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Research

Effects of nonnative species on the stability of riverine fish communities

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Ecography
00: 1–11, 2020
doi: 10.1111/ecog.04985

Subject Editor: Luis Mauricio Bini
Editor-in-Chief: Miguel Araújo
Accepted 8 April 2020

Despite the increasing ubiquity of biological invasions worldwide, little is known about the scale-dependent effects of nonnative species on real-world ecological dynamics. Here, using an extensive time series dataset of riverine fish communities across different biogeographic regions of the world, we assessed the effects of nonnative species on the temporal variability and synchrony in abundance at different organizational levels (population, metapopulation, community and metacommunity) and spatial scales (stream reach and river basin). At the reach scale, we found that populations of nonnative species were more variable over time than native species, and that this effect scaled up to the community level – significantly destabilizing the dynamics of riverine fish communities. Nonnative species not only contributed to reduced community stability, but also increased variability of native populations. By contrast, we found no effect of nonnative species dominance on local interspecific synchrony among native species. At the basin scale, nonnative metapopulations were again more variable than the native ones. However, neither native metapopulations nor metacommunities showed differences in temporal variability or synchrony as nonnative species dominance increased basin-wide. This suggests a 'dilution effect' where the contribution to regional stability of local native populations from sites displaying low levels of invasion reduced the destabilizing effects of nonnative species. Overall, our results indicate that accounting for the destabilizing effect of nonnative species is critical to understanding native species persistence and community stability.

Keywords: abundance fluctuations, biological invasions, interspecific synchrony, metacommunity, temporal variability, time-series

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Introduction

Knowledge of the mechanisms controlling the stability of ecological communities is a long-standing challenge in ecology (MacArthur 1955, May 1972, Pimm 1984) and remains central to inform ecosystem management in a changing world (Tilman et al. 2014, Wilcox et al. 2017). Both field and experimental studies suggest that community stability depends largely on the ecological properties (species composition and diversity) of the system being examined (Ives and Carpenter 2007, Donohue et al. 2013, 2016). Yet, it is also increasingly apparent that human-mediated stressors (e.g. land use change, nonnative species introductions) can also affect the stability of real-world communities – the patterns and mechanisms of which are largely not known and are currently an active area of scientific investigation (MacDougall et al. 2013, Hautier et al. 2015, Blüthgen et al. 2016).

Species invasions are expected to affect community variability (i.e. a measure of instability commonly quantified by the coefficient of variation in abundance or biomass across years) via changes in species composition and dominance (Ives and Carpenter 2007, Valone and Balaban-Feld 2018). However, less well recognized is that nonnative species may stabilize or destabilize community dynamics via their effects on population variability and the degree of synchrony in temporal fluctuations among species (Báez and Collins 2008, Wilsey et al. 2014). Theory predicts that smaller population sizes are associated with higher demographic stochasticity, and thus, temporal fluctuations and asynchrony in population dynamics are expected, particularly during the initial stages of invasion (Fauvergue et al. 2012, Trigal and Ruete 2016). When already established, nonnative species are also less likely to be synchronized with local processes related to resource availability and biotic interactions (Melbourne et al. 2007, Ruhi et al. 2015). Studies on stream fish communities suggest, for example, that interactions between native and nonnative species can be more intense in hydrologically less variable streams and rivers (Moyle and Light 1996, Gido et al. 2013) or within rivers in hydrologically stable flow periods, because nonnative species are less adapted to variable hydrologic conditions of the recipient habitat (Marchetti and Moyle 2001, Eby et al. 2003). This may result in stronger asynchrony among different co-occurring species at the local scale, as well as across metapopulations at regional scales.

The effects of nonnative species on the temporal variability and synchrony of native species are complex. Nonnative species can induce large fluctuations in the dynamics of native species via competitive or predatory interactions, which may in turn increase the temporal variability of aggregate community properties such as total abundance (Báez and Collins 2008). Moreover, the introduction of nonnative species can generate compensatory dynamics in which asynchrony among populations ultimately promote stability at the community level (Micheli et al. 1999, Tilman 1999, Gonzalez and Loreau 2009). In a manipulated grassland experiment, nonnative-dominated communities were as stable as their native counterparts, but with distinct mechanisms driving this stability: invaded communities were dominated by a few very stable species whereas communities composed only of native species had high response diversity, leading to asynchronous species dynamics and high temporal stability in total community biomass (Wilsey et al. 2014). Taken together, several mechanisms can be expected to operate independently or in concert to affect stability in invaded communities. Yet, to date, limited availability of long-term and spatially extensive datasets makes it challenging to draw inferences regarding these mechanistic pathways in heterogeneous, natural systems.

Empirical studies on the effects of nonnative species on community stability have been predominantly local in scale, although recent analytical frameworks emphasize the need to explore temporal variability across a variety of organizational levels (e.g. populations of species, communities) and spatial (i.e. local versus regional) scales (Wang and Loreau 2014, Wilcox et al. 2017, Wang et al. 2019). Under these frameworks, 'community variability' can be expressed as the product between average 'population variability', and the degree of synchrony among populations of the species present in the local community ('local interspecific synchrony'). 'Metapopulation variability' and the degree of synchrony among different metapopulations ('regional interspecific synchrony') then scale up to determine 'metacommunity variability' at the regional scale (Fig. 1). Temporal variability and synchrony can also vary in response to various ecological factors, as mediated by the effects of species diversity at both local (e.g. α-diversity) and regional (e.g. γ-diversity) scales (Wilcox et al. 2017, Wang et al. 2019). Although species diversity, temporal variability and synchrony are shown to interact at a variety of spatial scales to determine overall stability of communities and metacommunities (McCann 2000, Loreau and de Mazancourt 2008, Wilcox et al. 2017), the effects of nonnative species on temporal stability – and the scale-dependence of such impacts – remain largely unknown.

Here, we leverage long-term abundance time series of riverine fish communities across the world to examine the effect of nonnative species on community and metacommunity variability. Riverine systems are ideal systems to empirically test the effects of nonnative species on temporal variability. Biological invasions are frequently reported from both intentional and unintentional introductions resulting from various activities such as pet trade, recreational fishing, aquaculture practices or commercial shipping (Gozlan et al. 2010). As a result, nonnative fishes are numerous and are even dominant in many river basins around the world (Leprieur et al. 2008). In addition, the effects of nonnative species on native assemblages have long been studied and are thought to represent a key threat to the diversity and stability of these systems (Clavero and Garcia-Berthou 2005, Strayer 2010, Cucherousset and Olden 2011). Our study posed the following questions: 1) are the dynamics of

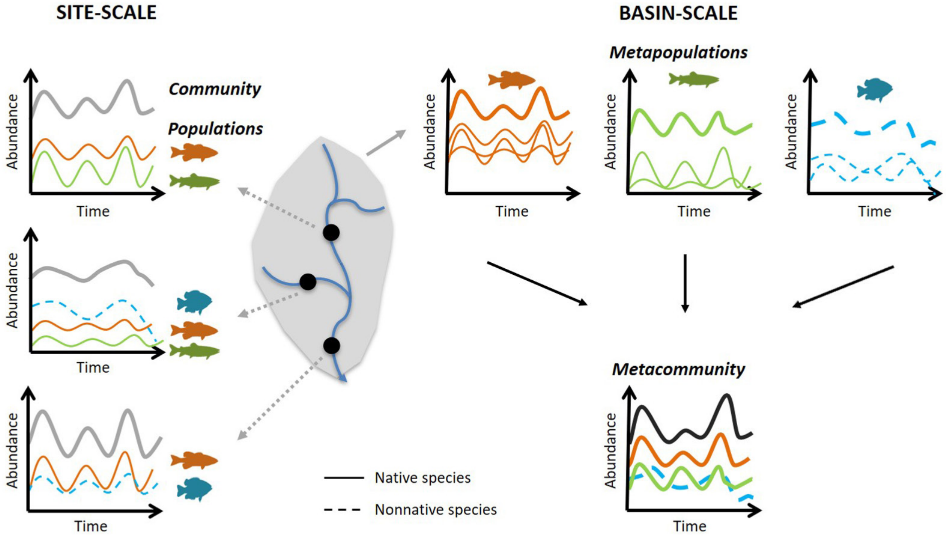

Figure 1. Conceptual figure illustrating temporal variability and synchrony in abundance for a theoretical stream fish metacommunity. At the site scale (stream reach; left panel), 'population variability' can be defined as the temporal variation in population abundance of native (solid colored lines) or nonnative (dotted colored lines), and 'community variability' as the temporal variations in total community abundance of the species present in the local community (thick grey lines). Likewise, site-scale 'local interspecific synchrony' can be defined as the synchrony in abundance among populations of the species present in the local community. At the river basin scale (here, watershed; right panel), 'metapopulation variability' can be defined as the temporal variations in total metapopulation abundance (thick colored lines) and 'metacommunity variability' as the temporal variations in total metacommunity abundance of the species present in the regional metacommunity (black thick line). Similarly, basin-scale 'regional interspecific synchrony' can be defined as the synchrony among different metapopulations present in the regional metacommunity. Population variability and interspecific synchrony scale up to determine community variability at the site scale; similarly metapopulation variability and regional interspecific synchrony scale up to determine metacommunity variability at the basin scale. Nonnative species are expected to influence temporal variability and synchrony at different organizational levels, but little is known about these scale-dependent effects.

nonnative species more variable and asynchronous than the native species? 2) Do nonnative species influence local and regional-scale stability via their effects on temporal variability and/or the degree of synchrony among native species? 3) How do the aforementioned effects of nonnative species scale up from local- to regional-scales (i.e. stream reach versus river basin)?

First, we predicted higher temporal variability and asynchrony of nonnative species, because these species may not be at 'equilibrium' with their new environment and might be subject to higher demographic stochasticity (Strayer et al. 2006, Václavík and Meentemeyer 2012, Ricciardi et al. 2013). Second, we hypothesized that nonnative species increase population variability over time and/or suppress population abundances of native species through competition or predation (Gozlan et al. 2010, Cucherousset and Olden 2011). We also hypothesized that population-level effects of nonnative species on the temporal stability of native species scale up to the community and metacommunity levels, causing higher variability in (meta)communities with increasing nonnative species dominance. Alternatively, we expected compensatory dynamics in native species in response to nonnative species (Gonzalez and Loreau 2009) to act as an opposite force so that aggregate (meta)community properties (i.e. total abundance) are stabilized via asynchronous (meta)population dynamics (Micheli et al. 1999).

Material and methods

Fish data

We assembled long-term (≥ 10 yr) fish monitoring time series from 27 river basins distributed among Europe, North America and Australia (Fig. 2, Supplementary material Appendix 1 Table A1). Each selected basin contained at least ten sampling sites (i.e. stream reach; mean = 25.78, range = 10–63), with the sites forming a gradient in the relative abundance of nonnative species (Supplementary material Appendix 1 Table A1). All surveys involved standardized protocols through time, where sampling occurred during low flow periods (summer–autumn) and predominantly using electrofishing methods (Oberdorff et al. 2001, Pont et al. 2006). Altogether 696 sites with local communities composed of 238 fish species were used for the study (min 0.8–max 22.6 species per site averaged across years). Species origin status (native versus nonnative) was defined at the basin scale following Tedesco et al. (2017).

Temporal variability, synchrony, diversity and nonnative species dominance

We calculated temporal variability and synchrony across spatial scales (site and basin) and organizational levels (population, community, metapopulation, metacommunity;

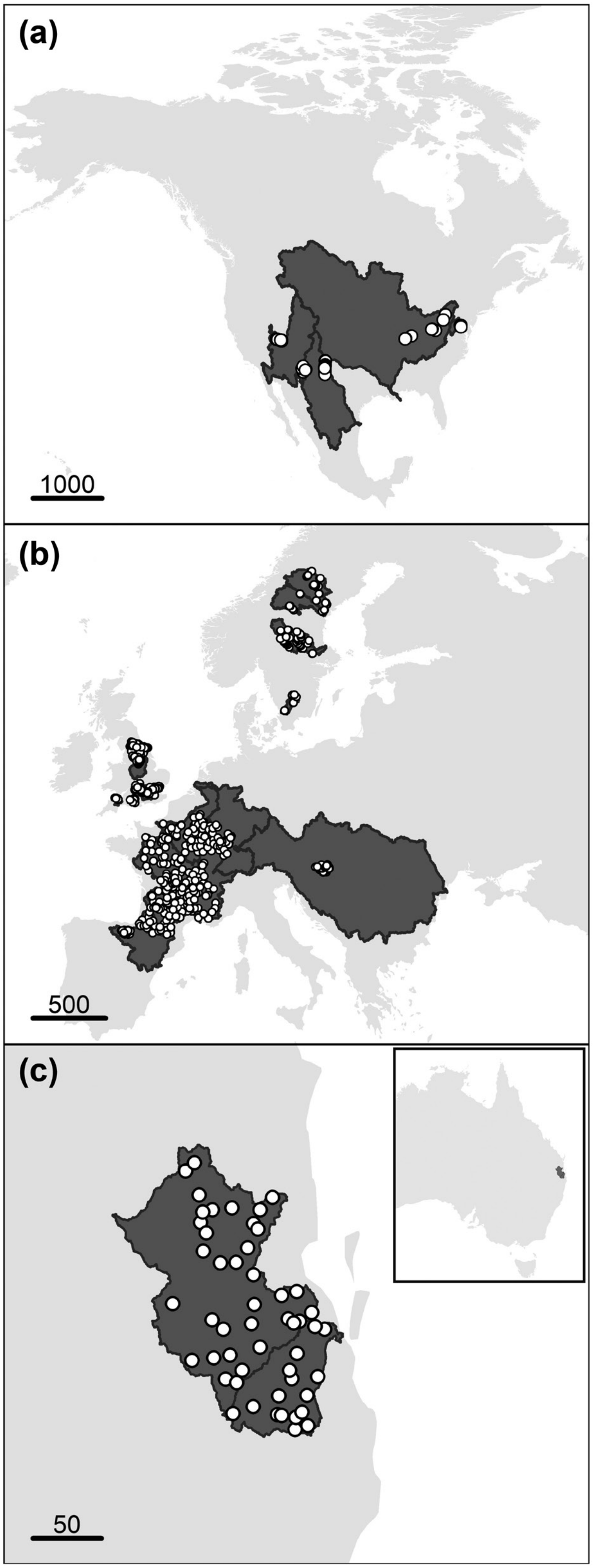

Figure 2. Map showing the studied sites (white dots) and associated basins (dark grey areas) located in (a) North America, (b) Europe and (c) Australia.

Fig. 1). Temporal variability at a given level of organization was defined as the coefficient of variation (CV) in abundance across years, and synchrony as the similarity of temporal fluctuations in abundance using a square-root version of Loreau and de Mazancourt's definition (Loreau and de Mazancourt 2008).

More specifically, we denoted $X_{i,s}(t)$ the abundance of species *i* in site *s* in year *t* within a given basin *b*, and used the subscripts *P* and *C* to represent 'population-level' and 'community-level', respectively. At the site scale, we calculated 'population CV' as the weighted average CV of population abundance ($CV_{i,s}$) of the species present within the local community in site *s* as:

$$CV_{P,s} = \sum_{i} CV_{i,s} \times \frac{\mu_{i,s}}{\mu_{\Sigma,s}}$$

where $CV_{i,s} = \sqrt{v_{ii,ss}} \big/ \mu_{i,s}$ with $\mu_{i,s} = \sum_{t=1}^{T} Xi,s(t) \big/ T$ and $v_{ii,ss}$ are the temporal mean (over *T* years) and variance of population abundance of species *i* in site *s*, respectively, and $\mu_{\Sigma,s} = \sum_{i} \mu_{i,s}$ is the temporal mean of total community abundance (i.e. sum of population abundances across species *i*) in site *s*. We also calculated 'community CV' as the CV of total community abundance among the species present within the local community in site *s* as:

$$CV_{C,s} = \frac{\sqrt{v_{\Sigma,ss}}}{\mu_{\Sigma,s}}$$

where $v_{\Sigma,ss}$ is the temporal variance of total community abundance in site *s*.

At the basin scale, we calculated 'metapopulation CV' as the weighted average CV of metapopulation abundance ($CV_{i,b}$) of the species present within the regional metacommunity in basin *b* as:

$$CV_{P,b} = \sum_{i} CV_{i,b} \times \frac{\mu_{i,\Sigma}}{\mu_{\Sigma,\Sigma}}$$

where $CV_{i,b} = \sqrt{v_{ii,\Sigma}} \big/ \mu_{i,\Sigma}$ with $\mu_{i,\Sigma} = \sum_{s} \mu_{i,s}$ and $v_{ii,\Sigma}$ are the temporal mean and variance of metapopulation abundance of species *i* in basin *b*, respectively, and $\mu_{\Sigma,\Sigma} = \sum_{i,s} \mu_{i,s}$ is the temporal mean of the total metacommunity abundance (i.e. sum of population abundances across species *i* and sites *s*) in basin *b*. We also calculated 'metacommunity CV' as the CV of total metacommunity abundance of the species present within the regional metacommunity in basin *b* as:

$$CV_{C,b} = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\mu_{\Sigma,\Sigma}}$$

where $v_{\Sigma,\Sigma}$ is the temporal variance of the total metacommunity abundance in basin *b*.

Similarly, we defined synchrony at the site and basin scales. At the site scale, we calculated 'local interspecific synchrony' as the synchrony in abundance among the species present within the local community in site *s* as:

$$\varphi_s = \frac{\sqrt{v_{\Sigma,ss}}}{\sum_i \sqrt{v_{ii,ss}}}$$

At the basin scale, we calculated 'regional interspecific synchrony' as the synchrony in abundance among the metapopulations present within the regional metacommunity in basin *b* as:

$$\varphi_b = \frac{\sqrt{v_{\Sigma,\Sigma}}}{\sum_i \sqrt{v_{ii,\Sigma}}}$$

We also computed alpha and gamma diversity as the mean species richness across years at the site and basin scale, respectively. All the metrics were tabulated for the native species only after excluding species of nonnative origin and for the entire community/metacommunity (both native and nonnative species pools). Lastly, we computed 'nonnative species dominance' as the mean ratio of total nonnative abundance to total community (site-level, range = 0–0.93) or metacommunity (basin-level, range = 0.0002–0.30) abundance. Time series of fish abundance together with the calculated metrics for two exemplar sites and basins are illustrated in Supplementary material Appendix 1 Fig. A1–A2.

Statistical analyses

Contribution of natives and nonnatives to temporal variability and synchrony

We tested whether the contribution of nonnative species to temporal variability and synchrony differ from native species at each level of organization. To do so, we first compared (site-scale) population CV and (basin-scale) metapopulation CV between native and nonnative species. Second, we assessed the contribution of individual species (native or nonnative) to community (site-scale; $\text{Contrib}_{i,s}$) and metacommunity (basin-scale; $\text{Contrib}_{i,b}$) dynamics by excluding one species at a time and recalculating the selected metrics (local interspecific synchrony, community CV, regional interspecific synchrony, metacommunity CV) each time (Yamane et al. 2018). At both the site and basin scales, we expressed Contrib_i as the percentage of change between the metric calculated with all the species ($\text{metric}_{\text{all}}$) and the same metric calculated when the species was excluded ($\text{metric}_{\text{without},i}$) as:

$$\text{Contrib}_i = \frac{\text{metric}_{\text{all}} - \text{metric}_{\text{without},i}}{\text{metric}_{\text{all}}} \times 100$$

If an individual species has a synchronizing effect, synchrony values should decrease when that particular species is excluded from the computations, resulting in positive contribution values. In contrast, if an individual species has a stabilizing effect, CV values should increase when that particular species is excluded from the computations, resulting in negative contribution values. For instance, when we exclude a native species, we expect an increase in community CV, resulting in a negative contribution, i.e. a destabilizing effect. At the site scale, we then calculated the average contribution of native ($\text{Contrib}_{\text{native},s}$) or nonnative ($\text{Contrib}_{\text{nonnative},s}$) species to local interspecific synchrony and community CV as the weighted average contribution among the subset of species (native or nonnative) present in the local community in site *s* as:

$$\text{Contrib}_{\text{native},s} = \sum_{i[\text{native}]} \text{Contrib}_s \times \frac{\mu_{i[\text{native}],s}}{\mu_{\Sigma,s}}$$

$$\text{Contrib}_{\text{nonnative},s} = \sum_{i[\text{nonnative}]} \text{Contrib}_s \times \frac{\mu_{i[\text{nonnative}],s}}{\mu_{\Sigma,s}}$$

Likewise, at the basin scale, we calculated the average contribution of native ($\text{Contrib}_{\text{native},b}$) or nonnative ($\text{Contrib}_{\text{nonnative},b}$) species to regional interspecific synchrony and metacommunity CV as the weighted average contribution among the subset of species (native or nonnative) present within the regional metacommunity in basin *b* as:

$$\text{Contrib}_{\text{native},b} = \sum_{i[\text{native}]} \text{Contrib}_b \times \frac{\mu_{i[\text{native}],\Sigma}}{\mu_{\Sigma,\Sigma}}$$

$$\text{Contrib}_{\text{nonnative},b} = \sum_{i[\text{nonnative}]} \text{Contrib}_b \times \frac{\mu_{i[\text{nonnative}],\Sigma}}{\mu_{\Sigma,\Sigma}}$$

Positive contributions of native or nonnative species on temporal variability and synchrony metrics thus indicate that on average native or nonnative species have a destabilizing or synchronous effect, respectively. Potential differences in contribution to temporal variability and synchrony between natives and nonnatives were then assessed using linear mixed models (Pinheiro and Bates 2000), using species origin (native versus nonnative) as a fixed effect, and site nested within basin (for the site-scale model) or basin (for the basin-scale model) as random effects.

Relationships between nonnative species dominance, temporal variability and synchrony

The potential effects of nonnative species dominance on temporal variability and synchrony were examined using multiple regressions controlling for the effect of varying species diversity among sites (alpha diversity) and basins (gamma diversity). At the site scale, we evaluated potential effects of nonnative species dominance on population CV and local interspecific synchrony, and tested whether these effects scale up to community CV (see Supplementary material Appendix 1

Fig. A3 for a conceptual illustration of the expected relationships). To do so, we built a linear mixed model for each response variable y (population CV, local interspecific synchrony or community CV): $y \sim$ alpha diversity + nonnative species dominance. We included random intercepts and random slopes for each basin on the covariates to account for potential regional effects (Pinheiro and Bates 2000). Similarly, at the basin scale, we tested whether nonnative species dominance may relate to metapopulation CV and regional interspecific synchrony, and how these effects may scale up to metacommunity CV (see Supplementary material Appendix 1 Fig. A4 for a conceptual illustration of the expected relationships). We built an ordinary least squares model for each response variable y (metapopulation CV, regional interspecific synchrony or metacommunity CV): $y \sim$ gamma diversity + nonnative species dominance. Alpha and gamma diversity, together with variability and synchrony metrics were *ln* transformed prior to model fitting to improve normality; nonnative species dominance was root-squared transformed. We performed separate models, one at the native species level and one at the entire community or metacommunity level in order to better tease apart the effects of nonnatives on community and metacommunity dynamics. All statistical analyses were conducted in the R statistical environment (R Development Core Team) using the package 'nlme' (Pinheiro et al. 2019).

Results

Population and community level effects at the site scale

Nonnative species demonstrated significantly higher population CV compared to native species ($df = 458$, $t = 25.15$, $p < 0.001$; Fig. 3a). However, native and nonnative species showed no differences in their contributions to local interspecific synchrony at the community level ($df = 458$, $t = 0.22$, $p = 0.83$; Fig. 3b). By contrast, the contribution of individual species to community CV was significantly lower for native species ($df = 458$, $t = -5.83$, $p < 0.001$; Fig. 3c), indicating that these species tended to stabilize community dynamics more than nonnative species.

We found that population CV, local interspecific synchrony and community CV were all significantly related to alpha diversity when considering the native species pool only (Table 1a–c). Importantly, both population and community CV increased significantly with increasing nonnative species dominance after accounting for variation in alpha diversity among sites (Table 1a, Fig. 4a, c). By contrast, no relationship was found with local interspecific synchrony (Table 1b, Fig. 4b). Overall, the same relationships were observed when analyzing the entire community (including native and nonnative species), except for local interspecific synchrony that decreased along the gradient of nonnative species dominance (Supplementary material Appendix 1 Table A2a–c, Fig. A5). Nonetheless, this effect was not strong enough to offset the effects of increased population CV on community CV.

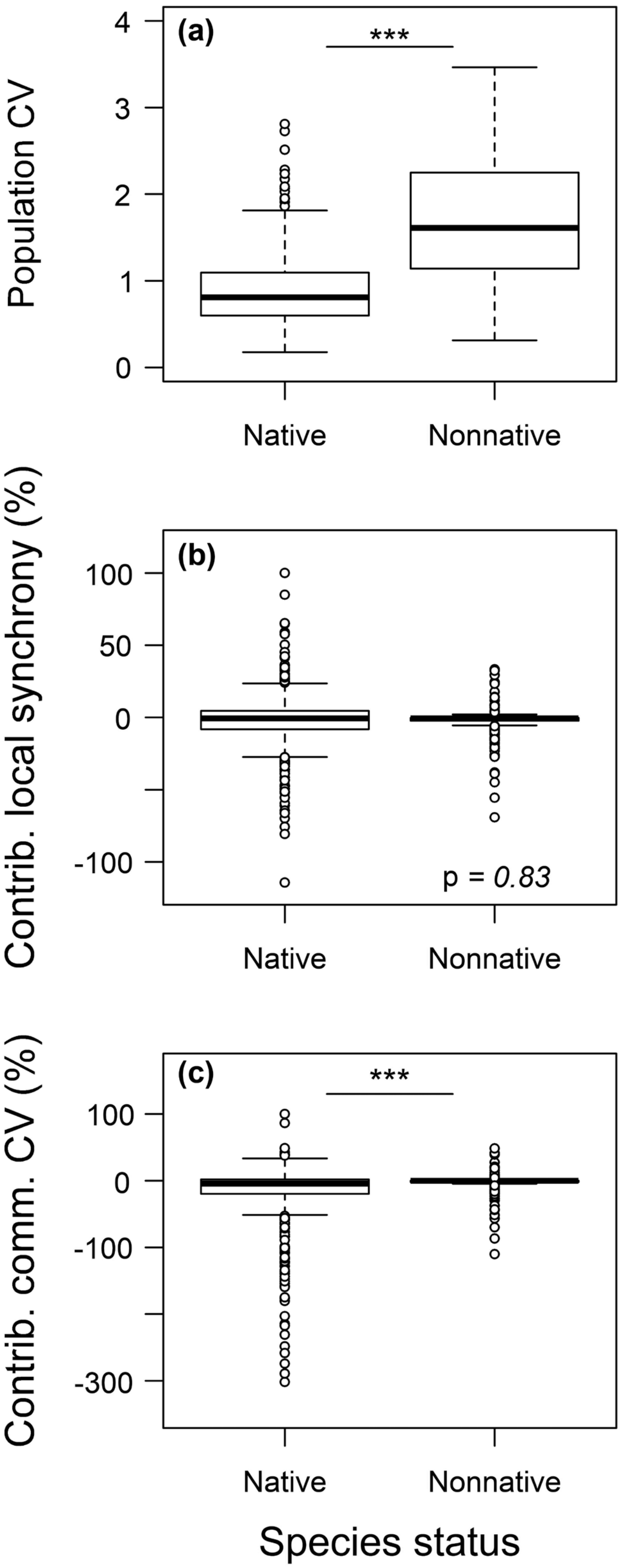

Figure 3. Comparison between native and nonnative species in terms of (a) population CV, (b) contribution of species to local interspecific synchrony (%) and (c) contribution of species to community CV (%). $^{*}0.01 \le p < 0.05$, $^{**}0.001 \le p < 0.01$, $^{***}p < 0.001$.

Table 1. Results of the multiple regressions revealing the effects of nonnative species dominance on (a) population CV, (b) local interspecific synchrony, (c) community CV, (d) metapopulation CV, (e) regional interspecific synchrony and (f) metacommunity CV, after accounting for variations in species richness among (meta)communities. Nonnative species dominance was defined as the mean ratio of total nonnative abundance to total (meta)community abundance. Alpha and gamma diversity, together with variability and synchrony metrics were *ln* transformed prior to model fitting; nonnative species dominance was root-squared transformed. The models were developed based on the native species pool only; see Supplementary material Appendix 1 Table A2 for the results including the entire community/metacommunity.

	Estimate	Standard error	df	t-value	p
(a) Population CV					
Alpha diversity	0.23	0.03	667	7.31	< 0.001
Nonnative species dominance	0.56	0.09	667	6.31	< 0.001
(b) Local interspecific synchrony					
Alpha diversity	−0.17	0.02	667	−9.21	< 0.001
Nonnative species dominance	−0.05	0.04	667	−0.90	0.203
(c) Community CV					
Alpha diversity	0.07	0.03	667	2.19	0.029
Nonnative species dominance	0.52	0.10	667	5.43	< 0.001
(d) Metapopulation CV					
Gamma diversity	0.09	0.15	24	0.56	0.584
Nonnative species dominance	0.15	0.58	24	0.27	0.792
(e) Regional interspecific synchrony					
Gamma diversity	−0.01	0.05	24	−0.23	0.821
Nonnative species dominance	−0.29	0.20	24	−1.44	0.164
(f) Metacommunity CV					
Gamma diversity	0.09	0.18	24	0.47	0.533
Nonnative species dominance	−0.37	0.69	24	0.31	0.593

Metapopulation and metacommunity level effects at the basin scale

Nonnative species demonstrated significantly higher metapopulation CV compared to native species (df = 25, t = 3.28, p = 0.003; Fig. 5a). However, native and nonnative species showed no differences in their contributions to regional interspecific synchrony at the metacommunity level (df = 25, t = 0.55, p = 0.589; Fig. 5b). The contribution of individual species to metacommunity CV tended to be lower for native species, indicating that these species tended to stabilize metacommunity dynamics more than nonnative species, but this effect was not significant (df = 25, t = −1.81, p = 0.082; Fig. 5c).

We found little evidence of an effect of gamma diversity on metapopulation CV, regional interspecific synchrony or metacommunity CV when considering the native species pool only (Table 1d–f). Likewise, no significant relationship was found between nonnative species dominance and metapopulation CV (Table 1d, Fig. 6a), regional interspecific synchrony (Table 1e, Fig. 6b) or metacommunity CV (Table 1f, Fig. 6c). The same relationships (or lack thereof) were observed when analyzing the entire metacommunity (including native and nonnative species; Supplementary material Appendix 1 Table A2d–f).

Discussion

We evaluated the influence of nonnative species on temporal variability and synchrony of riverine fish abundance at

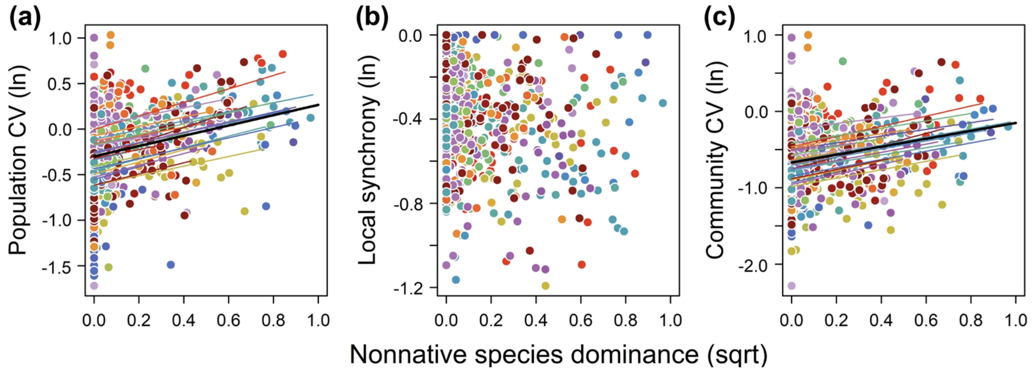

Figure 4. Effect of nonnative species dominance within communities (i.e. the mean ratio of total nonnative abundance to total community abundance) on: (a) population CV, (b) local interspecific synchrony, (c) community CV. Relationships are shown overall (fixed effects, black lines) and for individual basins (random effects, colored lines) after accounting for variations in alpha diversity (all $p < 0.05$; Table 1) by setting species richness to its mean value across communities. Each dot represents a site where the color represents a basin.

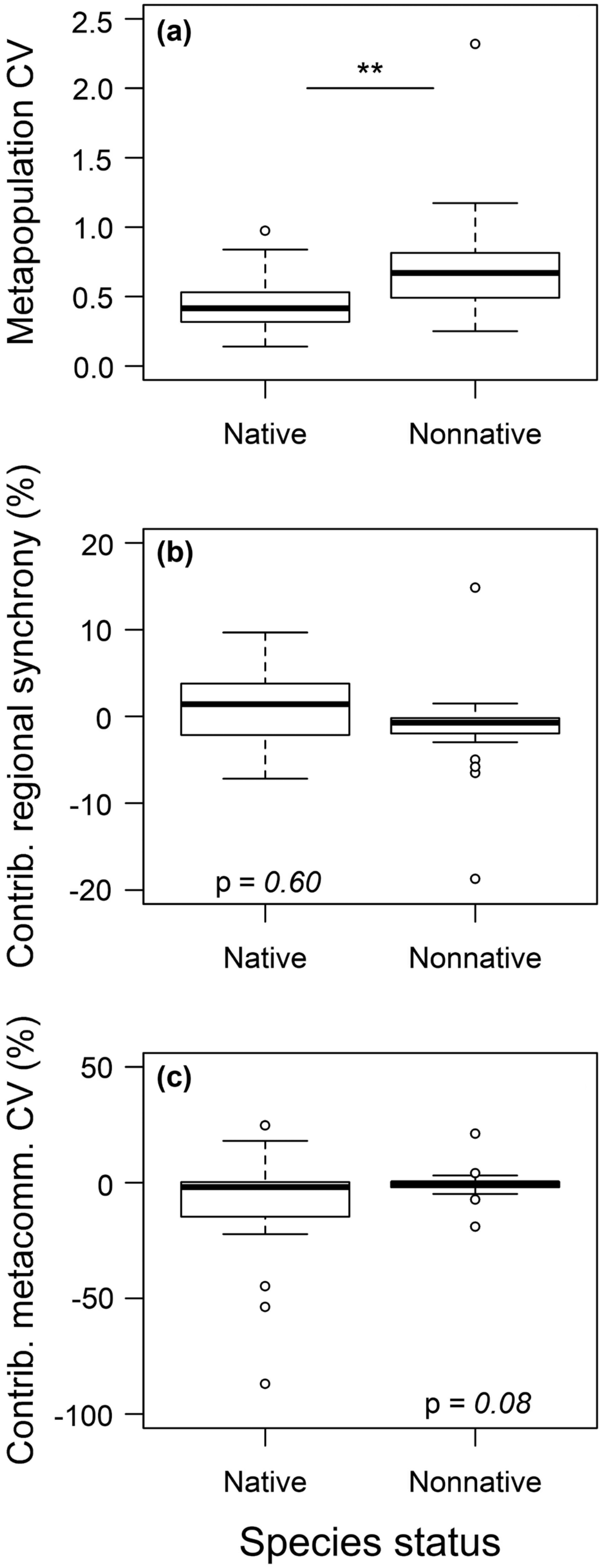

Figure 5. Comparison between native and nonnative species in terms of (a) metapopulation CV, (b) contribution of species to regional interspecific synchrony (%) and (c) contribution of species to metacommunity CV (%). $^*0.01 \leq p < 0.05$, $^{**}0.001 \leq p < 0.01$, $^{***}p < 0.001$.

the population, metapopulation, community and metacommunity levels, while controlling for species richness effects. Overall, our results demonstrated a significant destabilizing role of nonnative species, manifested across a variety of biogeographic contexts and mechanistic pathways.

We found that populations of nonnative species were more variable and contributed on average less to overall community stability (i.e. native and nonnative species together) compared to native populations. Yet, we found little evidence that native and nonnative species contributed differently to overall community synchrony. Beyond the impact of demographic stochasticity typical in small populations of newly introduced species (Fauvergue et al. 2012), these differences in the temporal variability of native and nonnative species suggest that nonnative species are more susceptible to the environmental conditions of the recipient habitat than their native counterparts, thus supporting the notion of environmental resistance and the importance of habitat conditions for successful invasion (Moyle and Light 1996, Howeth et al. 2016).

In contrast to many native fishes that are well adapted to fluctuating hydrological regimes of riverine habitats, many nonnative species are more likely to establish highly abundant, stable populations in standing water environments (Olden et al. 2006, Johnson et al. 2008). It follows that they often show source–sink dynamics between these hydrologically more stable habitats (source) and riverine (sink) habitats (Erős et al. 2012). A direct consequence is that such nonnative populations face an increased risk of local extinction unless multiple introductions (i.e. high propagule pressure) are distributed in time to lessen the effects of demographic and environmental stochasticity, or in space to support viable metapopulations (Simberloff 2009). This reinforces the view that propagule pressure-based policies should be explicitly considered to increase the effectiveness of national prevention programs aimed at minimizing the impact of nonnative species (Reaser et al. 2008). For riverine systems, these policies could include a stricter legislation for the introduction of nonnative fish to fishery ponds, effective control measures to prevent escapes from fish farms, and restrictions regarding the use of fish as life-bait.

Nonnative species were not only more variable but also destabilized the population dynamics of native species, plausibly through negative interactions such as interference, exploitative or apparent competition or predation (Ricciardi and Hoopes 2013, Giam and Olden 2016). In contrast to our expectations, we did not find evidence that local interspecific synchrony among native populations decreased along a gradient of nonnative species dominance, suggesting that the impact of nonnative species on native community level variability is mediated through increased population variability but not an effect on interspecific synchrony. Nonetheless, we found that the overall degree of synchrony within communities decreased with increased dominance of nonnative species, which likely indicates asynchronous population dynamics between native and nonnative species. However, this effect was not strong enough to offset the effect of increased population

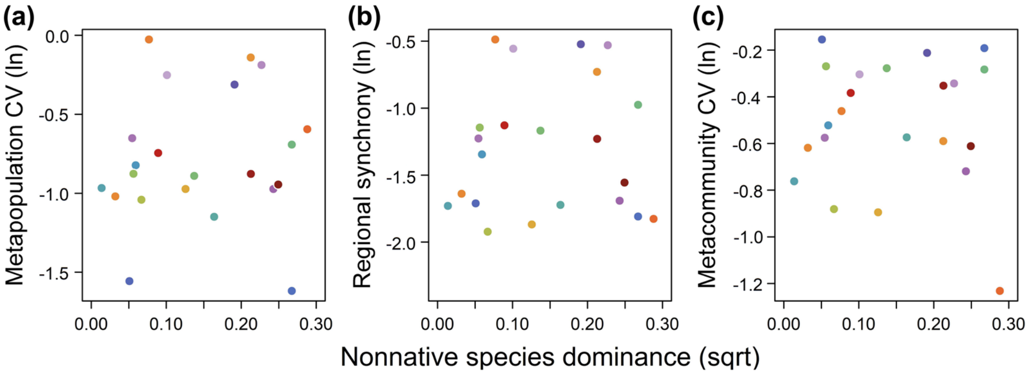

Figure 6. Effect of nonnative species dominance within metacommunities (i.e. the mean ratio of total nonnative abundance to total metacommunity abundance) on: (a) metapopulation CV, (b) regional interspecific synchrony and (c) metacommunity CV. Relationships are shown after accounting for variations in gamma diversity (all $p \geq 0.05$; Table 1) by setting species richness to its mean value across metacommunities. Each dot represents a basin using the same color legend than in Fig. 4.

CV (for both native and nonnative species) on community level CV. This indicates that increased dominance of nonnative species is associated with greater temporal variability of communities. Increasing temporal variability of ecological communities increases their vulnerability to environmental stochasticity (Inchausti and Halley 2003). This vulnerability may be further magnified in riverine systems, where current levels of fragmentation greatly reduce the chances of recolonization (Morita and Yamamoto 2002, Perkin et al. 2015). Our results therefore suggest that nonnative species introductions constitute a potentially major threat for the long-term persistence of riverine fish communities.

A longstanding question in community ecology is how stability is maintained across a hierarchy of spatial scales and organizational levels (Gross et al. 2014, Tilman et al. 2014). For riverine fish communities, we showed that nonnative species dominance can affect population and community variability beyond changes in species richness. This supports the few findings from terrestrial environments and demonstrates that species diversity alone is not sufficient to explain changes in real-world community dynamics (Wilsey et al. 2014, Blüthgen et al. 2016, Valone and Balaban-Feld 2018). Rather, human-mediated changes such as biological invasions can significantly obscure the relationship between diversity, stability and synchrony, and requires more attention in sustainable ecosystem management. We also found that, despite being always positive, the strength of the effect (i.e. slope) of nonnative species dominance on population variability varied among basins. In this regard, exploring how niche similarity related to resource acquisition and the distribution of native and nonnative species in this functional trait space mediate temporal variability and synchrony patterns represents a promising avenue for future research (van Klink et al. 2019). Similarly, incorporating biomass measurements or size-class distributions would likely provide complementary inferences about the determinants of community structure and dynamics (Morlon et al. 2009).

At the basin scale, metapopulations of nonnative species again displayed higher temporal variability than native species and tended to contribute less to overall metacommunity stability. However, this did not result in higher metacommunity variability. Our study also revealed that the temporal variability and synchrony of native metapopulations showed very modest changes along the gradient of nonnative species dominance. Overall, these results suggest a dilution effect where increased variability in individual populations have little effect at the metacommunity scale, likely due to the relatively low abundance of nonnative species at the metacommunity level in the examined basins. Dispersal processes of native populations from noninvaded sites can also partially offset some of the effects of nonnative species on native population variability at the metacommunity scale (Eriksson et al. 2014). Whether the destabilizing effects of nonnative species may scale up to affect the temporal stability of the entire metacommunity in more heavily invaded basins (cases where the number of nonnatives can represent up to 95% of the total species richness but that were not represented in the current study; Leprieur et al. 2008) thus remains a possibility.

There is increasing evidence that river network structure can significantly influence the dynamics of metapopulations and metacommunities (Yeakel et al. 2014, Erős 2017, Anderson and Hayes 2018). For instance, branching complexity has been shown to increase stability in riverine fish metapopulations because of differences in environmental conditions and mixing of individuals via dispersal among versus between river branches (Terui et al. 2018). Although we attempted to control for the contribution of species richness on temporal variability and synchrony at the metacommunity scale, we did not account for potential variation in network structure among basins. Regardless of these considerations, we caution against concluding that riverine fish metacommunities are buffered from the destabilizing effects of biological invasions. Rampant flow alteration and fragmentation by dams, ongoing climate change and increasing aquaculture needs will continue to facilitate invasions while challenging the persistence of native species, with potentially far-reaching consequences for the persistence and ecological integrity of these systems in the future (Reid et al. 2019).

Data availability statement

The source and link to each individual dataset used is provided in Supplementary material Appendix 1 Table A1. Data available from Figshare Digital Repository: <https://dx.doi.org/10.6084/m9.figshare.12214391> (Comte et al. 2020).

Acknowledgements – This paper is a joint effort of the international working group 'sYNGEO – The Geography of Synchrony in Dendritic Networks' kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

Author contributions – TE and LC contributed equally.

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Supplementary material (available online as Appendix ecog-04985 at <www.ecography.org/appendix/ecog-04985>). Appendix 1.

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