Haubrock, P.J., Pilotto, F., Soto, I., **Kühn, I.**, Verreycken, H., Seebens, H., Cuthbert, R.N., Haase, P. (2023):
Long-term trends in abundances of non-native species across biomes, realms, and taxonomic groups in Europe
Sci. Total Environ. **884** , art. 163808

https://doi.org/10.1016/j.scitotenv.2023.163808

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PII: S0048-9697(23)02429-4

DOI: https://doi.org/10.1016/j.scitotenv.2023.163808

Reference: STOTEN 163808

To appear in: *Science of the Total Environment*

Received date: 19 March 2023

Revised date: 22 April 2023

Accepted date: 24 April 2023

Please cite this article as: P.J. Haubrock, F. Pilotto, I. Soto, et al., Long-term trends in abundances of non-native species across biomes, realms, and taxonomic groups in Europe, *Science of the Total Environment* (2023), https://doi.org/10.1016/j.scitotenv.2023.163808

Long-term trends in abundances of non-native species across biomes, realms, and taxonomic groups in Europe

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Abstract:

Rates of biological invasion have increased over recent centuries and are expected to increase in the future. Whereas increasing rates of non-native species incursions across realms, taxonomic groups, and regions are well-reported, trends in abundances within these contexts have lacked analysis due to a paucity of long-term data at large spatiotemporal scales. These knowledge gaps impede prioritisation of realms, regions, and taxonomic groups for management. We analysed 180 biological time series (median 15±12.8 sampling years) mainly from Long-Term Ecological Research (LTER) sites comprising abundances of marine, freshwater, and terrestrial non-native species in Europe. A high number (150; 83,3%) of these time series were invaded by at least one non-native species. We tested whether (*i*) local long-term abundance trends of non-native species are consistent among environmental realms, taxonomic groups, and regions, and (*ii*) if any detected trend can be explained by climatic conditions. Our results indicate that abundance trends at local scales are highly variable, with evidence of declines in marine and freshwater long-term monitoring sites, despite non-native species reports increasing rapidly since the late 1970s. These declines were driven mostly by abundance trends in non-native fish, birds, and invertebrate species in three biogeographic regions (Continental, Atlantic, and the North Sea). Temperature and precipitation were important predictors of observed abundance trends across Europe. Yet, the response was larger for species with already declining trends and differed among taxa. Our results indicate that trends in biological invasions, especially across different taxonomic groups, are context-dependent and require robust local data to understand long-term trends across contexts at large scales. While the process of biological invasion is spatiotemporally broad, economic or ecological impacts are generally realised on the local level. Accordingly, we urge proactive and coordinated management actions from local to large scales, as invasion impacts are substantial and dynamics are prone to change.

Keywords: *long-term invasions; meta-analysis; eLTER; population dynamics; invasion dynamics*

Introduction

Globalization of trade and transport, increased use of non-native species in agro-, aqua-, and horticulture, combined with the effects of climate change, have progressively increased translocations of species outside of their native range (Rahel & Olden, 2009; Coyle et al., 2017; Seebens et al., 2017). This has resulted in the redefinition of historic biogeographic boundaries, with substantial detrimental effects on global biodiversity when non-native species spread and become invasive (Capinha et al., 2015; Brodie et al., 2018; Pyšek et al., 2020). Invasive species are those that spread (actively or passively) and can have negative impacts on human health and well-being, food production, ecosystem-services, and physical infrastructures, among others (Vilà et al., 2011; Simberloff et al., 2013; Shackleton et al., 2019), while presenting a major economic burden (Vilà et al., 2010, 2011; Pyšek et al., 2012; Castro-Díez et al., 2019; Diagne et al., 2021).

The rate of non-native species introductions has been rapidly increasing globally during the last 200 years (Seebens et al., 2017). Projections of future non-native species introductions expect established non-native species numbers to increase by ~36% towards 2050 (Seebens et al., 2021). Yet, knowledge about the temporal dynamics of non-native species accumulation with respect to population growth with time since invasion is still scarce. Further, how these dynamics may vary among taxonomic groups and environmental realms, and how environmental drivers, such as climate change, facilitate the spread of non-native species at large spatial scales (i.e., context-dependency of non-native species; Ricciardi et al., 2013), lack of investigation. Although past and projected detection rates of non-native species have varied among taxonomic groups and geographic regions, there is a lack of understanding of invasive species' population dynamics over time (Seebens et al., 2017, 2020; Bailey et al., 2020), which has implications for impact prediction and the application of effective management strategies (Parker et al., 1999; Ahmed et al., 2022). Populations that are establishing or stabilising from e.g., boom-bust dynamics (Januchowski-Hartley et al., 2011; Strayer et al., 2017) may have a reduced capacity to exert ecological and economic impact in the future (Schlaepfer, 2018), whereas populations could exhibit greatest risk within or beyond certain density thresholds (Ahmed et al., 2021b). For example, after introduction, populations may remain benign at low abundances, lacking detection through time and may only reach sufficient abundances that cause impact once triggered by environmental factors (i.e. sleeper populations; Spear et al., 2021). In turn, the nature of these differences among populations could vary depending on biogeographic contexts, taxonomic groupings, and realms.

Model predictions and future projections are currently challenged by context-dependencies (e.g., ecological novelty in recipient communities, mutualisms, environmental disturbances) that influence the rate of invasion success (Catford et al., 2009). Understanding how biological invasions respond to rapid environmental changes constitutes a major research priority in the field (Ricciardi et al., 2021). Until recently, the lack of suitable long-term data (White, 2019) — based on true time series — to allow the investigation of population dynamics of non-native species across large spatial (i.e., continental) scales, realms, taxonomic groups and biogeographic regions (i.e. in response to external e.g. climatic drivers), has limited our ability to understand past and project future population dynamics (Seebens et al., 2017, 2018). Current limitations therefore hinder a thorough understanding of how non-native species respond to current and future environmental characteristics, which in turn limits our ability to develop prioritisation protocols and additional actions urgently needed for effective non-native species management (Hastings et al., 2005; Haubrock et al., 2022a).

In this study, we collate a dataset consisting of 180 monitoring time-series of species communities. This dataset covers a European-wide geographic gradient, three realms (terrestrial, freshwater and marine), six taxonomic groups (fish, aquatic and terrestrial invertebrates, vascular plants, plankton, and birds) and seven biogeographic regions (Alpine, Atlantic, Boreal, Continental, Mediterranean, North Sea, Pannonian). In those 180 monitored community assemblages, we identified 150 time series of non-native species from 16 European countries. We used these time series to determine trends of non-native species over time and among taxonomic groups. We hypothesise that at the European scale, non-native species have increased in abundance (*i*) through time, and that the trends differ (*ii*) among taxonomic groups, and (*iii*) across biogeographic regions.

Methods:

We collected 180 European long-term community biomonitoring datasets: (1) 161 time-series originated from 89 LTER-Europe (Long-Term Ecological Research, Mirtl et al., 2018) sites (some with >1 time series) and 26 additional sources (originally compiled by Pilotto et al., 2020); (2) 13 site-specific time series collected along the Rhine River encompassing 35 years that originated from the State Office for Nature, Environment and Consumer Protection (LANUV NRW; Le Hen et al., 2023); and (3) six time-series monitoring the introduction of non-native fish species across Flanders (Belgium) obtained from the INBO-project (https://www.vlaanderen.be/inbo/en-GB/projects/monitoring-exoten-voor-eu-verordening-ias-coordinatie-voorbereiding-implementatie-en-opvolging; "Monitoring invasive species in connection with the EU IAS Regulation 1143/2014: Coordination, preparation, implementation and follow-up"). These time series fulfilled 5 criteria: (*i*) each individual time series covered at least 15 years; (*ii*) there were at least ten annual survey events during that time; (*iii*) sampling occurred at the same site (no space-for-time substitution); (*iv*) survey method, seasonal and taxonomic resolution were consistent throughout the whole study period for each respective time series; and (*v*) abundance of the monitored species was reported (Note S1).

Non-native species identification

We identified non-native species recorded in the 180 time series between 1921 and 2020 at the country-level by consulting four sources: '*Global Invasive Species Database*' (GISD; de Poorter et al., 2005), the '*Global Register of Introduced and Invasive Species*' (GRIIS; Pagad et al., 2018), the '*Invasive Species Compendium*' (CABI; Diaz-Soltero & Scott, 2014), and the '*Theory and Workflows for Alien and Invasive Species Tracking*' (sTWIST; Seebens et al., 2020). Further, all species were individually checked to exclude potential native species that had been misclassified by this approach due to e.g., a 'pest status'. Using the sTWIST data set (Seebens et al., 2020), we then extracted the year of the first record of the identified non-native species in each respective country using the *Global Alien Species First Record Database* (version 1.1; Seebens et al., 2017). In case the year of first record was not available, we used the first year of the invader's appearance in the respective time-series as the closest approximation.

The 180 community datasets contained altogether 150 time series of 63 non-native species that occurred for more than three years as a minimum requirement to calculate trends as found to be acceptable (Haubrock et al., 2022; Soto et al., 2022, 2023) (median sampling years: 15±12.8 SD). Four time series were repeated observations of single individuals reoccurring over time and were excluded based on the lack of variation in the data, making it impossible to determine if there is a trend present, thus resulting in a total of 146 non-native species time series after exclusion. The final dataset comprised non-native fish (n=60 observations, 11 species), invertebrate (n=53 observations, 22 species), vascular plant (n=13 observations, 12 species), plankton (n=4 observations, 4 species), and bird (n=16 observations, 14 species) time series, covering the marine (n=17 observations, 14 species), freshwater (n=92 observations, 21 species), and terrestrial (n=37 observations, 28 species) realms (Table S1). Further, this dataset covered the Alpine (n=4 observations), Atlantic (n=78 observations), Boreal (n=2 observations), Continental (n=40 observations), Mediterranean (n=7 observations), North Sea (n=13 observations), and Pannonian (n=2 observations) biogeographic regions (as classified according to European Economic Area, 2016).

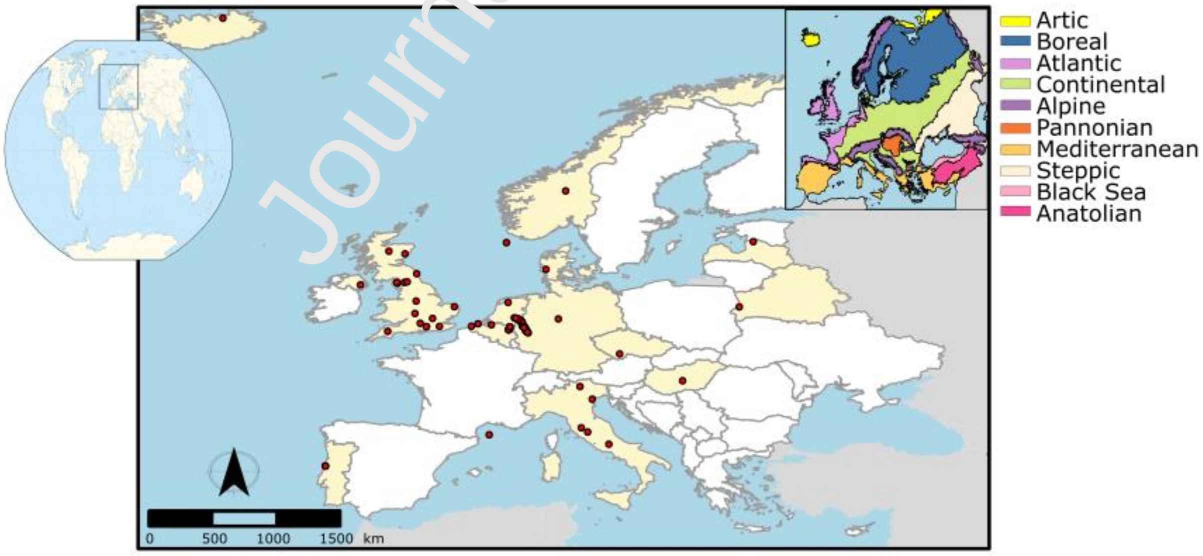

Figure 1: Distribution of the 146 non-native species time-series (red dots) used in the analyses. Note that one dot can represent multiple series in close locations.

Abiotic variables

We extracted the daily mean temperature and daily total precipitation data from the *ENSEMBLES daily gridded observational dataset for precipitation, temperature and sea level pressure in Europe* (E-OBS; spatial resolution: 0.1 degrees; Cornes et al., 2018). Using these data, we computed the mean annual temperature and precipitation of the 12 months prior to each respective sampling event of each site. Additionally, we obtained information on local anthropogenic pressure (e.g., urbanisation, sources of pollution, agriculture; described as ‘naturalness’) from each data provider for each site (ranked from 1 = low to 5 = high; see Pilotto et al., 2020).

Data analysis

We used a four-step procedure (Table 1) that allowed us to combine very heterogeneous original datasets. First, we analysed the ‘monotonic trends' of invader abundances across realms, biogeographic regions, and taxonomic groups, and applied a variance correction approach to account for temporal autocorrelation (Hamed & Rao, 1998) using the *S*-statistic (i.e., the slope identified by the Mann-Kendall test; see below for details) of the cumulative trends to synthesise and identify ‘broad’ common patterns. Secondly, we investigated the trends of the abundance of non-native species within each time series individually. In a third step, we used meta-regression models which allow the comparison between slopes considering the trends (*S*-statistics) of the individual time-series and their variance as an effect size to investigate potential drivers of the abundance of non-native species. In the fourth step, we used two generalised linear mixed models (GLMMs) to investigate drivers of raw abundances of non-native species trends that were identified as showing positive and negative trends respectively according to the Mann-Kendall trend test’s *S*-statistic.

Table 1. Four-step procedure for the analysis of the 146 European non-native species time series

Step	**Procedure**
1	Cumulative analysis of monotonic trends using Mann-Kendall trend tests
2	Species-specific analysis of monotonic Mann-Kendall trends
3	Comparison of trends with meta-regression models
4	Analysis of drivers of non-native species abundance with generalised linear mixed models

In the first step of the analysis, to infer trends on a broader scale, we pooled all time series trends for each (*i*) realm, (*ii*) taxonomic group and (*iii*) biogeographic region and used the Mann–Kendall trend test to identify monotonic trends (i.e. positive or negative) in the abundance of non-native species for each group separately (Mann, 1945; Kendall, 1949; Haubrock et al., 2022b) and used the *S*-statistic provided by the Mann-Kendall test and its variance as effect sizes (Kendall, 1948; Haubrock et al., 2022b). We then used meta-regression analysis mixed models using the *rma* function implemented in the `metafor` R package to examine ‘global’ trends within realms, taxonomic groups, and biogeographic regions, taking into account the variance of each clusters’ slope (Viechtbauer, 2010, 2015) and using the restricted maximum likelihood (REML) estimator which allows variation of true effects across time series trends. We included the factor realm (three levels: freshwater, marine and terrestrial), taxonomic group (six levels: fish, birds, aquatic invertebrates, terrestrial invertebrates, vascular plants, zooplankton), and biogeographic region (seven levels: Alpine, Atlantic, Boreal, Continental, Mediterranean, North Sea, Pannonian) as fixed effects in the models with no intercept under the assumption that species introductions initiate at zero, thus allowing comparability between slopes where all variables are included in the model as predictors. We further included the sites’ coordinates to account for spatial autocorrelation and examined changes in the slope for each non-native species by plotting the time-series-specific slopes over the time series midpoint. Finally, we also assessed heterogeneity (i.e., variance between time series), with 'low' heterogeneity defined as

<25%, indicating that the variation among effects is likely due to sampling error, and 'high' heterogeneity defined as >75%, indicating substantial variability among studies (Senior et al., 2016).

In the second part of the analysis, we first determined whether the number of time series was sufficient to describe all non-native species in the available time series, by plotting the cumulative number of identified non-native species against the cumulative number of years using the *specaccum* function of the `vegan` R package (Oksanen et al., 2013). Cumulative curves were considered to be saturating if ten previous values of the total number of non-native species were within ± 0.5 of the range of the asymptotic number of species, indicating the minimum monitored time series years required to describe the diversity of alien and native taxa (Huveneers et al. 2007). We then investigated the occurrence of unique species across all time series over time with an Empirical Cumulative Distribution Function (ECDF) by using the *stat_ecdf* function of the `ggplot2` R package (Wickham et al. 2016). The ECDF is a step function that increases by 1/k for each additionally occurring species, where k is the total number of non-native species identified, serving as an estimate of the cumulative probability distribution of species occurrences over time. We further described the composition of the trends within taxonomic groups, realms, and biogeographic regions by repeating the first analysis, but keeping individual time-series separated with these descriptive groupings. For this, we repeated the analysis from the first part, but for the total of all 146 site-specific time-series of non-native species abundances and included site_ID to account for random effects (i.e., source dataset), but in this case we used the function *rma.mv* implemented in the `metafor` R package (Vietchbauer, 2010) to run meta-regression mixed effect models. For this purpose, we classified trends into five classes based on whether they were ‘stable’, ‘increasing’, or ‘decreasing’. For ‘positive’ and ‘negative’ trends, we further distinguished between significant (p<0.05) and non-significant (p>0.05) trends.

In the third part of the analysis, we used the set of selected abiotic variables describing site characteristics and climatic conditions to identify potential drivers that affected the trajectory (i.e., slope) of non-native species abundances. For this, we used the slope (S-statistic) of each individual time-series as response variable in a meta-analytical approach and included the following explanatory variables: latitude and longitude to infer coarse spatial patterns between east and west as well as northern and southern Europe, site naturalness, mean temperature and precipitation over the study period from each site, temperature and precipitation trends of each site (S-statistics), the length of each time series to control for the duration of time series, and the species introduction year to infer periodic effects. All explanatory variables showed low collinearity (all $|r| < 0.5$); thus, they were all retained as predictors.

In the last step, we subsetted the abundance data based on the direction of trends identified by the modified Mann-Kendall trend test (i.e., positive or negative) and used generalised linear mixed models (GLMMs) using the R package `lme4` (Bates et al., 2011) to identify drivers thereof. For this, we analysed the abundance of both positive and negative non-native species abundance trends using a negative binomial distribution (with ‘log’ link). Each model consisted of the specific response variable (i.e., abundances) and the explanatory variables ‘Year’, ‘Latitude’, ‘Longitude’, ‘Temperature’, ‘Precipitation’, and the site’s ‘Naturalness’, as well as the random effects ‘Country’, ‘Realm’, ‘Species’ ‘Taxonomic group’ and ‘Site’ to control for unobserved heterogeneity and subject these to a statistically well-founded shrinkage. Note that “Country” was excluded due to collinearity with “Realm” $|r| > 0.8$. For both models, we performed a model selection as implemented in the `glmulti` package in R (Calgano et al., 2020) selecting the best predictors and models using the Akaike Information Criterion (AIC). Both final models consisted of the predictors “Year”, “Temperature”, and “Precipitation” and the random effects ‘Realm’ and ‘Site’.

Additionally, we ran a sensitivity analysis to test for any effect of imbalance in the underlying data (i.e., over- and underrepresentation of different clusters) on the results of the meta-regression mixed models. For this, we randomly sampled 10% of time-series within each realm, taxonomic group, and biogeographic region, repeated the random sampling 5 times, and, with those data pooled (without duplicating time-series), re-ran the meta-regression, as described above. Further, we computed outlier and influential case diagnostics (Viechtbauer & Cheung, 2010) using the *influence* function implemented in the `metafor` R package.

Results:

Trends in time-series trajectories

When pooled across taxonomic groups and biogeographic regions, we detected significant declines in the trajectories of non-native freshwater and marine (but not terrestrial) species' abundances (Figure 2a). This pattern was contrasted by an increasing, yet non-significant trend in the abundance of non-native terrestrial species over time (Figure 2a). Visualisation of the individual time-series trends temporally (Figure S1a) indicated that more recent marine and terrestrial time-series had predominantly declining and freshwater trajectories increasing positive trajectories—albeit being facilitated by few particularly long time series (Figure S1b)––with longer time-series indicative of stronger trends (Figure S1b). However, after ~ 2010, both increasing and decreasing trends in all realms levelled off and indicated no further change. These patterns were mainly driven by changes in fish, birds, and aquatic invertebrates, being the only taxonomic groups that showed significant changes (Figure 2b) but were also indicative of the longer duration of marine and terrestrial time-series (Figure S2). Further, we found that across the biotic regions covered by our data, the Atlantic, as well as Continental and North Sea regions all showed significantly decreasing abundance trends (Figure S1b). Mediterranean and Pannonian region trends were increasing and decreasing in abundance, respectively, though non-significant (p>0.05).

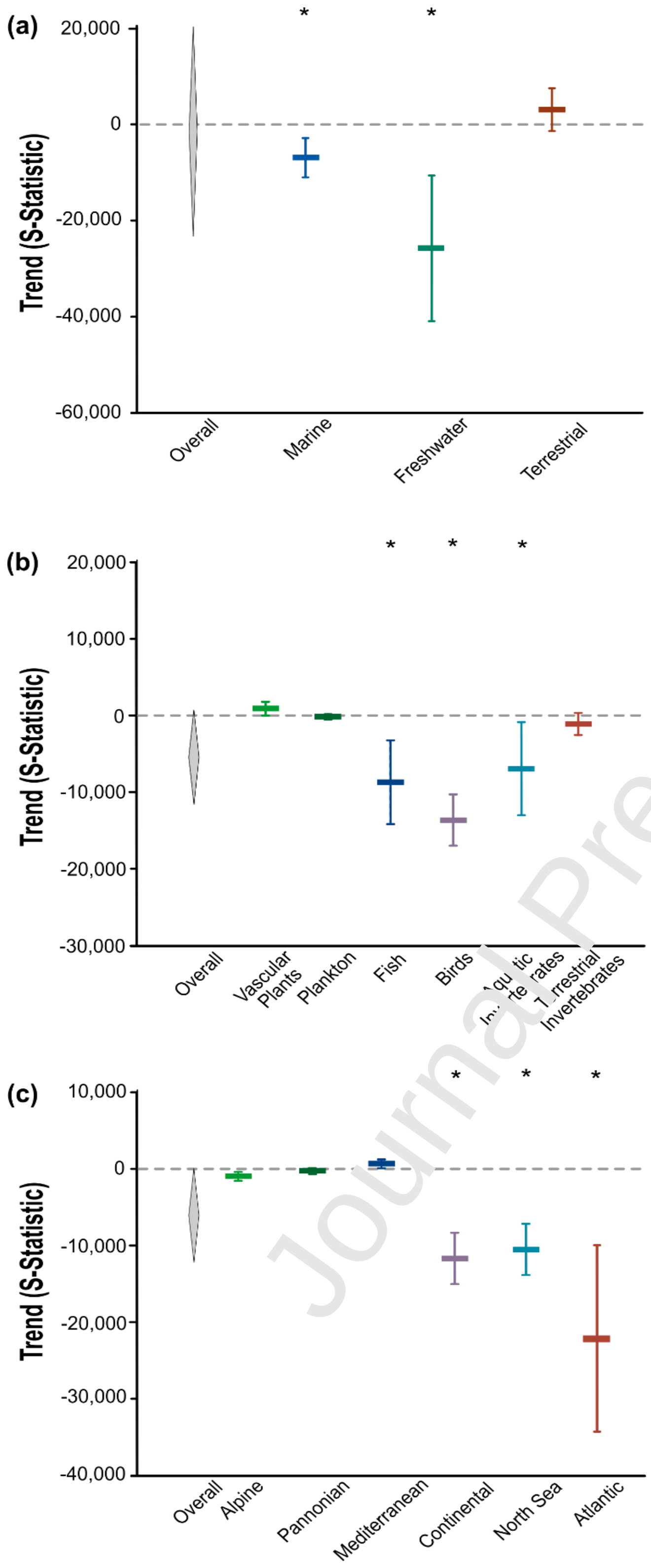

Figure 2: Direction of trends for the non-native species across the monitored realms (a), biotic groups (b), and biogeographic region (c). Results of the applied meta-analysis mixed models (values of S-statistics: model estimated mean, error bar: +/−C.I.) are displayed. Significant trends are highlighted with an asterisk. Number of species-specific time series (n): terrestrial: 37, marine: 17, freshwater: 92, plants: 12, plankton: 4, aquatic invertebrates: 36, terrestrial invertebrates: 18, fish: 60, birds: 16, Alpine: 4, Atlantic: 78, Boreal: 2; Continental: 40, Mediterranean: 7, North Sea: 13, Pannonian: 2.

Species-specific trends

The first records of non-native species in the analysed data were *Anthyllis vulneraria*, *Galium verum*, *Lotus corniculatus*, *Luzula campestris*, *Pimpinella saxifraga*, and *Rumex acetosella*, all firstly recorded in 1921. The most recent species to be recorded in our dataset were *Faxonius limosus* (year: 2013), *Ponticola kessleri* (2013), and *Pseudorasbora parva* (2014). Based on the limited availability of time-series, species detection was estimated to reach saturation (i.e., by becoming asymptotic) after 69.4 years (Figure 3a), whereas the empirical cumulative density function indicated an almost linear increase in non-native species over time since the late 1970s across all realms (Figure 3b).

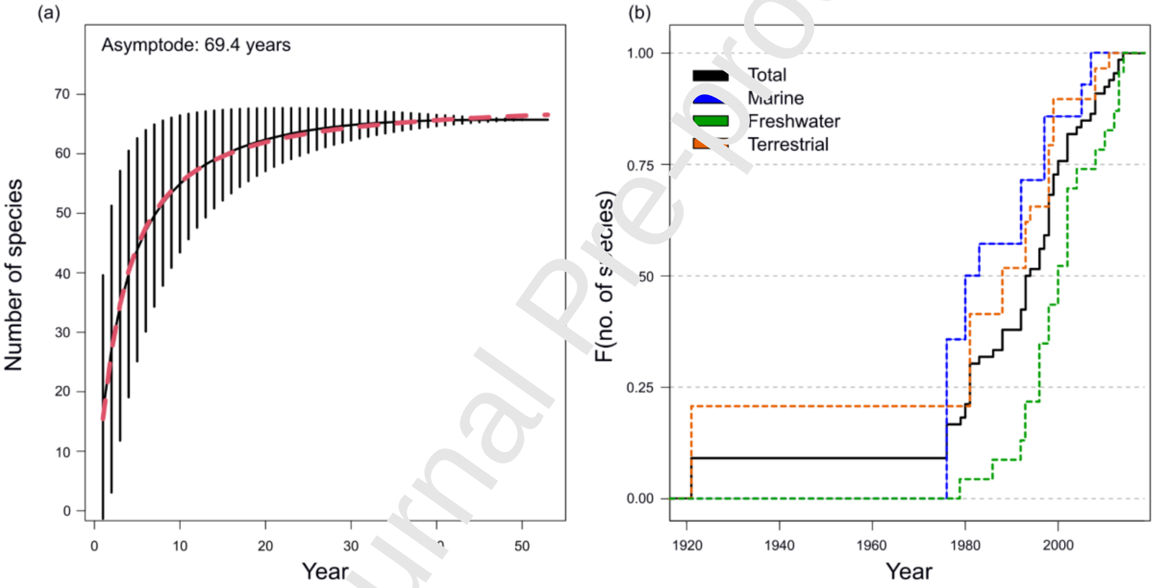

Figure 3: Species accumulation over the duration of monitoring years across all time series (a) and empirical cumulative density function of recorded species over time (b).

Investigating each non-native species time series individually, 15 non-native species abundance trends declined and 14 increased significantly ($p < 0.05$; Figure 4; Figure S3), whereas the majority of time-series exhibited no significant trend in the abundance of non-native species (positive: n=51 time-series; negative: n=61, zero slope; n=5). These trends further expressed considerable differences in the trajectories' variances (median variance of S-statistic: 44.3 ± 963 SD; min: 2.7; max: 5846). Consequently, the meta-regression model suggested low heterogeneity (I^2 = 18.75%) within time-series and trends, resulting in no overall significant trend in the abundance of non-native species (p>0.05). Within the marine realm, nine non-native species increased (including eight significantly), whereas eight species decreased (including three significant declines). In the terrestrial realm, 19 species declined (including five significant declines), and 16 increased (four significantly). Lastly, 62 freshwater species increased (two significantly), and 49 declined (seven significantly; Figure 4).

With regard to the individual taxonomic groups, the abundances of only two plant species expressed significant trends (negative and positive), while the majority were not significant (Figure S4). For plankton, the abundances of three out of four species showed significant trajectories (negative: n=1; positive: n=2; Figure S5). Aquatic invertebrates showed 21 decreasing trends (seven significant) contrasting the 12 positive trends (two significant; Figure S6). Terrestrial invertebrates were similar, with 12 declining trends (three significant) opposing the five non-significant increases (Figure S7). Vertebrates, namely fish and bird species, showed different trends: while only two non-native fish expressed significant trajectories (one positive and one negative out of a total of 60 species; Figure S8), ten out of 16 non-native bird species changed significantly (two negative and eight positive; Figure S9). As a result of this variation in effect direction within each group, the meta-regression model found no overall significant trend across realms, biogeographic regions, or taxonomic groups.

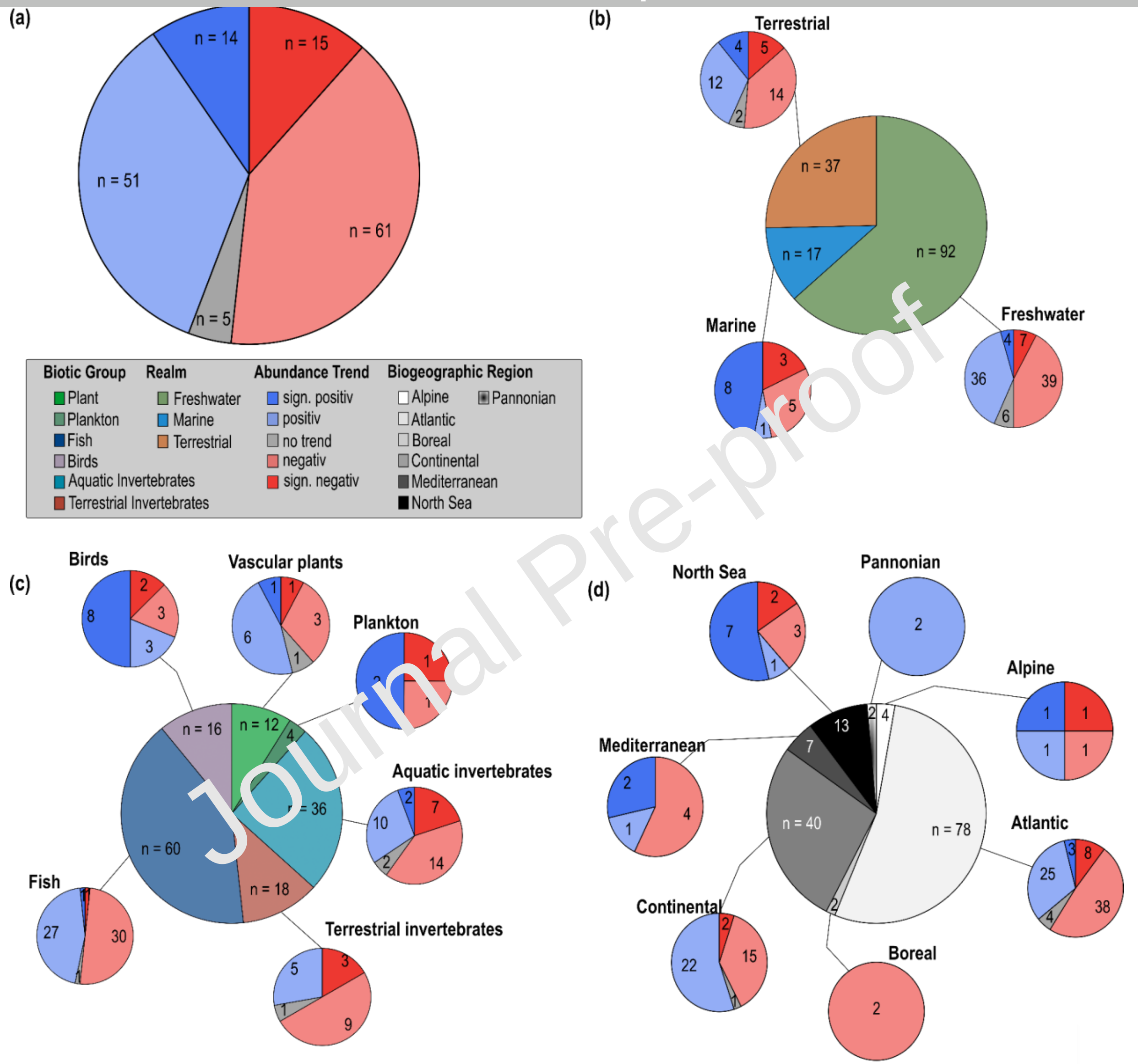

Figure 4: Trends in the abundance of individual non-native species overall (a), across realms (b), their taxonomic distribution (c), and for the biogeographic regions (d) according to the trend described by the Mann-Kendall trends. Positive trends are displayed in blue, negative trends in red, and undirected trends in grey, with darker shades indicating

significance. Number of species-specific time series (n): terrestrial: 37, marine: 17, freshwater: 92, vascular plants: 12, plankton: 4, aquatic invertebrates: 36, terrestrial invertebrates: 18, fish: 60, birds: 16, Alpine: 4, Atlantic: 78, Boreal: 2; Continental: 40, Mediterranean: 7, North Sea: 13, Pannonian: 2.

Meta-regression model trend drivers

Considering all individual non-native species abundance trends, we identified shifts in the rate changes of temperature and precipitation, i.e., major climatic drivers, which were both positively increasing and identified to be positively correlated to the changes in abundance of non-native species (Table 2). These two factors were identified to be the only significant predictors of changing trajectories in the abundance of non-native species.

Table 2: Influence of climatic trends and site characteristics on non-native species' trends considering all species' individual trends. Overall model: [τ^2: estimate of total amount of heterogeneity; τ: sqrt of the estimate of total heterogeneity; I^2: % of total variability due to heterogeneity of effects; H^2: total variability / within-study variance; QE: residual heterogeneity; QM: heterogeneity of moderators]; Predictors [se: standard error; z_{val}: number of standard deviations from the mean; p_{val}: level of significance; ci.lb: lower corresponding 95% confidence interval; ci.ub: upper corresponding 95% confidence interval].

Predictor	**τ^2**	**τ**	**I^2**	**H^2**	**$QE_{(df)}$**	**$QM_{(df)}$**
	3.64 ± 2.02	1.91	18.74 %	1.23	**69.73**	**53.36**
	Estimate	**se**	**z_{val}**	**p_{val}**	**ci.lb**	**ci.ub**
Latitude	-0.5841	0.7282	-0.8022	0.4224	-2.0113	0.8430
Longitude	0.6618	0.5749	1.1510	0.2497	-0.4651	1.7886
Temperature trend	5.9436	2.9301	2.0284	**0.0425**	0.2007	11.6865
Precipitation trend	16.3452	2.8999	5.6364	**<.0001**	10.6614	22.0290
Mean temperature	-0.2627	0.8565	-0.3067	0.7590	-1.9414	1.4159
Mean precipitation	0.0831	0.5674	0.1464	0.8836	-1.0289	1.1950
Naturalness	-0.4946	0.4739	-1.0438	0.2966	-1.4235	0.4342
StudyLength	-1.1647	0.7069	-1.6476	0.0994	-2.5503	0.2208

The meta-regression models applied to individual realms or taxonomic groups indicated that only precipitation was significantly positively related to abundance trends of terrestrial and freshwater non-native species (Figure 5a; Table S2). There were no significant predictors of the rate change in marine non-native species abundance.

For non-native fishes, the model identified that abundance changes were significantly negatively correlated with mean temperature (Figure 5b). Increases in the temperature and precipitation trends, however, affected the change of the abundance of non-native aquatic invertebrates positively, whereas terrestrial invertebrates responded significantly negatively to temperature trends, but significantly positively to naturalness (Table S3). There were no significant predictors of invasive bird or plant trends (Figure 5b).

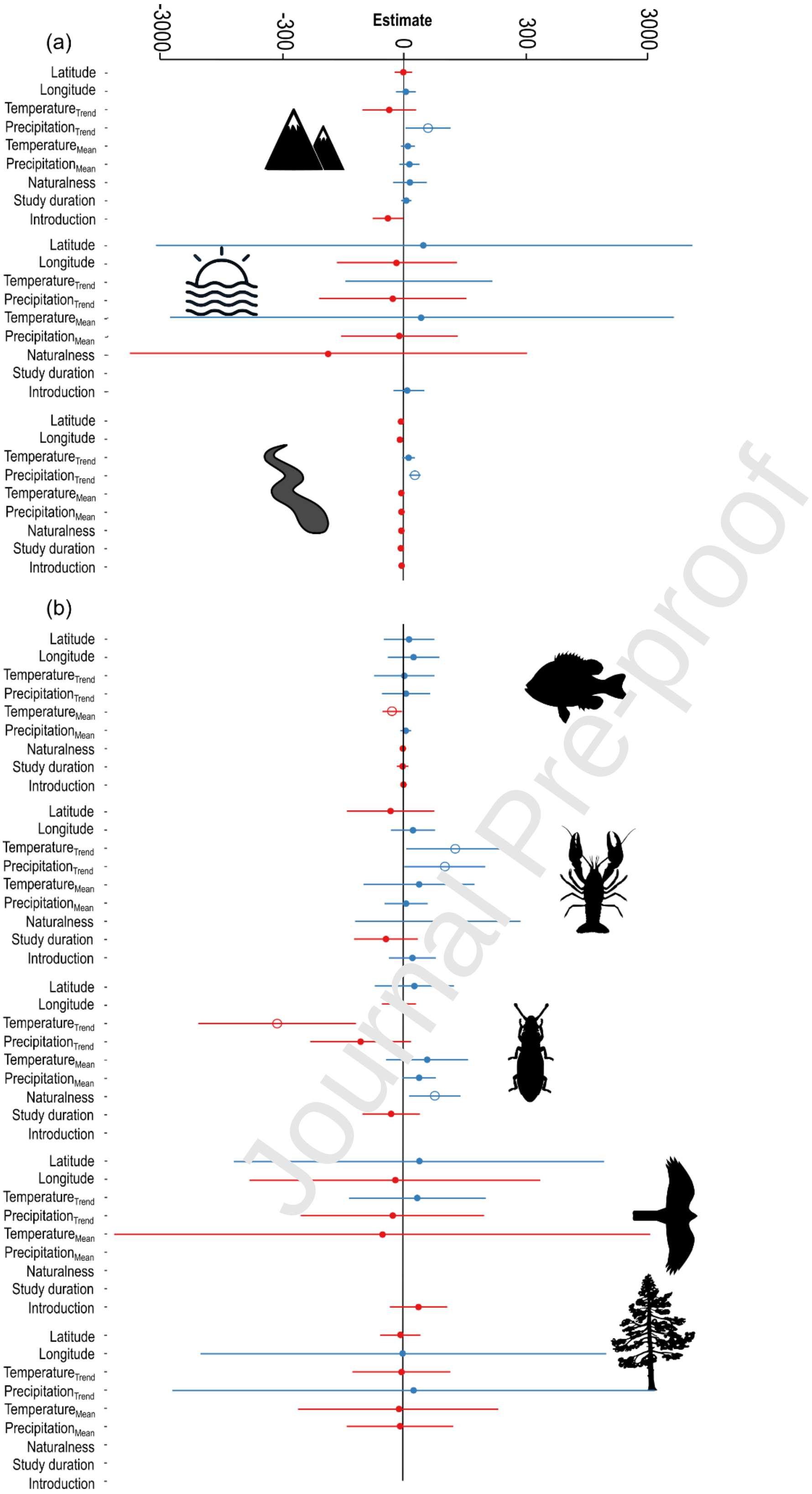

Figure 5: Influence of climatic trends and site characteristics on trends across terrestrial, marine, and freshwater environments (a) and taxonomic groups (b; fish, aquatic invertebrates, terrestrial invertebrates, birds and vascular plants) according to the meta-regression models. Missing predictors result from insufficient information within the relevant groups. Filled dots refer to no significant predictors (p>0.05), while hollow dots refer to significant predictors (p<0.05).

Across all biogeographic regions, only in the Atlantic and Continental regions significant predictors were identified, namely that sites with a positive precipitation increase tended to have higher abundances in the Atlantic region whereas with a decreasing average temperature tended to have lower abundances in the Continental region (Figure 6). All other predictors for all other regions were non-significant (*p*>0.05).

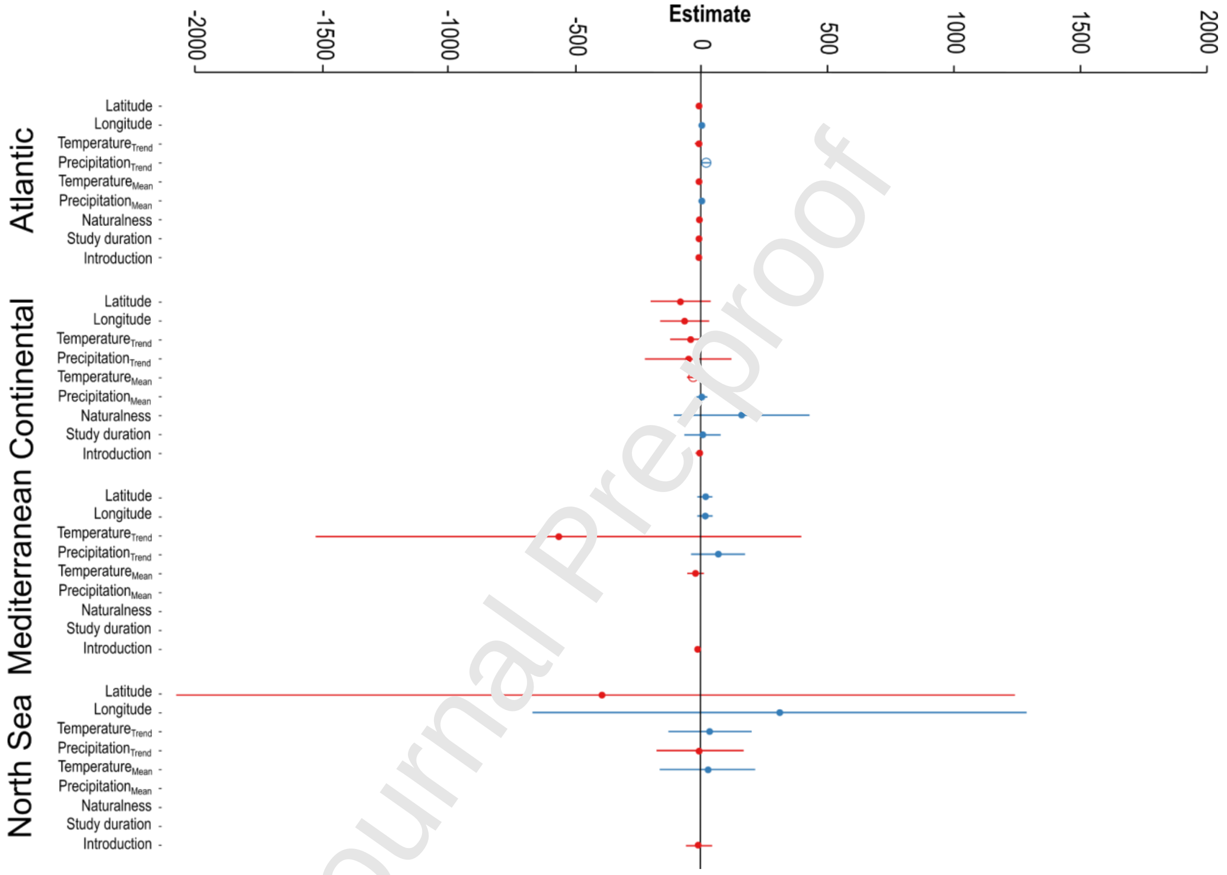

Figure 6: Influence of climatic trends and site characteristics on trends across biogeographic regions according to the meta-regression model. Missing predictors result from insufficient or redundant information within the relevant groups. Models could only be applied for four of the seven biogeographic regions. Filled dots refer to no significant predictors (p>0.05), while hollow dots refer to significant predictors (p<0.05).

After model selection, the GLMMs applied for “positive trends” identified “Year”, “Longitude”, and “Latitude” to significantly positively affect the abundance increase of non-native species, while for “negative trends”, “Longitude” and “Temperature”, predicted an increase in the abundance, while the trend over time (“Year”) was a significant negative predictor (Figure 7). These models also suggest that the magnitude in response is by far larger for species with negative trends, suggesting that the increase in positive trends stems from spatially structured, non-climatic drivers, while the increase in negative trends is mainly correlated with temperature.

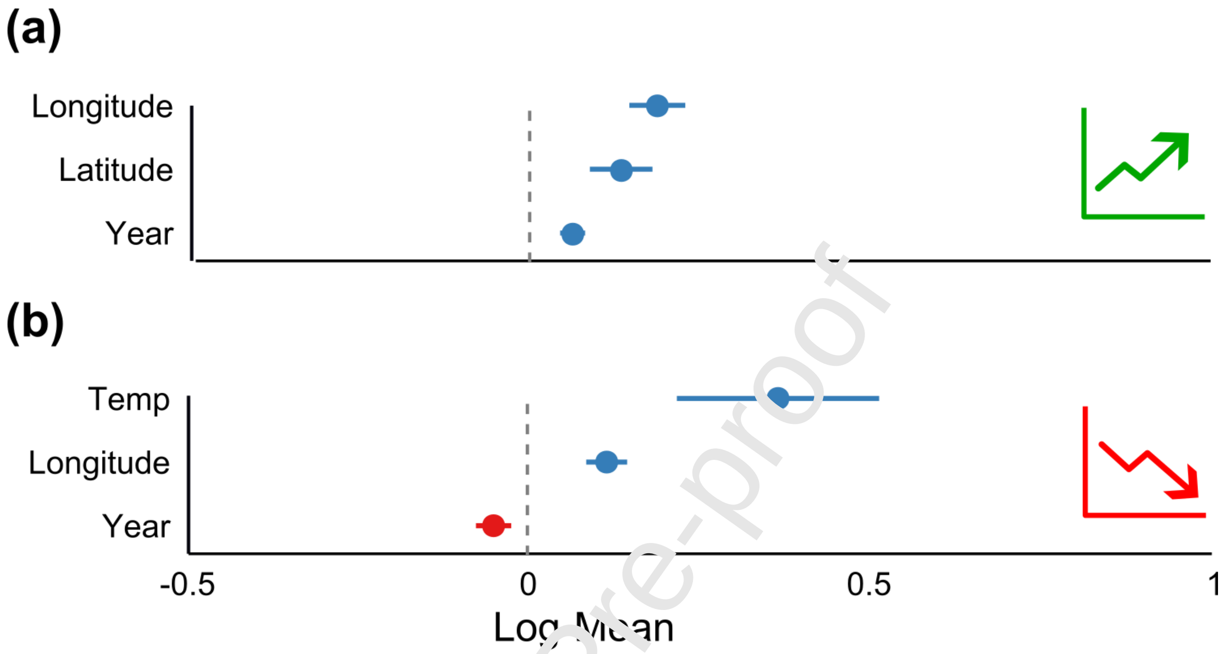

Figure 7: Estimates of significant predictors for the non-native species abundance within time series that were identified as showing a positive trend (a) and those identified to show negative trends (b).

From sensitivity analyses of the individual time-series based meta-regression, 14 of the 15 additional meta-regression conducted as a means to detect if the overall trend was subject to outliers, i.e., individual time-series, resulted in no significant trend, therefore confirming the results obtained for the full analysis as presented above. Contrastingly, the computed diagnostics (Figure S10) identified 16 time-series to have large residual deviances that may be considered outliers, from which three of those time-series were indicated to have a strong influence on the results.

Discussion:

Divergent patterns in invasion dynamics were exhibited in the present study among environmental realms, taxonomic groups, and biogeographic regions using long-term time-series, thereby confirming our hypotheses *i-iii*). Our results suggest that non-native freshwater and marine taxa (i.e., fish, birds and invertebrates) expressed decreasing abundance trends over time when pooled at the European level. At the level of individual time-series, occurrences especially of freshwater taxa appeared later compared to those in marine and terrestrial time-series, which generally showed decreasing trends over time. This difference was likely induced by a later onset of long-term monitoring in freshwater environments, resulting in shorter overall monitoring durations and a potential "perception bias", as non-native species in freshwater environments have typically been less recorded than terrestrial species in the last decades due to the inconspicuous nature of aquatic environments (Estévez et al., 2015; Kapitza et al., 2019; Coughlan et al., 2020; Cuthbert et al., 2021).

We also found large differences in trends of taxonomic groups (i.e., their slope). Significantly decreasing trends were exhibited in fish, birds, and aquatic invertebrates when pooled, thus mirroring the trends from the comparisons across realms. Birds showed the strongest decrease in trends. On the other hand, trends of non-native plants were not significant, albeit being positive. While we are not able to fully explain the stagnating trends with the unbalanced representation of taxonomic groups in our dataset (higher representation of fish and invertebrates), several reasons that can affect trends may be brought into perspective. These are, for instance, (a) diverse introduction histories of the varying species within the respective countries known to modulate establishment and population dynamics (Kulhanek et al., 2011; Pitt et al., 2017), (b) the varying and intertwined effects of drivers and stressors (Soto et al., 2023), and ultimately (c) timings in the implementation of non-native species management strategies (Mehta et al., 2017). Although the time a species was introduced into a respective country was not a significant predictor in our analyses, it should be noted that it could have a considerable effect on individual populations if the introduction coincided with times of favourable conditions or during a period with low investment in invasive species monitoring or prior to any government regulation. In addition, delays should be also considered in the detection of non-native species at regional and local scales, which may affect the interpretation of broader trends. The invader's introduction history may therefore play a significant but indirect role, as suggested by our results, showing that longer (and thus possibly older) time-series were indicative of stronger abundance trends. These results may, however, also indicate that short or recent time-series were inadequate in capturing the full species population dynamic (Lockwood et al., 2007; Haubrock et al., 2022b).

Conservation efforts significantly increased in the second half of the 20th century. This was well represented in our dataset. Freshwater environments, especially in Central Europe, have been subject to heavy anthropogenic modifications, such as riverbed and channel straightening (Vörösmarty et al. 2004). These modifications spiked in the early to mid-1900's, consequently resulting in more scientific attention in the second half of the 20th century, leading to gradually increasing monitoring and management (i.e. restoration efforts; Staehr et al., 2012). Similarly, greater numbers of freshwater time-series tended to start later (usually after 2000) compared to those of terrestrial and marine ones. This observed shift towards an increasing focus of monitoring efforts towards freshwater environments could have led to the observation of an increasing presence of non-native species, which is noteworthy, because such trends can affect the assessments of biodiversity changes (Pilotto et al., 2020). We further found that with the increasing lengths of time-series, trends were increasingly positive, indicating that non-native species abundances increase particularly at early invasion stages (Lockwood et al., 2007; Hui & Richardson, 2017), a common pattern in meta-regression (Nakagawa et al., 2022).

Despite considerable heterogeneity of the underlying data, three of the seven regions showed significant declines in the abundance of non-native species, whereas no region expressed significantly positive inclines. These were also the most representative regions as they had the highest number of available time series. Therefore, it is possible that regionally, non-native species are showing signs of declining abundances, albeit when based on individual time-series (i.e., without being pooled), we found no significant abundance increase in any taxonomic group, biogeographic regions or realms. This discrepancy highlights the importance of both localised monitoring as well as the scale and resolution of the conducted analysis, as our results suggest that population dynamics are localised, with some populations increasing and others decreasing, which in turn balance the diverging effects.

Nevertheless, we note that this result is purely based on the sites monitored in this study, and it does not account for further non-native species spread and trends of other sites that were not monitored.

When based on individual time-series, we identified significant effects of climatic trends, i.e., precipitation and temperature regime shifts. The effects of climatic trends, however, were likely to be stronger in freshwater environments than marine environments (Ficke et al., 2007; Woodward et al., 2010), as for instance precipitation only affected terrestrial and freshwater realms. Temperature changes in particular can facilitate ecological shifts in freshwater ecosystems via modulating the oxygen content (Burger et al., 2007), present a constraint for native species, pose a limiting barrier (Haase et al., 2019), or benefit non-native species directly (see e.g., Britton et al., 2010; Zerebecki & Sorte, 2011). However, temperature was not significant at the level of individual realms here. Precipitation increases, in turn, can affect the runoff in freshwater environments, leading to higher flows, often observed as a result of climate change (Baranov et al., 2020). Depending on the realm, decreases in precipitation can also lead to changes in nutrient availability in both terrestrial (Charles & Dukes, 2009) and freshwater environments (Dodds et al., 2019).

It is often reasoned that climatic drivers are the most relevant in determining an introduced species' success to establish and its successive potential for boom-bust population dynamics (Früh et al., 2012; Strayer et al., 2017). In line with this, we identified differing implications from the changes in the average annual temperature across the monitoring period: positive increases in temperature and precipitation predicted increases in the abundance of aquatic invertebrates, whereas a decrease in the average temperature over the monitoring period significantly predicted a decline in the abundance of non-native fish, underlining that some non-native species benefit from increasingly rapid environmental (or climatic) changes (Sutherst, 2000). A substantial share of our sites belonged to the LTER-Europe network (Mirtl et al. 2018), i.e., sites that can be considered more pristine and less anthropogenically affected due to past and ongoing efforts in biodiversity conservation (Haubrock et al., 2023), as shown by the high degree of 'naturalness' (Pilotto et al., 2020). Non-native terrestrial invertebrates also seemingly benefitted from high naturalness, potentially conferred by a reverse scenario than postulated by the 'biotic resistance' (Elton, 1958; Byers & Noonburg, 2003) and 'invasion meltdown' theories' (Silberloff & Holle, 1999; Von Holle, 2011). These theories describe that diverse, natural environment conditions present a higher resistance towards invasions due to a higher potential for competition from the resident native species, whereas previous or past invasions can lower this resistance towards future invasions (Catford et al., 2009; Jeschke, 2014).

While only indirectly included in our analysis through the use of the site’s 'naturalness’, it has often been shown that environmental degradation and pollution have facilitating effects on non-native species in aquatic and terrestrial environments (Davis et al., 2000; Uehara-Prado et al., 2009; Ellis, 2011). Nevertheless, our results have implications for management strategy towards non-native species. There are considerable taxonomic differences leading towards the applicability of management strategies: for example, non-native birds—which were found to be showing the strongest declines—are comparably more mobile than plants, making their management more challenging (Zarnetzke et al., 2010; Strubbe et al., 2011) due to high mobility and limited means of public perception (Verbrugge et al., 2013).

Conclusion:

We highlight the context-dependency across realms, taxonomic groups and regions in biological invasion dynamics. Having identified several individual time-series to significantly increase or decline, but no overall significant trend across realms, taxonomic groups, or regions, underlines the importance to portray invasions not only as a spatially broad problem, but also to manage them locally, as the economic or ecological impact and dynamics of non-native species populations are generally realised on the local level. Considering how efficient management can lower the long-term effects (in particular the economic and ecological impacts; Leung et al., 2002; Cuthbert et al., 2021), our results showing increasing abundances with increasing duration of monitoring suggest that the lack of early applied management could ultimately lead to often unhindered population growth. Our results therefore underline the need for improved implementation of non-native species management across realms, as well as the utility and importance of long-term monitoring initiatives. Our analysis has some limitations, mostly related to the availability and onset of time series. Although the duration of the time series was sufficient to adequately capture present non-native species, the ECDF revealed an increasing number of non-native species across all three major realms to a similar degree, which was limited by the availability of time series. Indeed, while the overall coverage of the original data was strong (Pilotto et al., 2020), the 150 non-native species' time series across Europe did not evenly cover all regions and environmental gradients, arguably partly resulting from regional monitoring gaps. This gave rise to a few influential time-series with large residuals affecting the results. Further, our analysis mostly covered climatic variables over comparatively short periods, considering that the effects of climate on biodiversity can only be determined by time-series of 30 years or longer (McMichael et al., 2004). Otherwise, important drivers often postulated to drive population dynamics (i.e., local site-specific dynamics) could not be included due to limited data availability. This rendered our results as nearly exclusively non-significant, whereas changes in disturbance, land-use type, and biotic interactions might have had stronger impacts than climatic trends if these data were available.

Author contributions

PJH and PH conceived the study. PH, FP, HV provided data. PJH and IS performed the analyses. PJH and RNC wrote the first draft. FP, PJH, and IK conceptualised the analyses. FP, HS, IK and IS commented and contributed to the writing.

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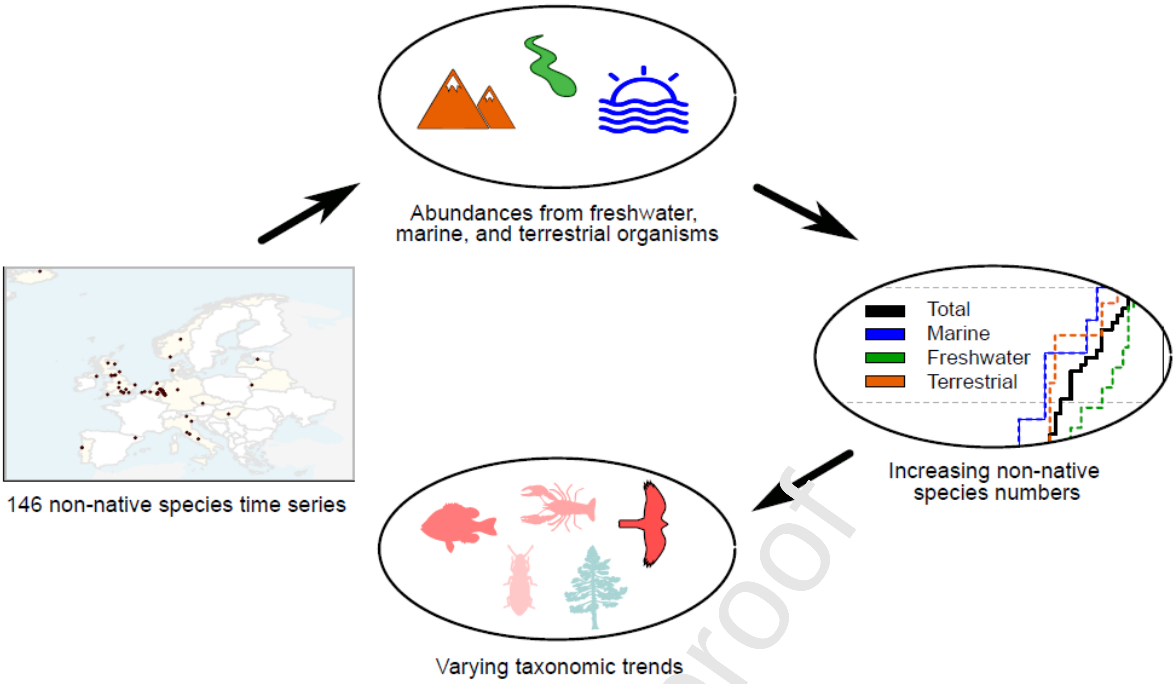

Graphical Abstract

Highlights

- Biological invasion rates are increasing with human vectors and climate change.
- Analyses of non-native species abundance trends are still scarce due to data gaps across realms, taxa and regions.
- Abundance trends of non-native species in Europe are highly variable among contexts.
- Temperature and precipitation change are important predictors of abundance trends.