temperature in streams (Allan & Castillo, 2007; Grabowski et al., 2009), but also larger rivers having a greater level of confluence with smaller streams, functioning as shipping canals and therefore being prone to higher invasion rates. These results could be also affected by differences in sampling effort and the sampling methods among time series, which could have created biases and delays in detecting *D. villosus* at local and regional scales.

4.4 | Impact of *D. villosus* on community metrics

Understandings of how invasive alien species impact the recipient ecosystems and the potential synergistic effects of anthropogenic stressors (abiotic and biotic factors) have become priorities in invasion science (Ricciardi et al., 2021). Supporting our fourth hypothesis, we identified a negative relationship between temporal changes in the number of sampled *D. villosus* individuals and in three metrics representing macroinvertebrate communities: taxon richness, temporal turnover and Shannon diversity. The negative impacts of *D. villosus* on invaded ecosystems are well-documented and include the depredation of a wide range of macroinvertebrates (e.g. chironomids, leeches, isopods and juvenile crayfish; Buřič et al., 2009; Dick et al., 2002; Platvoet et al., 2009), including via "wasteful" killing (Dick et al., 2002). Invasive amphipods have also been shown to display lower levels of omnivory than native species (Cuthbert, Kotronaki, Hütt, et al., 2022). This predatory capacity can reduce or replace functionally equivalent species via intraguild predation (e.g. native *Gammarus duebeni* by alien *G. tigrinus*; Rewicz et al., 2014). *Dikerogammarus villosus* also has negative effects on ecosystem functioning, including alteration of habitat structure, leaf litter decomposition and energy flows through food webs, potentially causing large-scale trophic cascades (Koester et al., 2016; MacNeil et al., 2011; Piscart et al., 2011; Van Riel et al., 2006). These impacts can create vacant niches that increase community susceptibility to other invasions and exacerbate the collective impacts of invasive alien species (Boets et al., 2010, 2011).

However, we stress that changes in community trends cannot be attributed exclusively to the effect of *D. villosus*, as correlation does not indicate causation, and were likely also altered by other anthropogenic and natural stressors not included in our models, including changes in water quality, disturbance events or even other invasive alien species (Didham et al., 2005; Haubrock et al., 2020; Pilotto et al., 2020). The combination of invasive alien species and other human impacts can promote the local extirpation of native species, reducing community diversity and driving biotic homogenization (Dormann et al., 2007; Ekroos et al., 2010; McKinney, 2004; McKinney & Lockwood, 1999), but can also promote or prevent invasions and/or increases in invader populations (Simberloff & Von Holle, 1999; Beaury et al., 2020).

4.5 | Implications and conclusions

The scope of our study was limited by the time series represented in our database. Invasive alien species, such as *D. villosus*, can affect food webs through either bottom-up or top-down regulation, potentially triggering trophic cascades that cause major disturbances in invaded ecosystems (Van Riel et al., 2006). The greater effects of *D. villosus* following steeper increases in its abundance suggest that the main effects on invaded communities are driven by high population densities, which overwhelm the ecological resistance of the recipient community. Surprisingly, the data from GBIF and our time series do not overlap in some cases, highlighting areas for future abundance survey efforts. *Dikerogammarus villosus* was first recorded in Italy in 1992 (Seebens et al., 2018), Belgium in 1998 (Seebens et al., 2018), France at the beginning of the 2000s (Devin et al., 2001) and the United Kingdom in 2010 (Bacela-Spychalska et al., 2013; Seebens et al., 2018), but *D. villosus* was not present in any time series from these countries, perhaps because our data are restricted to lotic systems. Our study was therefore limited by our focus on rivers and streams. *Dikerogammarus villosus* also occurs in lentic freshwaters including lakes, ponds, and brackish waters, and has marked impacts on these ecosystems (Bacela-Spychalska et al., 2013; Bollache et al., 2004; Minchin et al., 2019). Its occurrence in other countries could also be underestimated, resulting in relatively few time series, for example the Netherlands or Switzerland (Altermatt et al., 2014; Bij de Vaate & Klink, 1995). As such, further research would be needed to comprehensively characterize *D. villosus* impacts across all European freshwaters. Notwithstanding these data gaps, our results allow broad-scale inference of impacts using standardized time series across a range of invaded lotic European freshwaters.

Overall, our results show that *D. villosus* is well-established across the vast majority of Europe. Considering that *D. villosus* has invaded many freshwater and brackish ecosystems beyond those sites covered by the time series we considered in our analyses, it remains impossible to conclude anything about the capacity of *D. villosus* to expand further in Europe. Nonetheless, our documentation of *D. villosus* highlights the need for greater effort to reduce delays in the detection of invasive alien species to implement management techniques in an early stage of invasion, when such methods can be more effective (Ahmed et al., 2022; Lodge et al., 2016) and less expensive (Cuthbert, Diagne, et al., 2022; Fantle-Lepczyk et al., 2022; Hulme et al., 2009). These measures are especially important in those regions currently uninvaded, such as the North American Great Lakes that can act as "stepping stones" to assist further spread across the continent. Our use of long-term, large-scale time series also emphasizes the importance of long-term data in ecology (Crooks et al., 1999). Further long-term studies are necessary to increase our understanding of the population dynamics of *D. villosus* and other aquatic invaders across the breadth of ecosystems, and the context-dependencies that differentiate such dynamics, to provide better management information for stakeholders and governments.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in a GitHub reposit at https://github.com/IsmaSA/Dikerogammarus-villosus-population-dynamics.git.

PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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