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The negative ecological impacts of a globally introduced species decrease with time since introduction

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Abstract

While there is a long-history of biological invasions and their ecological impacts have been widely demonstrated across taxa and ecosystems, our knowledge on the temporal dynamic of these impacts remains extremely limited. Using a meta-analytic approach, we investigated how the ecological impacts of non-native brown trout (*Salmo trutta*), a model species with a 170-year-long and well-documented history of intentional introductions across the globe, vary with time since introduction. We first observed significant negative ecological impacts immediately after the species introduction. Second, we found that the negative ecological impacts decrease with time since introduction and that the average ecological impacts become nonsignificant more than one century after introduction. This pattern was consistent across other ecological contexts (i.e., geographical location, levels of biological organization, and methodological approach). However, overall negative ecological impacts were more pronounced at the individual and population levels and in experimental studies. While the mechanisms leading to this decrease remain to be determined, our results indicate that rapid response of native organisms (e.g. adaptation, but also local extinction) may play an important role in this dynamic. Changes in native species traits and local extinction can have important conservation implications. Therefore, we argue that the decline of the negative ecological impacts over time should not be used as an argument to neglect the negative impacts of biological invasions.

KEYWORDS
biodiversity, exotic species, global anthropogenic changes, global invasion, salmonids

1 | INTRODUCTION

Humans have facilitated the transport of other species outside their native ranges for millennia, and the rate of human-facilitated invasions has accelerated in the past few centuries. The earliest introductions of non-native species were associated with domestication and development of agriculture in the Neolithic (Preston, Pearman & Hall, 2004) and emblematic examples include the introduction of the dingo dog *Canis dingo* from Asia to Australia more than 4,600 years ago (Oskarsson et al., 2011), the introduction of wormseed wallflower *Erysimum cheiranthoides* to the British Isles in the Bronze Age (West, 2000) or the later introduction of common carp *Cyprinus carpio* from Eastern to Western Europe 2,000 years ago (Balon, 1995). The frequency of human-mediated introductions of non-native species have increased significantly since the 1800s as globalization progressed, and the number of introductions has increased exponentially during the last decades (Seebens et al., 2017). Biological invasions of non-native species introduced by humans are a key component of the current biodiversity crisis (Bellard, Cassey & Blackburn, 2016; Naeem, Duffy & Zavaleta, 2012) and while there is a rich scientific literature quantifying their ecological impacts across taxa and ecosystem types, our knowledge on the temporal dynamic of their ecological impacts remains extremely limited (Jeschke et al., 2014; Simberloff et al., 2013).

The ecological impacts of biological invasions can be defined as any direct or indirect change in phenotypic and fitness parameters of native organisms and ecological parameters of recipient ecosystems that result from coexistence with a non-native species (Jeschke et al., 2014). The ecological impacts of non-native species are commonly assessed by comparing (spatially or temporally) sites with and without the invasive species (Parker et al., 1999). Ecological impacts of non-native species can be positive or negative, depend on local context such as community structure and environmental conditions (Davis, 2009; Vander Zanden, Olden, Thorne & Mandrak, 2004), and also preadaptation of native organisms (Strauss, Lau & Carroll, 2006). Often used in invasion ecology, correlative studies based on observational approaches contain natural variations that can disguise the subtle impacts of non-native species (Parker et al., 1999; Simberloff & Vitule, 2014), highlighting the importance of experimental approaches in the field. Ecological impacts of non-native species have been primarily quantified at the individual and population levels, while impacts at higher levels of biological organization (i.e., recipient community and ecosystems) remain understudied (Cucherousset & Olden, 2011; Parker et al., 1999). Therefore, explicit consideration of local conditions, increment of temporal and spatial scales, combination of observational and manipulative studies, and studies at different levels of biological organization are needed to improve our knowledge on the ecological impacts of non-native species and their temporal dynamic (Parker et al., 1999).

Theoretical predictions about the temporal dynamic of ecological impacts of biological invasions are equivocal and can be generalized in two alternative hypotheses, which both primarily assume negative ecological impacts and monotonic temporal dynamic. The first hypothesis suggests that the ecological impacts of non-native species should increase over time due to (a) a lag in population growth and dispersal following the introduction (Crooks, 2005; Pyšek & Jarošík, 2005), (b) the evolutionary responses (e.g., local adaptation) of the non-native species to the novel environment (Colautti, Alexander, Dlugosch, Keller & Sultan, 2017; Engel, Tollrian & Jeschke, 2011), and (c) the accumulation of negative impacts caused by the non-native species over time (Peltzer, Allen, Lovett, Whitehead & Wardle, 2010). The second hypothesis suggests that the ecological impacts of non-native species should decrease over time due to local adaptation of native organisms to the invader (Sih et al., 2010), limiting the initial advantage of the non-native species over naïve native prey (Langkilde, 2009), predators (Carlsson, Sarnelle & Strayer, 2009), and pathogens (Mitchell, Blumenthal, Jarošík, Puckett & Pyšek, 2010). Clearly, this conundrum unveils a lack of empirical studies regarding the direction and the magnitude of the temporal changes (Strayer, 2012; Strayer, Eviner, Jeschke & Pace, 2006), limiting our understanding of long-term impacts of non-native species.

The two alternative hypotheses derived from the theory might not be mutually exclusive, leading to a nonmonotonic temporal dynamic. For example, stabilizing processes in the recipient communities and ecosystems can reduce the negative ecological impacts of a non-native species after an initial stage of fast growth of invasive population (i.e., boom-bust dynamic, Strayer et al., 2017). In a rare empirical investigation on this topic, Dostál, Müllerová, Pyšek, Pergl and Klinerová (2013) have reported that the local temporal dynamic of the ecological impacts of invasive giant hogweed (*Heracleum mantegazzianum*) was nonmonotonic. Specifically, over a 48-year period, negative ecological impacts on community richness of native plants were initially increasing with time since introduction, but dismissed after ~ 30 years. However, the scarcity of studies quantifying the temporal dynamic of the ecological impacts of non-native species over a sufficiently long period of time and at a large spatial scale precludes a full understanding of biological invasions and the resilience capacity of ecosystems facing accelerating global anthropogenic changes (Seebens et al., 2017; Strayer, 2012).

Suitable model organisms to fulfill this knowledge gap should have a long-term history of multiple introductions across the globe and well-documented records of their ecological impacts. Brown trout (*Salmo trutta*) is a species matching these criteria. This salmonid fish species is native to Europe, Northern Africa, and western Asia and has a history of ~ 170 years of deliberate introductions across the globe that begins with increasing immigration of European settlers to North America and Australasia in the mid-19th century (Figure 1; McIntosh, McHugh & Budy, 2011; Budy et al., 2013). British acclimatization societies were among the first ones to introduce brown trout outside its native range (Halverson, 2010; McIntosh et al., 2011), shipping fertilized eggs overseas from Europe in wooden containers filled with a wet moss and ice (Halverson, 2010; Westley & Fleming, 2011). The efforts invested in its transport and stocking clearly demonstrate the high social and economic value of brown trout. The same reasons have motivated its later introductions in South America, Asia, and Africa during the 20th century (McIntosh et al., 2011). The ecological impacts of non-native brown trout are well-described in the literature, ranging from behavioral changes in native aquatic invertebrates (McIntosh & Townsend, 1998), to fitness reductions of native fishes (Jones & Closs, 2015; Zimmerman & Vondracek, 2007), and to changes of ecosystem functioning in recipient stream ecosystems (Nyström, McIntosh & Winterbourn, 2003).

Using a meta-analytic approach, we quantified the temporal changes in the ecological impacts of non-native brown trout across the globe. We specifically tested the existence of a nonmonotonic quadratic relationship between time since introduction and the ecological impacts (i.e., negative ecological impacts initially increase with time since introduction and subsequently decrease to become not significantly different from zero) or a monotonic linear relationship as an alternative hypothesis. We then compared this temporal dynamic between geographical locations, levels of biological organization, and studies using observational and manipulative approaches.

2 | MATERIALS AND METHODS

2.1 | Literature search and study selection

We used the Institute of Scientific Information Web of Science online database (http://webofknowledge.com) to identify peer-

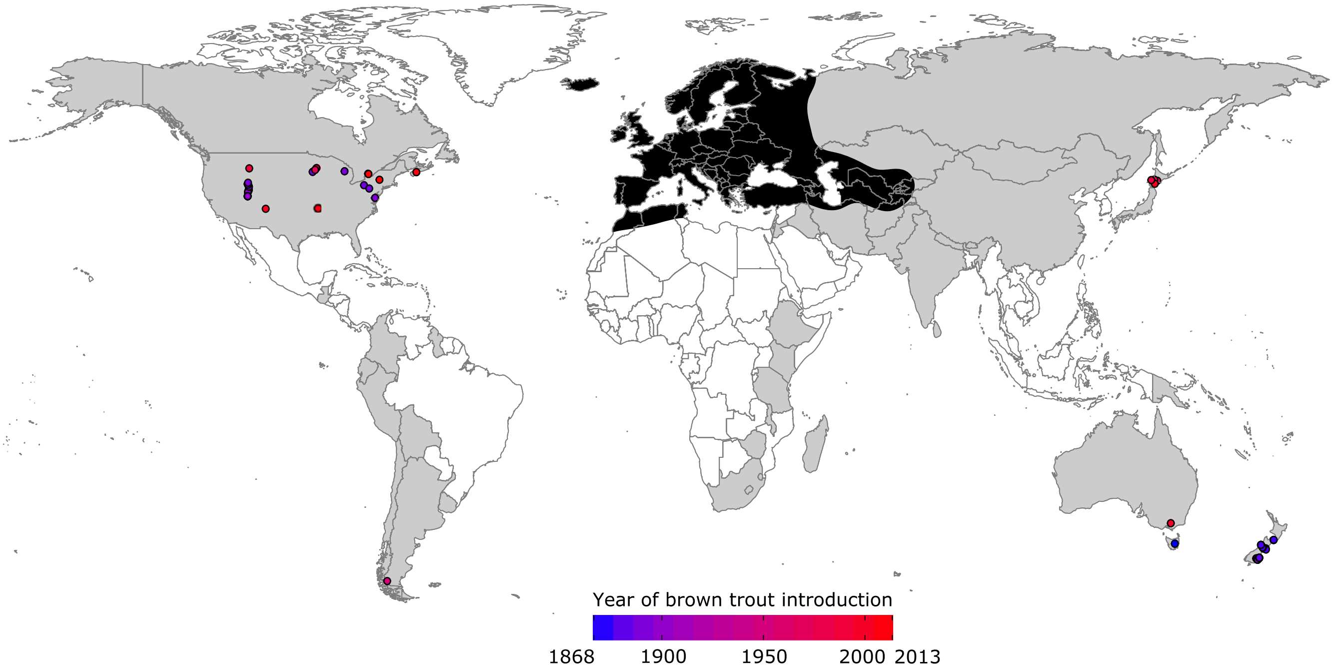

FIGURE 1 Global distribution of brown trout and spatial-temporal extent of the dataset. The 'maximum' native range (black) and 'minimum' non-native range (gray) are depicted, note that there is a high level of uncertainty in the actual distribution of the species given anecdotal and conflicting reports. Non-native range was defined at the country level. The circles represent the geographical location of studied sites from studies included in the meta-analysis. The fill color of the circles corresponds to the year of brown trout introduction for each study. Native and non-native range of brown trout are based on Fishbase (www.fishbase.org), FAO (www.fao.org), Baglinière and Maisse (1991) and McIntosh et al. (2011) [Colour figure can be viewed at wileyonlinelibrary.com]

reviewed articles published through the end of 2016 that quantify the effects of introductions of non-native brown trout on native organisms and recipient ecosystems. A full list of the search string employed to identify relevant papers by topic is provided in the Supporting Information Appendix S1. Our protocol followed those defined in Buoro, Olden and Cucherousset (2016), but we considered both manipulative and observational studies.

Our initial literature search identified 4,234 published articles. Based on a screening of titles and abstract, 265 full-text articles were subsequently assessed for their eligibility in the analysis (Supporting Information Figure S1 in Appendix S1). Only studies that compared organism/ecosystem responses when exposed to non-native brown trout (i.e., treatment) versus without non-native brown trout (i.e., control) were included. We then reviewed the references section of each relevant article to identify additional articles. Using this procedure, we identified additional 58 potential articles for inclusion, which in total created a dataset of 323 articles. However, a large number was excluded from the final analysis because (a) they lacked clear sympatric (i.e., coexistence between native and non-native) or allopatric (i.e., control with natives only) treatments or (b) treatments contained several non-native salmonid species or (c) they did not report raw results per treatment and control (sample size, mean, standard error or standard deviation values, or confidence interval) but only overall statistical results (e.g., *p*-values).

2.2 | Data extraction

The final dataset contained 54 studies that comprised 277 assays quantifying the ecological impacts of non-native brown trout (see full list of references in Supporting Information Appendix S2).

We then classified variables to measure impacts across different evolutionary and ecological contexts. First, for each study, we extracted the geographical location and discriminated studies conducted in the southern and the northern hemisphere. Indeed, salmonid fishes are native only to the northern hemisphere and thus we expected that organisms in northern hemisphere that coevolve with the local native salmonid species may have higher resistance and resilience to invasion by non-native brown trout than the organisms in southern hemisphere which did not coevolve with native salmonid fishes (Strauss et al., 2006). Among the studies matching our inclusion criteria, 26 were performed in North America, 23 in Australasia, 4 in Asia, and 1 in South America. No study was conducted in Africa despite multiple introductions reported in this continent (Figure 1). Second, we extracted the response variables that were classified at four different levels of biological organization, that is, individual, population, community, and ecosystem (Cucherousset & Olden, 2011). Indeed, no study in the final dataset reported impact at the genetic level. Levels of biological organization were subsequently group into two categories: individual and population levels (intraspecific responses) and community and ecosystem levels (interspecific responses). Complex interactions between native organisms at the community and ecosystem levels can buffer ecological impacts of non-native species at the large spatial scale (Levine, 2000), therefore, we expected that ecological impacts of non-native brown trout at the individual and population levels will be stronger and last for a longer period after the non-native trout introduction than the ecological impacts at the community and ecosystem levels. We also categorized each study based on the methodological approach used, that is, manipulative (mesocosms and laboratory studies, and studies using experimental manipulation of the studied system such as species translocation, removal, or caging) and observational (studies based on observation of a natural system, which was not manipulated for the study). We expected that manipulative studies will report stronger negative ecological impact of non-native brown trout than observational studies, because size of the ecological impacts are more likely to be dampened by confounding variables in observational than in manipulative studies. We also expected that ecological impacts measured in observational studies will decrease faster with time since introduction than ecological impacts measured in manipulative studies, because extirpation of a native species can reduce apparent ecological impacts of biological invasions measured by observational studies. This is because species extirpation disables researchers to compare allopatric and sympatric situation in observational studies. We extracted statistics for control and treatment group sample sizes, means, and variations (standard deviations, standard errors, or confidence intervals), from tables and results in the articles. When necessary, we extracted data from published figures using DataThief (Tummers, 2006). For articles that did not report those statistics, we requested the data from the corresponding author. Finally, the time since introduction (in years) was measured as time between the first brown trout introduction in the studied system and data collection in each study. The year of brown trout introduction was obtained for each study in the following ways, listed in preferential order: (a) directly reported in the article, (b) from other published peer-reviewed sources or government websites, and (c) from the corresponding authors. In the cases of manipulative studies, the time since introduction was defined according to experience of native organisms with non-native brown trout. Therefore, if native organisms originated from allopatric population (i.e., naïve to non-native brown trout), time since introduction was considered equal to zero.

2.3 | Data analysis

We quantified the ecological impacts on recipient ecosystems and native organisms by evaluating the difference of the effects (i.e., means) between treatment and control, adjusted for the differences in scale between studies (i.e., standardized mean difference). We used Hedges' g as an estimate of the standardized mean difference because it is a unit-free metric (ranging from $-\infty$ to $+\infty$), insensitive to unequal sampling variance, and is not biased by small sample sizes (Koricheva, Gurevitch & Mengersen, 2013). Hedges' g gives the magnitude of the impact and its direction. We scaled all Hedges' g so all expected negative ecological impacts point in the negative direction and expected positive ecological impacts point in the positive direction (see Supporting Information Appendix S3). We calculated the Hedges' g and corresponding sampling variance for each essay using the R package 'metafor' (Viechtbauer, 2010). We quantified the temporal trends related to the year of publication using cumulative meta-analyses (Leimu & Koricheva, 2004). Cumulative meta-analysis can uncover temporal bias in studies caused by changes in scientific knowledge (e.g., improvement of taxonomic knowledge or methodologies) and scientific paradigm (e.g., changes in perception of non-native species, Simberloff & Vitule, 2014) over time. To conduct the cumulative meta-analysis, assays in the dataset were sorted by the year of publication in chronological order. The earliest available assays were entered into the analysis first and, at each step of the cumulative meta-analysis, assays published in the following year were added in chronological order and the distribution of effects size were re-evaluated (median and uncertainty) at each step. To quantify potential publication bias associated with the tendency of journals to publish studies with significant results (i.e., leading to an asymmetry of effects size), we examined the robustness of our analysis via inspection of funnel plots, trim-and-fill analysis, and fail-safe numbers. We identified and removed one outlying assay from the analysis based on inspection of funnel plot, but our results were overall deemed robust (for details see Supporting Information Appendix S4).

To test whether time since introduction induced changes in ecological impacts and if this relationship differed across ecological context and methodological approach of studies, we used a linear mixed-effects model. Mixed-effects models allow testing for a significant effect of a continuous variable (here, time since introduction) and differences in effect sizes between grouping variables while assuming that random sources of variation in effect sizes exist between studies and that sampling error accounts for heterogeneity within studies. Thus, we assumed that the observed Hedges' g^{obs} of assay i followed a normal distribution such that:

$$g_i^{\text{obs}} \sim \mathcal{N}\left(g_i^{\text{true}}, \sigma_i^{\text{within}}\right) \tag{1}$$

with g_i^{true} being the true effect size and σ_i^{within} the within-study variation, that is, known sampling error for assay i. Then, the true effect size g_i^{true} is normally distributed with the average effect size μ_i and the between studies variation σ^{between}:

$$g_i^{\text{true}} \sim \mathcal{N}\left(\mu_i, \sigma^{\text{between}}\right) \tag{2}$$

Finally, to evaluate the type of temporal dynamic of the ecological impacts and the effect of study ecological context and methodological approach, we fitted both linear (i.e., monotonic) and quadratic (i.e., nonmonotonic) regressions between the average effect size μ_i and the centered time since introduction time_i for the assay i:

$$\mu_i = \alpha_{\text{context}_i} + \beta_{\text{context}_i} \times \text{time}_i + \gamma_{\text{context}_i} \times \text{time}_i^2 \tag{3}$$

With α being the intercept, β the slope term of the linear relationship, the γ quadratic term and context (i.e., geographical location, biological levels of organization, or methodological approach of study) for the assay i. We first analyzed the model without time effect to assess the overall ecological impacts as $\hat{g}^{\text{true}}$. When nonsignificant, quadratic (i.e., nonmonotonic) term of regression was removed from the model.

The model was fitted within a Bayesian framework allowing inferences for true effect size for each assay that take into account uncertainty about parameter estimates. The joint posterior distributions of model parameters were obtained by means of Markov Chain Monte Carlo (MCMC) sampling as implemented in the JAGS software in R using the package rjags (Plummer, 2003). We ran three parallel MCMC chains and retained 25,000 iterations after an initial burn-in of 5,000 iterations. Convergence of MCMC sampling was assessed using Brooks–Gelman–Rubin diagnostics (Brooks & Gelman, 1998). We ensured that the MCMC convergence criteria Rhat was below 1.1 for all model parameters. Uncertainties in model parameters were reported using credible intervals at 95% ($CI_{95\%}$). We evaluated the statistical significance of time since introduction and effect sizes for each grouping variables by ensuring that the $CI_{95\%}$ did not overlap with 0. We compared models between the contexts by calculating the gap Δ between categories for each parameters of interest ($\hat{g}^{true}$, α, β and γ). For example, we evaluated the difference of intercept ($\Delta\alpha$) between geographical location by calculating $\Delta\alpha = \alpha_{Northern} - \alpha_{Southern}$ at each iteration. Medians of effect sizes, $CI_{95\%}$ (within brackets) and confidence that the parameter is significantly positive or negative (i.e., do not overlap with 0 and differ from the sign of the median; hereafter, $P_{</>0}$) are subsequently reported.

3 | RESULTS

Overall, non-native brown trout caused significant negative ecological impacts on native organisms and recipient ecosystems ($\hat{g}^{true} = -0.350$, $CI_{95\%}$ [-0.490; -0.209], $P_{>0} < 0.001$). The global ecological impacts of non-native brown trout did not differ significantly across geographical locations as there was no significant difference in its impacts in southern and northern hemispheres (see Supporting Information Appendix S5). The ecological impacts measured at low (i.e., individual and population) and high (i.e., community and ecosystem) levels of biological organization were significantly different, with significant overall negative ecological impacts only at the individual and population levels. The ecological impacts measured in manipulative and observational studies were significantly different, with only manipulative studies reporting significant overall negative ecological impacts (Supporting Information Appendix S5).

Time since introduction ranged from 0 to 138 years and was not correlated with the year of study publication (rho = -0.04) that was ranging from 1981 to 2016. There was no obvious linear relationship between the intensity of the ecological impacts of brown trout and the year of study publication (Figure 2).

Estimates of the coefficients of regression indicate a significant positive linear term (slope term: $\beta = 0.003$, $CI_{95\%}$ [0.000; 0.006], $P_{<0} = 0.017$; Table 1), but no significant quadratic term (quadratic term: $\gamma = 2.661\ e^{-5}$, $CI_{95\%}$ [$-6.785\ e^{-5}$; $2.000\ e^{-4}$], $P_{<0} = 0.289$) between the time since introduction and average ecological impacts of non-native brown trout, suggesting the existence of a monotonically increasing linear relationship. Immediately after introduction, non-native brown trout induce significant negative ecological impacts on native organisms and recipient ecosystems, that is, the average ecological impact estimated at introduction were significantly negative ($\hat{g}^{true}_{time=0\,year} = -0.564$, $CI_{95\%}$ [-0.811; -0.323], $P_{>0} < 0.001$). However, average ecological impact became nonsignificantly different from zero approximately 130 years after introduction ($\hat{g}^{true}_{time=130\,years} = -0.167$, $CI_{95\%}$ [-0.388; 0.050], $P_{>0} = 0.066$, Figure 3).

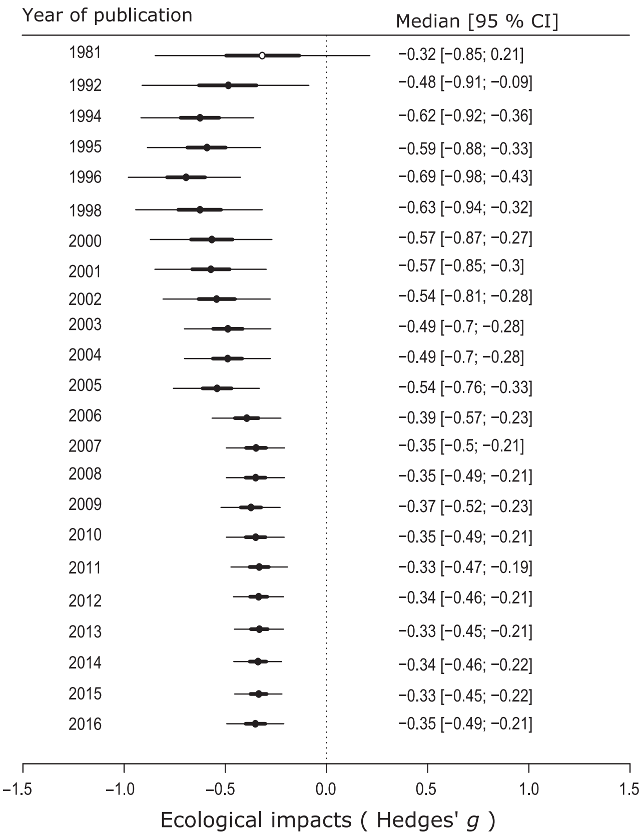

FIGURE 2 Cumulative effect sizes over publication year for the 277 assays used in the meta-analysis. Medians (circles), 50% (thick segments), and 95% (thin segments) credible intervals are reported. Significant and nonsignificant impacts are indicated using black and white circles, respectively

Importantly, $\Delta\beta$ was not significant in any tested context model, which indicates that there was no significant difference in the linear relationship between time since introduction and ecological impacts of non-native brown trout across the three contexts that were tested (Figure 4; Table 1). Similarly, there was no significant difference in the quadratic relationship between time since introduction and ecological impacts across these three contexts (Supporting Information Appendix S6).

4 | DISCUSSION

Our results reject the hypothesis of a nonmonotonic quadratic relationship between ecological impacts of biological invasion and time

TABLE 1 Model outputs fitted with linear (i.e., monotonic) regressions between the average effect size and the centered time since introduction and their comparison (Δ). Models were fitted in a Bayesian framework. Medians and 95% credible interval are reported. $P_{</>0}$ provides the proportion of negative or positive posterior values, that is, confidence that the effect is negative or positive, respectively. Effects were considered significant when $p < 0.05$

			Median effect size [95% CI]			
Context	**Category**	**# of assays**	**α**	**β**	**Δα**	**Δβ**
Overall	–	276	−0.350 [−0.490; −0.210] $P_{>0} < 0.001$	0.003 [0.000; 0.006] $P_{<0} = 0.017$	–	–
Geographical location	Southern hemisphere	130	−0.365 [−0.559; −0.175] $P_{>0} < 0.001$	0.006 [0.000; 0.011] $P_{<0} = 0.019$	0.029 [−0.249; 0.308] $P_{<0} = 0.112$	−0.002 [−0.009; 0.004] $P_{>0} = 0.239$
	Northern hemisphere	146	−0.334 [−0.537; −0.134] $P_{>0}<0.001$	0.003 [−0.001; 0.008] $P_{<0}=0.058$		
Level of biological organization	Individual and population	209	−0.390 [−0.525; −0.260] $P_{>0} = 0.001$	0.002 [−0.001; 0.004] $P_{<0} = 0.066$	0.259 [−0.161; 0.682] $P_{<0} = 0.113$	0.006 [−0.006; 0.019] $P_{<0} = 0.158$
	Community and ecosystem	67	−0.133 [−0.537; 0.267] $P_{>0}=0.234$	0.008 [−0.004; 0.021] $P_{<0}=0.090$		
Methodological approach	Manipulative	180	−0.428 [−0.564; −0.297] $P_{>0} < 0.001$	0.001 [−0.001; 0.004] $P_{<0} = 0.158$	0.303 [−0.056; 0.658] $P_{<0} = 0.048$	0.005 [−0.007; 0.017] $P_{>0} = 0.195$
	Observational	96	−0.127 [−0.461; 0.202] $P_{>0}=0.222$	0.007 [−0.005; 0.018] $P_{<0}=0.132$		

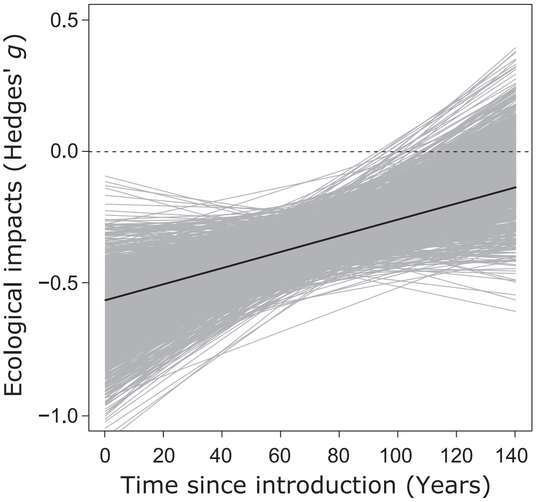

FIGURE 3 Relationship between time since introduction and average ecological impacts of non-native brown trout. Predicted curve drawn based on parameter values from randomly chosen 1,000 MCMC samples. The median (black line) and randomly chosen 1,000 MCMC subsamples (dark gray) are displayed

since introduction at the global scale. Instead, they support the alternative hypothesis of the existence of a monotonic linear relationship. Specifically, we found that the average ecological impacts of non-native brown trout were significantly negative in recent introductions and became nonsignificant where the species was introduced more than one century ago. This temporal dynamic was not significantly different across the three contexts tested (i.e., geographical location, level of biological organization, and methodological approach). In addition, there was no indication of a bias related to publication year that was not correlated with time since trout introduction, suggesting that changes in scientific knowledge and paradigm over time were unlikely to affect our main findings (Leimu & Koricheva, 2004; Simberloff & Vitule, 2014).

Immediate negative ecological impacts after non-native trout introduction observed in our study contrast with the general pattern of biological invasions, which often includes a lag stage between the introduction and the moment when ecological impacts of biological invasion become noticeable (Crooks, 2005; Dostál et al., 2013). However, the lag stage can be reduced by increasing propagule pressure (i.e., number of introduced individuals) (Blackburn, Cassey & Lockwood, 2009; Colautti, Grigorovich & MacIsaac, 2006). Species with high social and economic values, such as brown trout (Halverson, 2010; McIntosh et al., 2011), are often deliberately released in favorable habitat in high numbers resulting in high propagule pressure that could facilitate their immediate negative ecological impacts in natural systems (Saul et al., 2017). Immediate negative ecological impacts of non-native species can be also reinforced by their phenotypic plasticity (Colautti et al., 2017; Westley, 2011). For instance, due to plasticity, brown trout usually achieve a 30% larger body size and have a high preference for piscivory outside of its native range (Budy et al., 2013), which is likely to rapidly magnify its negative

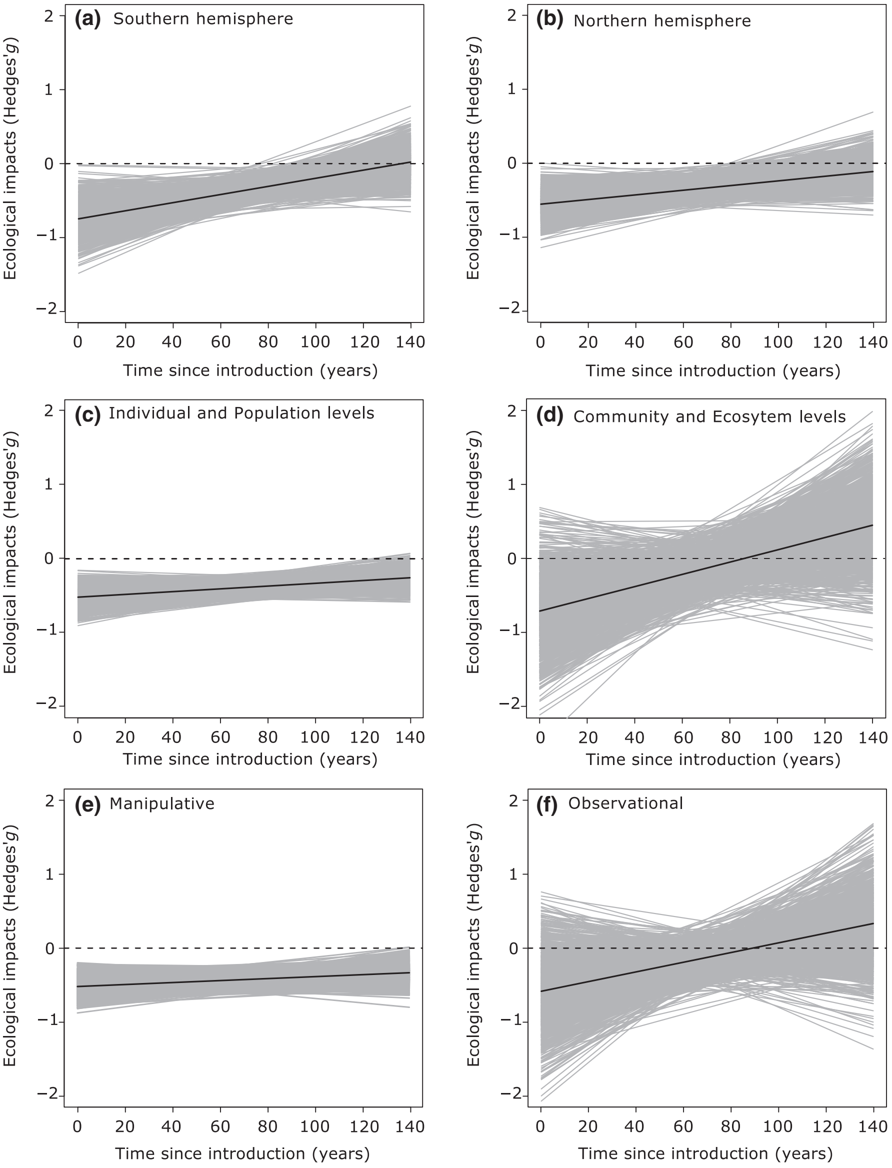

FIGURE 4 Relationship between time since introduction and average ecological impacts of non-native brown trout in (a) Southern hemisphere, (b) Northern hemisphere, at (c) individual and population levels, (d) community and ecosystem levels, and in (e) manipulative, and (f) observational studies. Predicted curve drawn based on parameter values from randomly chosen 1,000 MCMC samples. The median (black line) and randomly chosen 1,000 MCMC subsamples (dark gray) are displayed

ecological impacts (Pereira, Agostinho & Gomes, 2015). Similarly, phenotypic plasticity has been shown to facilitate invasion of a zooplankton species *Daphnia lumholtzi* in Northern America (Engel et al., 2011), which indicate that non-native species with high phenotypic plasticity have a pronounced potential to quickly become successful invaders.

Our finding that the negative ecological impacts decrease monotonically over time could be driven by two mutually nonexclusive hypothetical mechanisms. First, rapid adaptive response of native organisms and selection against native organisms sensitive to the biological invasions should lead to the development of resistant populations and communities, thus rapid evolutionary response of individuals can mitigate the negative ecological impacts of the biological invasion. For instance, native prey species can develop an antipredation strategy against the non-native predators (Carthey & Banks, 2016; Langkilde, 2009) and simultaneously non-native species can over time become an important resource for native predators (Carlsson et al., 2009). Thus, native predators can regulate a population of non-native species and prevent their strong ecological impacts (Pereira et al., 2015). Decrease in the ecological impacts over time has been observed also for competitive interactions, with the competitive capacity of non-native plants decreasing with increasing time since introduction (Iacarella, Mankiewicz & Ricciardi, 2015). Second, native species that are not preadapted to coexist with non-native species can rapidly become locally extinct (i.e., extirpation) (Bellard et al., 2016; Strauss et al., 2006). Extirpation represents one of the most intense impacts of biological invasions. Extirpation of a native species can reduce apparent ecological impacts of biological invasions measured by observational studies. Indeed, impacts at these levels cannot be measured on a native species that does not coexist anymore with the invader. In another words, some impacts of biological invasions can go so quickly that they might pass us by, before we can record them by observational studies. However, the effect of such coexistence can be tested using experimental manipulation of the studied system. Our results demonstrated that there was no significant difference in the temporal patterns measured in manipulative and observational studies, suggesting that extirpation of native species was unlikely the main driver of the decrease in the ecological impacts over time that we observed.

In addition, our result might be explained by the cumulative effects of multiple stressors such as an interaction between biological invasions and other components of anthropogenic global changes (Rahel & Olden, 2008; Strayer, 2012). For example, the interaction between environmental perturbations induced by climate change and biological invasions has been suggested to magnify negative ecological impacts of these phenomena (Dukes & Mooney, 1999; Engel et al., 2011). Studies included in our meta-analysis compared sympatric (with non-native species) and allopatric (control without non-native species) sites, which where sampled from 1977 to 2013. However, at some of these sites, brown trout was present since the mid-19th century and native species may have had time to adapt to the biological invasion before the rapid increase in average global temperature that began in the second half of 20th century (Hansen et al., 2006). Consequently, the communities at the sites with older brown trout introduction may be more resistant to negative ecological impacts of the interaction between climate change and biological invasion than the communities exposed to recent introductions that are co-occurring with the ongoing rapid climate change. Historical perception and management of non-native species may also cause a relative change in ecological impacts of biological invasions over time. Populations of species with high social and economic values (e.g., some salmonid fishes), which were spread by acclimatization societies, were often carefully managed and protected in their new environment (Halverson, 2010; Seebens et al., 2017). Paradoxically, this careful management may cause that non-native species had in the past a function of an umbrella species (Simberloff, 1998), therefore, native organisms and recipient ecosystems at the sympatric sites were spared of additional anthropogenic stressors like water pollution or habitat loss due to the coexistence with a non-native species with high social and economic values. This attitude has likely changed, as a negative perception of non-native species currently prevails among the scientists and stakeholders (Schlaepfer, Sax & Olden, 2011; Simberloff, 2011), and sites with recent introductions are less likely to be spared from additional anthropogenic stressors due to the presence of non-native species.

We found evidence that reported average intensity of negative ecological impacts of non-native brown trout was higher in the studies using manipulative than observational methodological approach. This can be simply caused by higher number of confounding factors in observational studies that can disguise the net ecological impacts of non-native species. However, trim-and-fill analysis suggested that positive ecological impacts were under reported in our dataset of manipulative studies, implying that impacts of non-native brown trout in the manipulative studies may be less negative than stated (Supporting Information Appendix S4). This could be explained by higher probability to bias by the prejudgement view on non-native species in manipulative studies that results in an emphasis on documenting the negative ecological effects (Schlaepfer et al., 2011). The response of native organisms to the pressures induced by non-native species may also depend on evolutionary and ecological contexts of the invasion (Levine, 2000; Strauss et al., 2006; Vander Zanden et al., 2004). We found that the ecological impacts of non-native brown trout were significantly higher at the individual and population levels than at the community and ecosystem levels, suggesting that the ecological interactions among native organisms might buffer the ecological impacts at the higher levels of biological organization.

Our study represents a rare quantitative assessment of the temporal dynamic of the ecological impacts of a biological invasion at large spatial and temporal scales. We found that the negative ecological impacts of non-native brown trout decrease with time since introduction to become not significant after more than one century after introduction. The mechanisms leading to this decrease in ecological impacts remain to be determined, but the temporal pattern seems to be overall robust as it is consistent across contexts and indicates that rapid evolutionary processes may play an important role in this dynamic. However, we argue that the decline of the negative ecological impacts over time should not be used as an argument to neglect the conservation implications of the effects of biological invasions (Dostál et al., 2013; Simberloff, 2011) or to naturalize an introduced species (Pelicice, Vitule, Lima Junior, Orsi & Agostinho, 2014), which can be extremely harmful. In addition, the existence of strong negative ecological impacts immediately after introduction highlights that prevention of first introductions and eradication or containment of non-native species shortly after introduction are the most efficient methods to limit their negative ecological impacts. Long-term longitudinal monitoring (including before species introduction) of native organisms and recipient ecosystems receiving non-native species is a priority to fully appreciate the temporal dynamic of their responses to biological invasions and their drivers. Finally, quantifying the temporal dynamic of the ecological impacts across taxonomically and functionally distinct invasive species is needed to quantify the relative contribution of the history of biological invasions and the ecological traits of invasive species on the temporal dynamic observed.

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AUTHOR CONTRIBUTION

JC, MB, and LZ designed the research. LZ and MB prepared the dataset and analyzed the data. LZ, JC, and MB wrote the article.

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We have no competing financial interest to report.

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SUPPORTING INFORMATION

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

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