LETTER

Global Salmonidae introductions reveal stronger ecological effects of changing intraspecific compared to interspecific diversity

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Abstract

The introduction of organisms within the native range of wild conspecifics is a widespread phenomenon and locally modifies patterns in intraspecific diversity. However, our knowledge of the resulting ecological effects, as opposed to those caused by invasion-induced changes in interspecific diversity, is still limited. Here, we investigated the ecological effects of native and non-native invaders across levels of biological organisations and recipient organisms using the global and long history introductions of salmonids. Our meta-analysis demonstrated that the global effects of native species introductions exceeded those induced by non-native invaders. The impacts of native invaders were primarily manifested at the individual level on wild conspecifics, but remained largely unexplored on other native organisms and at the community and ecosystem levels. Overlooked and poorly appreciated, quantifying the impacts of native invaders has important implications because human-assisted introductions of domesticated organisms are ubiquitous and likely to proliferate in the future.

Keywords

Biological invasions, domesticated species, ecosystem functioning, experimental studies, meta-analysis, native invaders, salmonids.

INTRODUCTION

Ecologists have only recently begun to appreciate how intraspecific variability in biological diversity, referring to diversity in individual genetic, physiological or phenotypic traits within a population or a species, may play a critical role in ecological processes (Bolnick *et al.* 2011; Violle *et al.* 2012). Emerging evidence, for example, has revealed that intraspecific variation in the phenotypic traits of consumers can cascade across levels of biological organisation, ultimately altering prey community structure and ecosystem functioning (Harmon *et al.* 2009; Palkovacs & Post 2009). Despite these recent advancements, our knowledge of the ecological consequences of human-induced changes in intraspecific diversity, as opposed to interspecific diversity, is still limited (Palkovacs *et al.* 2012).

The worldwide reshuffling of species distributions via human-assisted introductions provides a powerful, yet unexploited, opportunity to investigate this question (Olden *et al.* 2004; Sax & Gaines 2008). First, the introduction of non-native species beyond their original distributional range (hereafter, *non-native invaders*) is a widespread phenomenon involving countless taxonomic groups, thus facilitating an investigation of the consequences of changes in interspecific diversity. Second, despite only fleeting recognition by ecologists, biological invasions can also alter intraspecific diversity

through the release or promotion of *native invaders*. This refers to distinct genotypes or phenotypes of species that add to existing or establish new populations within their native range (Simberloff 2011; Carey *et al.* 2012).

Captive-breeding for conservation programmes, supplemental stocking of waterways with fish and agriculture practices for food production have led to the selection of particular attributes of many organisms that include enhanced genetic diversity, elevated growth rate and disease resistance (Diamond 2002; Larson & Fuller 2014). Such domesticated plants and animals have been widely released, both intentionally (e.g. stock enhancement) and accidentally (e.g. escaped from farms, horticulture and aquaculture facilities), into new and existing parts of their native range. This may ultimately lead to the alteration of intraspecific diversity of wild populations with potential adverse ecological impacts (Laikre *et al.* 2010; Carey *et al.* 2012; Champagnon *et al.* 2012); a burgeoning concern given the growing production and potential release of transgenic (i.e. genetically modified) organisms in the wild (Devlin *et al.* 2015).

Here, we use global-scale introductions of freshwater fishes, specifically salmon and trout (family Salmonidae), as a robust biological model to investigate the ecological effects of changing intraspecific and interspecific diversity. Salmonids have been the focus of artificial breeding and selection programs since the mid-1800s, and the production of hatchery-raised

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specimens ushered in a century of widespread intentional introductions (Stankovic *et al.* 2015). The first stockings of non-native salmonids were performed in North America and Europe by acclimatisation societies primarily to satisfy recreational fisheries. This was followed by broad-scale introductions of predominantly brown trout (*Salmo trutta*) and rainbow trout (*Onchorynchus mykiss*) in numerous regions lacking native salmonids, such as Chile, South Africa, and New Zealand (e.g. Hutchings 2014; Stankovic *et al.* 2015). Concurrently, aquaculture and stocking programmes were developed within the native range of many salmonids species to enhance commercial and recreational fisheries, as well as for conservation purposes (Lorenzen *et al.* 2012). The commercial production of salmonids for human consumption in aquaculture facilities has flourished worldwide. For instance, 94% of Atlantic salmon (*Salmo salar*) on Earth are located in aquaculture, with close to two million of these domesticated fish escaping from farms each year in the North Atlantic (Schiermeier 2003). Then, stocked and escaped salmonids modify intraspecific diversity within their native area. More recently, concern has emerged regarding the potential consequences of transgenic salmonids (e.g. Sundström *et al.* 2007; Devlin *et al.* 2015) growing twice as fast as its wild counterpart and being the first genetically engineered animal to be approved for human consumption in the United States and representing a new form of potential native invaders.

Despite crucial concerns about the expansion of human-assisted introductions of domesticated and genetically modified organisms across the world, quantifying the effects of changing intraspecific diversity on recipient ecosystems and comparing them to those induced by changes in interspecific diversity remain poorly appreciated. Here, we capitalise on the rich history of global salmonid introductions to provide a meta-analytic comparison of the ecological consequences of human-induced changes on both intraspecific and interspecific diversity. We also investigate whether the magnitude of ecological impacts induced by native and non-native invaders vary across levels of biological organisation and the resident native organisms. According to ecological theory and a growing body of empirical evidence, we posit two main hypotheses. First, we predict that at lower levels of biological organisation (i.e. genetic, individuals and populations), native invaders will have stronger impacts on wild conspecifics but weaker impacts on other native organisms when compared to non-native invaders. This prediction is supported by the fact that by virtue of high ecological and phenotypic similarity between native invaders and their wild conspecifics, the strength of intraspecific competition should exceed interspecific competition (Forrester *et al.* 2006; Clark 2010) and that non-conspecific organisms (e.g. native prey, competitors and predators) are already adapted to native invaders. Second, when compared to native invaders, we predict that the introduction of non-native invaders will be associated with greater impacts at higher levels of biological organisation (i.e. communities and ecosystems). This prediction is supported by the fact that non-native invaders are ecologically distinct from native species and represent a novel ecological actor for native prey, competitors and predators that lack shared evolutionary histories ('naiveté hypothesis', Sih *et al.* 2010; Saul & Jeschke 2015). Therefore,

it is expected that the introduction of non-native salmonids will impact a wide range of native organisms through the establishment of novel biotic interactions and modify multiple components of the recipient ecosystems more dramatically compared to the introduction of native salmonids.

METHODS

Literature search and study selection

Our protocols for search and selection followed those outlined by Pullin & Stewart (2006) for a systematic review, which included formation of search protocol and data inclusion, data extraction and analysis. We initiated a literature search using the Institute of Scientific Information Web of Science online database (http://webofknowledge.com) to identify peer-reviewed articles published through the end of 2015 that used manipulative studies to quantify the effects of salmonids introductions (native and non-native invaders) on native organisms and recipient ecosystems. We employed the following search string to identify relevant papers by topic (i.e. using key words combinations): (salmonid* or trout* or salmon* or char or Salmo or Salvelinus or Oncorhynchus) AND (invasi* or invader or alien or exotic or nativ* or nonnative or non-native or introduc* or naturaliz* or domesticated* or non-indigenous or nonindigenous or indigenous or stocked or stocking or hatchery-reared*) AND (experiment* or manipulation* or manipulated* or treatment or control or laboratory or channel* or river* or stream* or lake* or tank* or mesocosm* or enclos* or removal or eradication or suppression) AND (impact* or effect* or consequence* or interaction* or affect* or comparison* or change* or modif* or influence). We filtered search results within subject areas of Genetic, Infectious Diseases, Environmental Science, Ecology, Zoology, Demography, Behavioural Science and Marine Freshwater Biology.

Our initial literature search identified 3908 published papers. Based on a screening of titles and abstract, 326 full-text articles were subsequently assessed for their eligibility in the analysis (Fig. S1). Criteria for final inclusion were: (1) studies that compared organism/ecosystem responses when exposed to introduced native and non-native salmonids (i.e. *treatment*) vs. without introduced salmonids (i.e. *control*) and (2) manipulative experimental studies (i.e. removal or addition of non-native species, using laboratory condition, outdoor mesocosms, or *in situ* enclosures/exclusions) to avoid the potential effects of other confounding factors (e.g. Twardochleb *et al.* 2013; Thomsen *et al.* 2014). We then reviewed the references section of each relevant article to identify potential articles and also performed a forward search on Web of Science to identify recent articles. With this procedure, we identified 339 potential studies in total for inclusion. However, the majority of these studies were excluded from the final analysis because (1) they were based only on observational approaches (no manipulation), (2) they lacked sympatric (i.e. control with native only) or allopatric (i.e. coexistence between native and non-native) treatments and (3) they focused exclusively on non-native organisms (Fig. S1). In addition, we excluded studies when non-native treatments contained several species of

invaders to avoid accounting for their potential interactions. Finally, as we were interested in studies reporting raw data (mean and standard error or standard deviation values), it was necessary to exclude studies for which sample size, standard error or standard deviation were missing and studies that only reported statistical results (e.g. *P*-values).

Data extraction

The final database contained 64 studies that included 481 assays quantifying the ecological impacts of native and non-native salmonids (see full list of references in supplementary material). For each article, we extracted the identity of the introduced species and its origin (native or non-native), the geographical location, the species name and taxonomic group of native organisms (fish, amphibians and invertebrates) and the response variables measured (e.g. testosterone, reproductive success, species richness or energy flux; see Table S1 for full list). We classified the impacts into different levels of biological organisation (i.e. genetic, individual, population, community and ecosystem) following Cucherousset & Olden (2011). Response variables were subsequently grouped into various classes of traits (Table S1). We then coded each study based on the experimental approach, i.e. laboratory or outdoor mesocosms (*ex situ*) and sections or cages (*in situ*) to investigate potential influence of the study type on impacts measured. To assess the largest potential impacts (Twardochleb *et al.* 2013), we included the data from the treatment with the highest density when different fish densities were used in the experiment. When several temporal measurements were performed, we selected data from the last sampling date. Finally, we extracted statistics for control and treatment groups, including sample sizes, means and variations (standard deviations, standard errors or confidence interval), from tables and results in the articles. When necessary we extracted data from published figures using ImageJ (Rasband 1997–2015). For articles that did not report those statistics, we requested the data from the corresponding author. To retain as much information as possible across levels of biological organisation and response traits, we did not pool statistics across different assays originating from the same study (e.g. different non-native species or response traits measured). We considered each experiment separately because they correspond to independent measures of ecological impacts (see next section about investigating potential pseudo-replication).

Among the studies reporting ecological impacts of introduced salmonids, 64% (*n* = 41) were performed in North America, in which 42% for USA (*n* = 27), and only 11 studies were from Europe, 5 from Asia, 6 from Oceania (New Zealand Australia), 1 from South America and 1 from Africa (Fig. S2). A geographic bias commonly observed for aquatic studies on invasive species (Thomsen *et al.* 2014) and more broadly all invasive species (Pyšek *et al.* 2008). Studies were dominated by three introduced species, namely brown trout (28%), rainbow trout (21%) and brook trout *Salvelinus fontinalis* (14%). Most studies reported ecological impacts at the individual and population levels (60.5 and 23.9% of assays respectively), followed by a lower proportion of studies reporting impacts at the community (12.5%) and the

ecosystem (2.9%) levels. Only one study in our database quantified the genetic impacts of introduced salmonids (Caudron *et al.* 2011), therefore this level of biological organisation could not be considered further.

Data analyses

We quantified the response of native organisms and recipient ecosystems to the introduction of salmonids using standard meta-analytical approaches. Meta-analyses are based on the comparison of 'effects' (e.g. means) between treatment (T) and control (C). We used Hedges'*d* as an estimate of the standardised mean difference that is not biased by small sample sizes (Borenstein *et al.* 2011) (eqn 1):

$$d = \frac{X'_T - X'_C}{S} g \qquad (1)$$

where X' is the mean of the response variable of the treatment (X'_T) or control groups (X'_C), S is the pooled standard deviation (eqn 2) and g is the weighting factor accounting for sample size bias (eqn 3) calculated as:

$$S = \sqrt{\frac{(N_T - 1) \times \sigma_T^2 + (N_C - 1) \times \sigma_C^2}{N_T + N_C - 1}} \qquad (2)$$

and

$$g = 1 - \frac{3}{4 \times (N_T + N_C) - 9} \qquad (3)$$

where N is the sample size of the treatment (N_T) or control (N_C) groups and σ^2 is the variance of the treatment (σ_T^2) or control groups (σ_C^2) (eqn 2).

Hedges'*d* is a unit-free metric, ranging from $-\infty$ to ∞, which gives the intensity of the impact and its direction. Here, we considered any changes induced by introduced salmonids, irrespective of the direction of the Hedges'*d*, as an ecological effect on native species and the recipient ecosystem. To do so, we ensured that all the scales point in the same direction by multiplying the mean values of some traits (namely aggressiveness, agonism, primary production, migration, movement, activity mortality and hormones) by -1, whatever the sign of the mean values, so that an increase in these traits was interpreted as a negative impact (see Table S1).

Meta-analyses were conducted using the R package 'metafor' (Viechtbauer 2010). For all analyses, we used random-effects and mixed-effects models (with grouping variables). Random-effects models assume that random sources of variation in effect sizes exist between studies and that sampling error accounts for heterogeneity within studies. Mixed-effects models allow testing for significant differences in effect sizes between grouping variables. To test whether introduced native and non-native salmonids induce global ecological impacts, we used a mixed-effects model to measure the effect sizes for each type of introduced species (i.e. native vs. non-native introductions). We also used mixed-effect models with levels of biological organisation, response traits or type of native organisms as grouping variables to compare the intensity of the ecological impacts induced by native and non-native invaders. Means of effect sizes, bootstrapped 95% confidence

intervals (CI, within brackets) and *P*-values (based on 10 000 iterations) are subsequently reported. We evaluated the statistical significance of effect sizes for each grouping variables by ensuring that the 95% CI did not overlap with 0. We examined heterogeneity in effect sizes by means of Higgins'I^2, the percentage of 'unexplained' variance, and the Q-test (hereafter, Qt) which is the weighted deviations about the summary effect size. Note that Q-test has low power when the number of studies and/or sample sizes is small and should be interpreted with caution. To evaluate whether variation among studies in effect size is associated with group differences, we also reported the test of moderators (Qm) from mixed-effect model. The test of moderators Qm is used to determine whether the differences in the average effect of one group (e.g. native invaders) differ from the average effect of another group (e.g. non-native invaders) and corresponds to the square of the z-score for pairwise comparisons. Qm values and *P*-values are subsequently reported.

Many studies reported data on the effect of the same non-native species on different response traits. Considering all measures simultaneously may contribute to pseudo-replication in the meta-analysis. To test the influence of pseudo-replication, we followed the same procedure as Vilà *et al.* (2011) by randomly selecting a single effect size per article (i.e. 'sampled datasets'), for (1) both native and non-native salmonid invaders, (2) levels of organisation (non-native invaders only), (3) groups of organisms and (4) three response variables with the largest sample sizes: indirect fitness, demography and biomass. We then compared the impacts measured from the 'sampled datasets' to those estimated with the entire dataset (i.e. all effects size included). Specifically, we fitted two separate random-effects models for each type of datasets. To test for the existence of a difference between the two, we then compared the two estimated effects size using a fixed-effect model with data source (entire vs. sampled datasets) as a covariate. Influence of pseudo-replication is evident if the difference of effects size was not null and the 95% CI did not overlap with 0. Our results did not indicate an influence of pseudo-replication (Table S2) and, as a consequence, we felt confident to include all the data in our analyses.

Meta-analyses can be influenced by a publication bias associated with the tendency of journals to publish studies with significant results (i.e. leading to an asymmetry of effects size), therefore we examined the robustness of our results via inspection of: (1) funnel plots, (2) Egger's regression test, (3) the trim-and-fill method and (4) the 'fail-safe number'. The funnel plot is a scatter plot of the effect sizes from individual studies against their precision. A bias is visually identifiable by an asymmetrical appearance of the funnel plot, for example because studies without statistically significant effects remain unpublished. The level of significance of the asymmetry is also tested using the Egger's regression method (i.e. a linear regression between effect sizes from individual studies against their precision). The trim-and-fill method helps correct for publication bias by inspecting the symmetry of effect sizes and precisions (due to the suppression of the most extreme results on one side of the funnel plot). The method estimates the number of missing studies to add to the observed data to attain symmetry, i.e. the funnel plot is more symmetric

(provided in Tables S3–S6). Finally, the fail-safe number (*Fs*, Rosenberg 2005) indicates the number of non-significant unpublished studies that would be needed to reduce the significant level of the meta-analysis to *P* = 0.05. Fail-safe number is considered robust when $Fs > 5N + 10$ with N being the number of assays included in the analysis. In the present, the overall Fs was 31426 which is larger than $5 \times 481 + 10 = 2415$, suggesting that much more assays than those included in our meta-analysis would be needed to reduce the significance of the meta-analysis (also reported in the text). However, the funnel plot was noticeably asymmetric (Fig. S3). This visual observation is confirmed by Egger's test, which yields a statistically significant *P*-value (t-score = −2.5, *P* = 0.0127). Taken together, this indicates that our results are robust and, although the actual impacts may be smaller than reported, they are unlikely to be null.

RESULTS

Introduced salmonids have caused significant ecological impacts (d = −0.32 [−0.40; −0.24], *P* < 0.001; Fig. 1) and the global impacts were significant for both native (d = −0.66 [−0.96; −0.36], *P* < 0.001, Fs = 1053) and non-native (d = −0.29 [−0.36; −0.21], *P* < 0.001, Fs = 20 742) invaders. Importantly, the global effect differed significantly between the two types of invaders (Qm = 6.37, *P* = 0.01) with a stronger impact for native invaders compared to non-native invaders. We observed a high level of variability in the effect sizes (Table S3), indicating that ecological impacts varied significantly across levels of ecological organisation and taxonomy but not between the type of experimental approach (i.e. *ex situ vs. in situ*; Qm = 3.01, *P* = 0.09).

The ecological impacts of native invaders were significant at the individual level (d = −0.78 [−1.13; −0.44], *P* < 0.001, Fs = 1000) but not at the population level (Fig. 2, Table S4). We found only one manipulative study quantifying the impacts of native invaders at the community level (no significant impact) but none at the ecosystem level. For non-native invaders, significant impacts across all levels of biological organisation were observed (Fig. 2) despite a slight publication bias at the population and community levels (Table S4). However, the intensity of impacts did not differ significantly between levels of biological organisation, except for the population level that displayed significantly stronger impacts than at the individual (Qm = 5.65, *P* = 0.02) and the community (Qm = 4.54, *P* = 0.03) levels. The impacts were significantly higher for native than for non-native invaders at the individual level (Qm = 11.48, *P* < 0.001) while no significant difference (Qm = 1.53, *P* = 0.21) was observed at the population level between the two invader types.

Native invaders were found to induce significant effects on physiological and indirect fitness traits of native organisms (Table 1). Significant impacts of non-native invaders were observed on individual foraging and indirect fitness traits and, at the population level, on direct fitness and demography. At higher levels of biological organisation, we also observed significant impacts of non-native invaders on the biomass of native organisms and primary production (Table 1). Overall, the impacts on response traits at the individual level were not
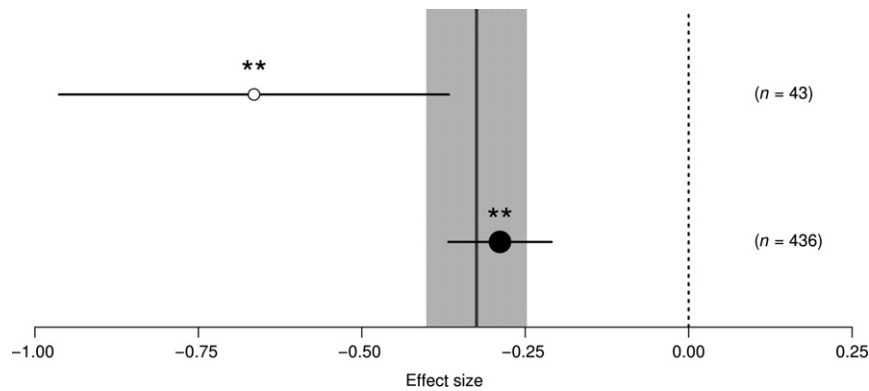
Figure 1 Overall ecological impacts of native (white circle) and non-native (black circle) salmonids. The size of the circles represents the mean effect size and is scaled to the precision of estimates. Error bars represent bias-corrected 95%-bootstrap confidence intervals (based on 10 000 permutations). A significant effect is found when error bars do not overlap zero (significant effects are indicated: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). The number of assays (n) considered in the analysis is indicated in parentheses. Overall impact (all invaders included) is also displayed: mean (dashed line) and 95% CI (grey envelop).
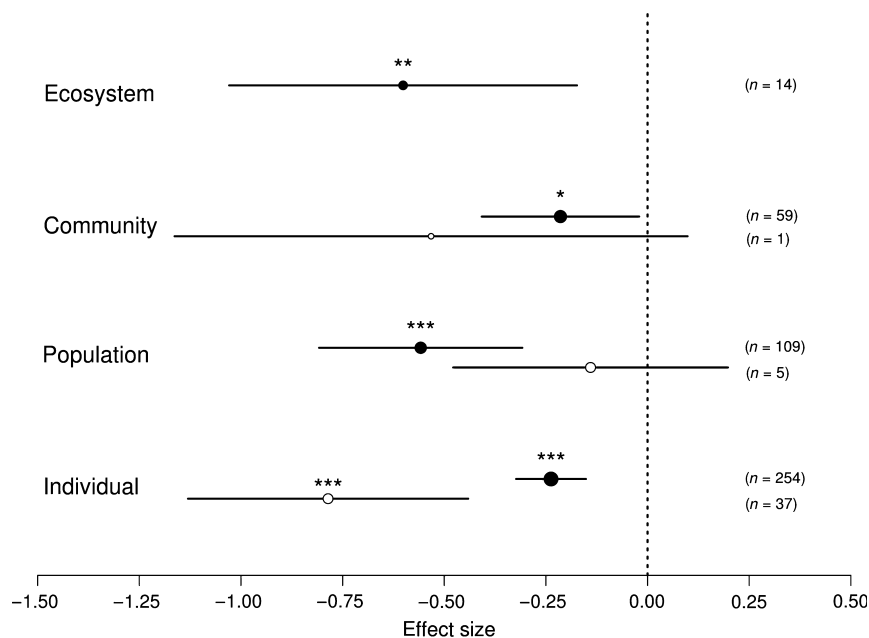

Figure 2 Ecological impacts of native (white circles) and non-native (black circles) salmonids across levels of biological organisation. The size of the circles represents the mean effect size and is scaled to the precision of estimates. Error bars represent bias-corrected 95%-bootstrap confidence intervals (based on 10 000 permutations). A significant effect is found when error bars do not overlap zero (significant effects are indicated: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). The number of assays (n) considered in the analysis is indicated in parentheses.

significantly different between native and non-native invaders, except in the case of physiological traits where native invaders induced stronger effects than non-native invaders ($Qm = 30.72$, $P = 0.001$).

Overall, introduced salmonids induced significant impacts on all native organisms investigated (Fig. 3; Table S6). For native invaders, significant impacts on native fish were observed ($d = -0.67$ [-0.98; -0.36], $P = 0.002$, Fs = 988). It was also the case for non-native invaders ($d = -0.26$ [-0.34; -0.17], $P < 0.001$, Fs = 8618) whose intensity of impacts on native fish was significantly lower than those induced by native invaders ($Qm = 7.46$, $P = 0.004$). Only one manipulative study quantified the impacts of native invaders on

invertebrates and the effect was not significant. The effects of non-native invaders differed between native organisms, i.e. significantly stronger on amphibians than on fishes ($Qm = 6.37$, $P = 0.012$) and marginally significant on invertebrates ($Qm = 3.71$, $P = 0.053$).

DISCUSSION

Using the widespread introduction history of salmon, trout and charr, we demonstrated that changing intraspecific diversity by introducing native invaders have stronger overall ecological effects than those associated with changes in interspecific diversity caused by non-native species

Table 1 Summary statistics of ecological impacts induced by native and non-native salmonids across response traits at different levels of biological organisation (I = individual, P = population, C = community and E = ecosystem)

Response trait	Native invaders			Non-native invaders		
	n	Hedges'd (95% CI)	P-value	n	Hedges'd (95% CI)	P-value
Physiology (I)	9	−2.30 [−3.41; −1.19]	**0.008**	25	0.02 [−0.24; 0.29]	0.862
Behaviour (I)	2	0.51 [−0.34; 1.37]	0.500	45	−0.22 [−0.48; 0.03]	0.089
Activity (I)	1	−0.52 [−1.93; 0.88]	1.000	15	−0.31 [−0.66; 0.02]	0.100
Foraging (I)	4	−0.93 [−1.60; −0.27]	0.125	41	−0.41 [−0.58; −0.24]	**< 0.001**
Habitat use (I)	1	−0.39 [−2.01; 1.21]	1.000	42	−0.09 [−0.41; 0.22]	0.562
Indirect fitness (I)	20	−0.34 [−0.56; −0.11]	**0.012**	86	−0.28 [−0.37; −0.19]	**< 0.001**
Direct fitness (P)	5	−0.14 [−0.48; 0.19]	0.687	27	−0.94 [−1.46; −0.43]	**< 0.001**
Migration (P)				1	0.54 [−1.08; 2.17]	1.000
Demography (P)				66	−0.57 [−0.92; −0.21]	**0.002**
Displacement (C)				23	−0.03 [−0.35; 0.28]	0.819
Biomass (C)	1		1.000	49	−0.25 [−0.46; −0.05]	**0.017**
Diversity (C)				2	−0.32 [−1.30; 0.67]	0.500
Energy flux (E)				3	−0.46 [−1.61; 0.69]	0.750
Primary production (E)				11	−0.65 [−1.13; −0.17]	**0.015**

The number of assays (n), mean estimated effect sizes (Hedges's d) and bias-corrected 95%-bootstrap confidence intervals (CI; based on 10 000 iterations) are reported. Bold values indicate a statistically significant P-value.

introductions. As predicted, we revealed that native invaders induced more pronounced impacts at the individual level when compared to non-native invaders. Our meta-analysis also demonstrated significant knowledge gaps regarding the ecological consequences of introduced native salmonids on recipient communities and ecosystems, precluding a robust evaluation of our second prediction. Together, these findings highlight the need to further consider the potentially changing ecological role of introduced native organisms (Carey *et al.* 2012). We also found that, for non-native invaders, ecological impacts differed between levels of biological organisation and native organisms, with higher impacts reported on amphibians than on fish and invertebrates.

Our study suggests that the ecological impacts of invader-induced changes to intraspecific diversity exceed those associated with changes to interspecific diversity, and that this difference was primarily driven by stronger impacts of native invaders at the individual level. Recent investigations have revealed higher invasion success and stronger ecological impacts of non-native plants (e.g. Li *et al.* 2015) and freshwater fishes (e.g. Ricciardi & Atkinson 2004) that were closely related to native species. Indeed, according to the 'pre-adaptation hypothesis' (Ricciardi & Mottiar 2006), native invaders that share similar ecological traits with resident species should benefit both in terms of population establishment and the

acquisition of resources. Extending this idea, we suggest that native invaders induce higher ecological impacts because enhanced local abundances are favoured in pre-adapted environments, which when combined with high ecological similarity can lead to heightened intraspecific competition with conspecifics. Moreover, native prey, competitors and predators are already adapted to native invaders so that impacts should be mainly directed toward native conspecifics, limiting the impacts at higher levels of organisation. Correspondingly, most of studies available in our meta-analysis investigated the impacts of native invaders on conspecific salmonids (with the exception of one study on invertebrates), precluding to test the prediction of lower impacts of intraspecific introductions on other native organisms than non-native invaders. This highlights a significant knowledge gap addressing the potential effects of native invaders on non-conspecific organisms, limiting our understanding of the ecological impacts of changes in intraspecific diversity.

Our finding that changes in interspecific diversity induced significant global ecological impacts across all levels of biological organisation is supported by ecological theory positing that non-native invaders should benefit from reduced biotic interactions with resident species compared to native invaders because ecological similarity diminishes with decreasing phylogenetic relatedness (encapsulated in the 'Darwin's
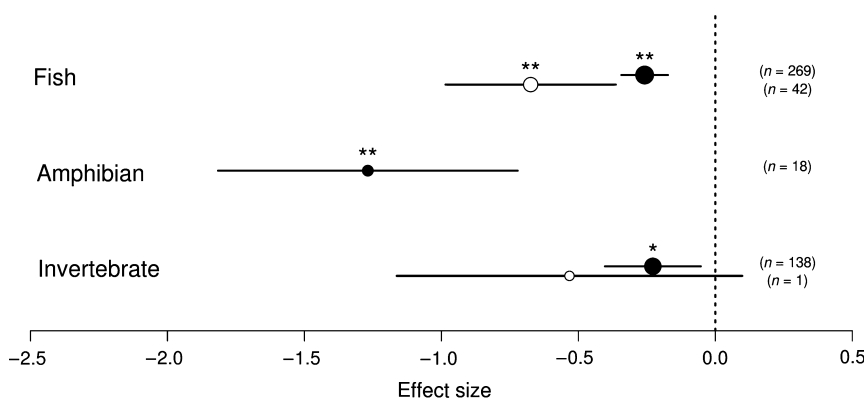
Figure 3 Ecological impacts of native (white circle) and non-native (black circles) salmonids on organism groups: Fish, Amphibians and Invertebrates. The size of the circles represents the mean effect size and is scaled to the precision of estimates. Error bars represent bias-corrected 95%-bootstrap confidence intervals (based on 10 000 permutations). A significant effect is found when error bars do not overlap zero (significant effects are indicated: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). The number of assays (n) considered in the analysis is indicated in parentheses.

naturalization hypothesis'; Burns & Strauss 2011). Moreover, prey, parasites and predators lack shared evolutionary histories with non-native species ('naïveté hypothesis'; Saul & Jeschke 2015) while native invaders should face stronger biotic pressures from co-adapted predators and parasites in the recipient ecosystems (Vilà *et al.* 2011; Ricciardi *et al.* 2013). Empirical tests of these hypotheses are still limited and somewhat inconclusive (e.g. Diez *et al.* 2008; Bezeng *et al.* 2015), potentially because the success of non-native invaders is highly context-dependent and influenced by local abiotic conditions (Ricciardi & Mottiar 2006; Korsu *et al.* 2010; Strecker & Olden 2014).

We observed that native invaders displayed significantly stronger impacts than non-native invaders at the individual level. Despite a bias toward conspecific salmonids and low sample size for some traits, and thus the requisite caution must be associate with these findings, we found that physiological traits (mainly associated with stress response) were most impacted by native invaders. This suggests that the physiological traits measured here are likely to be the basis of the initial response of organisms facing introduced conspecifics, although this would require further investigation. Our study also highlighted the existence of significant impacts of native invaders on indirect fitness (e.g. growth, condition), suggesting that evolutionary consequences could be expected. Moreover, despite a limited number of experimental studies at the genetic level, genetic effects could be largely anticipated based on field observations (see Laikre *et al.* 2010; Lorenzen *et al.* 2012 for review). Introgression with domesticated strains is indeed far more common than interspecific hybridisation, modifying evolutionary trajectories and then playing an important role in the evolution of many taxa (Allendorf *et al.* 2001; Laikre *et al.* 2010). Uninterrupted introduction of native invaders might lead to introgression (e.g. Caudron *et al.* 2011), impacting genetic diversity with a homogenisation or replacement of local genotypes and in turn, a disruption of local adaptation (Andow & Zwahlen 2006; Bourret *et al.* 2011). Time since invasion can also modulate the evolutionary and ecological impacts induced by invaders (Strayer 2012; Dostál *et al.* 2013) and it is important to note that our meta-analysis used only

manipulative studies that are usually performed on short-term periods and failed to report the length of time native organisms have been exposed to non-native salmonids. If the introduction dates of the species in the recipient ecosystems are known, such information can be used to determine whether the length of exposure modulates the ecological impacts of introduced salmonids and whether the time since invasion modifies differentially the impacts induced by native and non-native invaders. Both are ripe areas for future investigation.

Perhaps, the most striking result is the lack of knowledge regarding the ecological consequences of native salmonids introductions on recipient communities and ecosystems. Our systematic literature survey revealed no studies investigating the impact of native invaders at the ecosystem level and research focusing on population and community levels was very limited ($n \leq 5$). This made it impossible to evaluate our prediction of stronger impacts of non-native invaders at higher levels of biological organisation compared to native invaders. Similarly, high uncertainty associated with low sample sizes at higher levels of organisation influenced our capacity to explore patterns for non-native invaders. In addition, we observed that non-native salmonids induced significant effects on all taxonomic groups with the amplitude of impacts being significantly stronger on amphibians. This result suggested that amphibians are more susceptible to salmonids predation than fish and invertebrates. This is likely driven by the fact that, in most cases, studies investigating the impacts of introduced salmonids on amphibians were performed in fishless lakes where amphibians demonstrated complete naïveté to fish predators, as opposed to invertebrates and other fish species that are likely to have prior experience with predatory fish. We also found that native invaders induced stronger impacts on native fish compared to non-native invaders. This might be driven by a potential taxonomic asymmetry across native fish species on which impacts were quantified. Indeed, for native invaders, recorded impacts focused mainly on *Oncorhynchus* (50% of assays), *Salmo* (41%) and *Salvelinus* (9%) genus as recipient species while impacts of non-native invaders were measured on native *Salmo* (51%), *Salvelinus* (28%), *Oncorhynchus* (13%) and other non-salmonid fishes

(8%). This highlights a lack of knowledge on the impacts of introduced salmonids on non-salmonid fishes in experimental studies; a topic that deserves attention.

Overall, our findings suggest that the ecological impacts of native invaders rival, or possibly exceed, those associated with non-native invaders. However, studies examining the impacts of native salmonids were found only at the lowest levels of biological organisation and focused primarily on conspecific organisms, emphasising important knowledge gaps regarding potential ecological consequences on non-conspecific organisms and at the community and ecosystem levels. Such studies are greatly needed because a growing body of literature has shown that variations in individual traits within a species can affect ecosystem functioning (e.g. Harmon *et al.* 2009). We argue that understanding the community and ecosystem consequences of changes in intraspecific diversity induced by native invaders should be a priority because volunteer and accidental introductions of native species will continue to grow in the future.

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AUTHOR CONTRIBUTIONS

JC, JDO and MB designed research; MB and JC prepared the database; MB analysed data; and MB, JC and JDO wrote the article.

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