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Do trout respond to riparian change? A meta-analysis with implications for restoration and management

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Summary

1. There are strong conceptual links between riparian zones and freshwater fish via riparian influences on water quality, habitat quality and availability, and trophic dynamics. Many of the world's riparian zones are, however, severely degraded, and the key functions they provide for fish lost or compromised. In response to their on-going degradation, extensive works are underway globally to restore the structure and

function of riparian zones. Despite intense effort, we lack clear empirical evidence of how fishes respond to changes to riparian zones.

2. We conducted a systematic review and meta-analysis to explore how trout (specifically brook, brown, cutthroat, rainbow and steelhead), fishes with globally important social, cultural, economic and ecological value, respond to key drivers of riparian alteration. We also identified where and with which species current research is being undertaken and examined the broad characteristics of different studies (e.g. location, focal species, length of study, study design) to better understand potential knowledge gaps in our understanding of how trout respond to changes in riparian zones.

3. ISI Web of Science and Google Scholar were searched for relevant peer-reviewed studies, and from an initial 6514 papers, 55 were included in the formal meta-analysis. From these, we extracted data to calculate response ratios comparing biological attributes at sites with altered riparian characteristics to suitable unmanipulated control sites. We used linear mixed effects models to assess general and species-specific trout responses to eight key 'drivers' of change in riparian condition.

4. Most studies were undertaken in North America using control-impact designs. We found little evidence for species-specific responses to riparian change, and surprisingly, many drivers deemed important in the literature (e.g. revegetation, managed canopy removal, grazing, and forestry clearing) did not consistently influence trout population- or individual-level metrics. Nonetheless, trout populations did respond positively to increasing woody debris and livestock exclusion (+87.7% and +66.6% respectively), and negatively to bushfire and afforestation (-67.4% and -88.2%, respectively). We found some evidence that positive riparian changes may just attract fish (i.e. increased abundance or density) rather than enhance actual population production (i.e. individual size and growth). Whilst this conclusion necessarily needs to be interpreted with caution, it does suggest that targeted research on the 'production vs. attraction' hypothesis would be beneficial.

5. Several key drivers of riparian change, such as revegetation activities, have been the focus of only limited research. More generally, long-term data are lacking for most drivers. Both of these key information gaps limit our ability to predict the likely timing and trajectory of responses to riparian management. Robust monitoring programs in areas with altered riparian zones – particularly using BACI designs to

allow changes to be attributed to management – are required. The knowledge gaps present for fishes as ecologically, socially and environmentally important as trout are likely to be even more pronounced for the majority of less-studied freshwater fish species.

Introduction

Riparian zones are the interface between terrestrial and lotic environments and play a critical role in modulating a range of ecosystem processes that affect aquatic organisms, including fish (Gregory *et al.*, 1991; Naiman & Decamps, 1997; Pusey & Arthington, 2003). The multitude of pathways linking fish to riparian zones can be categorised into three main groups: riparian influences on water quality, habitat quality and diversity, and trophic dynamics (see Pusey & Arthington, 2003). Fish are likely to be affected by processes in the riparian zone that have resultant impacts on bank stability and erosion, stream flow, water temperature and quality, and inputs of sediments, nutrients and organic matter. Whilst many studies have demonstrated clear links between fish and the condition of riparian zones (e.g. Baxter, Fausch & Saunders, 2005; Kawaguchi & Nakano, 2001), a solid understanding of the spatial and temporal scales of fish response to riparian change is less well understood.

Human population expansion and associated intensification of land clearing, forestry and agriculture have all impacted on waterways and their riparian zones with resultant serious consequences for freshwater fishes (Meyer & Turner, 1992; Tilman, 1999; Jones *et al.*, 2010). For example, increases in stream sedimentation and turbidity can affect in-stream primary and secondary productivity, and when coupled with reductions in terrestrial food inputs due to lost riparian vegetation, can severely limit food resources for stream fishes (Meehan, 1991; Saunders & Fausch, 2012; Wipfli, 1997). In addition, the riparian canopy plays an important role in regulating the temperature of lotic systems and its removal may result in increased water temperatures beyond levels fish can tolerate (Broadmeadow *et al.*, 2011). Conversely, for cold-climate streams the removal of riparian shading may have positive impacts on fish assemblages through increasing solar radiation and thus water temperature, primary and secondary productivity, and increasing feeding efficiency (Riley *et al.*, 2009; Wilzbach *et al.*, 2005; Bilby & Bisson, 1992; Wipfli, 1995). As these examples demonstrate, there is a strong conceptual basis for predicting that fish are likely to respond to riparian restoration.

Efforts have increasingly been directed towards management activities that attempt to restore the ecological function of damaged riparian zones (Naiman & Latterell, 2005). Most commonly, these activities involve adding woody debris, replanting riparian vegetation, or erecting fences to exclude livestock (Lehane *et al.*, 2002; Ryder *et al.*, 2011; Summers, Giles & Stubbing, 2008). Many of these activities are implemented on the presumption they will lead to desired ecological outcomes. However, concurrent monitoring to assess progress towards these outcomes is generally lacking, as is the empirical research necessary to understand the potential pathways of effect (Palmer *et al.*, 2005). Without this information, it is impossible to evaluate the efficacy of different riparian management activities in meeting their desired outcomes.

In this study, we systematically assess evidence for how trout respond to key drivers of riparian change. Trout are one of the most important and charismatic freshwater fish, and are now distributed throughout most of the globe where they form important components of both recreational and commercial fisheries (Crawford & Muir, 2008; MacCrimmon, Marshall & Gots, 1970). Trout also fulfill key ecological roles such as being major predators in their native and introduced range (Quinn, 2011) and linking terrestrial and aquatic food webs and nutrient flows through interactions with riparian zone species (Baxter *et al.*, 2004; Epanchin, Knapp & Lawler, 2010; Courtwright & May, 2013).

Trout declines across their native range have been linked to pollution, exotic species introductions, forestry and agricultural practices, catchment modification, river regulation, over-exploitation, and climate change-related temperature and hydrological changes (Clews *et al.*, 2010; Marschall & Crowder, 1996; Kovach *et al.*, 2016). Many of these factors directly impact riparian zones and have prompted targeted riparian rehabilitation and restoration programs, along with in-channel focussed restoration efforts (Whiteway *et al.*, 2010). For example, managing grazing regimes and constructing fences to exclude livestock from streams can enhance trout populations through the preservation and regrowth of riparian vegetation, a reduction in bank erosion, and the promotion of terrestrial invertebrates inputs (Summers, Giles & Stubbing, 2008; Saunders & Fausch, 2012). Despite widespread implementation of riparian management activities based on our conceptual understanding of fish-riparian linkages, we still lack a broad quantitative and comparative assessment of how trout respond to changes to riparian zones. Such an assessment would help us better understand the links between trout and riparian zones, and more specifically how riparian management might affect trout.

We use a systematic review and meta-analysis to assess how trout (specifically brook, brown, cutthroat, rainbow and steelhead) respond to eight common and ubiquitous drivers of riparian change: woody debris addition, forestry clearing, grazing, stock exclusion, managed canopy removal, afforestation, bushfire and revegetation. Systematic reviews and meta-analyses provide the framework and tools to quantitatively summarise the results from many empirical studies (Pullin & Stewart, 2006) and examine the potential generality of responses to environmental change. Meta-analysis provides an opportunity to increase statistical power, determine large-scale patterns across geographical regions, and greatly assist evidence-based conservation and management (Stewart, 2010). The use of meta-analysis in ecology has progressed rapidly (Kettenring & Adams, 2011; Mantyka‐Pringle, Martin & Rhodes, 2012; Rodríguez‐Castañeda, 2013) as appreciation of the benefits have become apparent (Stewart, 2010). Using such an approach here allows us to make a broad-scale assessment of how trout respond to riparian management, and provides a ready means for identifying which restoration strategies are likely to be most successful.

We had three aims: (1.) extract and analyse published data to quantify how trout respond to different drivers of riparian change, (2.) identify where and with which species current research is being undertaken to examine trout responses to changes in riparian zones, and (3.) evaluate the characteristics of study designs (i.e. time since riparian change; design type: Before-After/Control-Impact vs. Control-Impact vs. Before-After) implemented to measure trout responses to riparian changes. We use our results to evaluate evidence linking trout responses to riparian management, and to identify knowledge gaps that limit current understanding of these responses.

Methods

Literature search

We conducted literature searches using ISI Web of Science and Google Scholar on 3rd August 2016 (see Table S1 in Supporting Information). Google Scholar results were restricted to the first 50 papers for each of the search terms. In addition, we examined the available grey-literature and reference lists of selected papers, including related meta-analyses and reviews for additional studies. It should be noted that our grey literature search was not exhaustive due to the complexities of finding and obtaining unpublished government and consultancy reports. Nonetheless, our focus was primarily on understanding research efforts rather than monitoring more generally which is often the focus of grey literature studies. Excluding duplicates, 6514 papers were systematically screened for inclusion in the meta-analysis (Figure 1). Four criteria determined study inclusion: (i) focused on the following species of 'trout' (and their variants; family Salmonidae): brook trout/charr (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarkii*), or rainbow or steelhead trout (*Oncorhynchus mykiss*), (ii) published quantitative data on trout responses to riparian change, (iii) utilised a before-after (BA), control-impact (CI) or before-after control-impact (BACI) design, and (iv) the effects of individual drivers of riparian change could be isolated from other changes that may have taken place.

Defining the question and outlining the scope for a quantitative review is an essential step and necessarily involves comprise between holistic and reductionist approaches (Pullin & Stewart, 2006). We selected 'trout' species because they have strong cultural, economic and environmental values and are the focus of major management actions across their native and introduced ranges. Some studies pooled observed responses across species; in these cases the data were categorized as 'genus *Oncorhynchus*' (if rainbow, cutthroat and steelhead combined) or '*combined species*' (if combinations of brown, brook, rainbow or cutthroat). We did not include studies focusing on Atlantic and Pacific salmon (migrating or landlocked) as we were primarily interested in how trout respond to riparian change, and resources did not permit a larger scoped study.

Data extraction, classification and effect-size calculation

Human-induced changes to riparian zones can occur via numerous pathways, and studies were only included if there was a reference to the driver directly affecting the riparian zone. We defined eight 'drivers' of riparian change (see Table 1 for driver descriptions and what we classified as a treatment and control for each). Stock exclusion and grazing were analysed as separate drivers as they differ in what constitutes the relevant control site for comparison. For grazing studies, treatment (i.e.

grazed) sites were compared to controls that had never been grazed, while for stock exclusion currently grazed sites (control) were compared to treatment sites that are fenced and currently ungrazed but with a history of grazing. Although the addition of woody debris is not technically an alteration to the riparian zone, we included it as a driver due to its commonality as a restoration technique, and the fact that wood entering streams and rivers often comes as inputs from the riparian zone and thus is impacted by riparian change (reviewed in Roni *et al.*, 2015).

We extracted a range of information from each study, including: geographic location (continent, country), study design (i.e. BACI vs. CI vs. BA), trout species, the driver of riparian change, how long ago the change occurred (years), the biological response type measured (individual: size or survival; population: density, biomass or abundance), and also the life stage at which these responses were measured (simplified to juvenile or adult).

We extracted treatment and control group data from the text, tables or figures (using graphical digitiser software) of each paper, allowing the calculation of log response ratios following published methods (Hedges, Gurevitch & Curtis, 1999). For BA and CI studies: RR = ln[I or A] - ln[C or B], and for BACI studies: $RR = \ln[I_A / C_A] - \ln[I_B / C_B]$, where RR is the response ratio, I is the impacted site mean, C is the control site mean, A is the after mean, and B is the before mean.

Response ratios greater than zero, thus, indicate a positive individual- or population-level response within impacted/altered sites compared to control/reference sites (CI studies), or for post-alteration compared to pre-alteration (BA studies). A log response ratio cannot be defined for situations when the numerator or denominator is zero (Hedges, Gurevitch & Curtis, 1999). Adding a constant to these values can induce serious bias (Rosenberg, Rothstein & Gurevitch, 2013), so we took the more conservative approach of excluding these data from further analysis. This resulted in 35 site or time observations of trout response to riparian change to be excluded from our analysis (5.8% of the total data).

If papers recorded data for multiple years, log response ratios were calculated for each year. Similarly, if papers recorded data from multiple experimental sites or species, we calculated separate response ratios for each. In some circumstances, we swapped the sign of the response ratio to ensure that its interpretation was consistent with all studies in a category (i.e. drivers are operating in the same direction). This was only done for one driver (woody debris addition) where the negative impacts of 'woody debris removal' were reversed so that they reflect the benefit of 'woody debris addition'. There was no significant difference in response ratio values between these two types of woody debris study (p=0.691). We exponentiated response ratios throughout to provide more easily interpretable percentage differences.

Data analysis

Initial modelling (approach outlined below) suggested that there was minimal difference in the direction and magnitude of driver effects within each individual- or population-level response type (see Figure S1). These results, and the low sample size for some response types (e.g. just one paper estimating survival response ratios), meant that for subsequent analyses we pooled data under 'individual' or 'population' groups. As such, throughout the manuscript changes to population-level 'response' refer to general changes in abundance, densities and biomass, whilst individual-level changes refer to general changes in the size, growth and survival of trout.

We used linear mixed effects models to quantify overall (all species combined), then species-specific, responses of trout to each riparian driver. Response ratios pertaining to individual and population level data were modelled separately. Driver (eight levels) was fit as a fixed effect and the model intercept was suppressed so that we could estimate a separate coefficient for each driver. We adopted a two stage modelling approach, first analysing all species pooled (with species fit as a random effect, see below), then each species separately. We did this because not all species were exposed to each driver, precluding the exploration of species by driver interactions (i.e. formal comparison of species' responses to each driver). A purely additive model (driver + species) is not informative because it is irrelevant to compare absolute differences in species-specific response ratios in isolation (e.g. in general brown trout have bigger response ratios than rainbow trout)

In our first suite of models we fit a complex random effect structure to the combined-species data for individual and population level responses. 'Species' (7 levels based on lowest possible taxonomic resolution: brown, rainbow, brook, cutthroat, steelhead, *Oncorhynchus* combined, undefined trout) was nested within 'site' (unique identifier), which in turn was nested within 'study' (i.e. paper). 'Species' nested within 'site' induced a correlation amongst RRs from the same species collected at the same time and site (e.g. between rainbow trout size and density) or through time at a site (i.e. repeated surveys). 'Site' nested within 'study' induced a correlation amongst all observations (across species) at a given site and accounted for common local environmental or contextual effects. The 'study' random effect accounted for any systematic differences due to, for example, common regional environmental conditions or study-specific methodologies or biases. In our second suite of species-specific models, we used the same random effect structure illustrated above but dropped the redundant 'species' random effect. Overall, our model structures allowed us to analyse the specific response ratio data from each species, site or time point within a given study rather than having to simplify data to a single mean value per study, removing the need to weight response ratio estimates by sample size as is commonly done in other aggregate-based methods of meta-analysis.

Where appropriate, competing models with different fixed effects structures were fit using maximum likelihood (ML) and compared using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). These values were rescaled as the difference between each model and the model with the lowest AIC_c (ΔAIC_c) for a given data set. The optimal response ratio model as selected by ΔAIC_c was then re-fit using REML to produce unbiased parameter estimates. Analyses were performed using the lme4 package (Bates *et al.*, 2013) in 3.3.1 (R Development Core Team, 2016).

Results

Fifty-five of the initial 6514 papers were relevant at the full-text level (see Appendix S1), and we extracted 129 individual- and 370 population-level response ratios (499 total) from these papers. The majority of studies focused on the effects of adding woody debris and forestry clearing, and most studies were conducted in North America and Europe, with a small number from South America and Australia (Figure 2). Many studies reported effects on multiple trout species, from multiple impact sites and/or for several years after the alteration.

Study design

The primary experimental design used was control-impact comparisons (CI: 64%), followed by before-after control-impact (BACI: 20%) and before-after (BA: 16%). The overall average time after the riparian alteration when trout monitoring was conducted (based on all RR) was 8.28 years (±0.57 SE, range: 0.08-65 years), although there was considerable variation among the primary drivers analysed (Table 1). Grazing studies had the longest (22.9 years) and revegetation studies the shortest (1.5 years) average interval between riparian change and fish monitoring.

Overall responses to drivers of riparian change

Our models showed that overall alterations to the riparian zone strongly affected population-level trout responses (AIC_c null model (no driver effect, k=5): 955.3 vs. AIC_c driver model (k=12): 931.1; ΔAIC_c : 24.2), but had little effect on individual level responses (AIC_c null model (no driver effect k=5): 156.8 vs. AIC_c driver model (k=10): 160.4; ΔAIC_c : 3.6; Figure 3). At a population level, trout responded positively to increases in the amount of large woody debris and livestock exclusion (average increase of 87.7% and 66.6%, respectively) and responded negatively to bushfire and afforestation (average decrease of 67.4% and 88.2%, respectively). Despite reasonable sample sizes (≥20 RRs), we detected no significant directional effect (95% CI overlapping zero) of forestry clearing, grazing, or managed canopy removal on trout populations (Figure 3). Limited data was available for studies investigating the effects of revegetation (11), making it difficult to draw conclusions on the effects of this driver. There was no clear effect of any riparian driver on individual level responses, despite large sample sizes being present for woody debris addition (20 RRs) and forestry clearing (72 RRs).

Species-specific responses

A total of 384 of 499 response ratios were resolved to the species level (see Table S2) and used in species-specific models of driver impact (Figure 4a,b). At the individual level there was little evidence of any driver affecting trout (bar a negative response of rainbow trout to bushfire), most likely due to small sample sizes. At the population level, small sample sizes also resulted in decreased confidence of effect size magnitude. We did however detect strong positive responses of brook trout populations to stock exclusion and forestry clearing, positive impacts of woody debris addition on cutthroat and rainbow trout populations, and negative effects of afforestation on brown and rainbow trout populations.

Discussion

Overall responses to drivers of riparian change

Our review provides an important assessment of how changes to riparian zones affect trout. In summary, trout populations responded positively to increases in woody debris and excluding livestock, negatively to bushfires and afforestation, and not consistently to the other drivers of riparian change.

Adding instream woody debris is a common strategy to enhance fish populations (Howson *et al.*, 2012; Stewart *et al.*, 2006; Roni *et al.*, 2015), and can increase habitat complexity, provide food or habitat for prey species, or alter the stream channel by reducing water velocity and increasing stream depth and pool frequency (Keim, Skaugset & Bateman, 2002; Urabe & Nakano, 1998). Our results are consistent with previous work that has demonstrated the benefits of woody debris to trout (Sweka & Hartman, 2006; Degerman *et al.*, 2004; Gustafsson, Greenberg & Bergman, 2014; Whiteway *et al.*, 2010).

We found that trout responded positively to livestock exclusion, likely due to subsequent improvements in instream habitat condition. Bank erosion and bare ground are typically higher in grazed riparian zones, which often also have less woody vegetation, and fewer shrubs and groundcover plants (Kauffman & Krueger, 1984; Robertson & Rowling, 2000). Habitat conditions adjacent to grazed riparian zones can be worse for trout (e.g. less nutrient filtration, less shading) and reduce fish growth and abundance (Saunders & Fausch, 2012; Summers, Giles & Stubbing, 2005). Removing livestock may also alter channel geomorphology, improve water quality and increase terrestrial food supply (Opperman & Merenlender, 2004; Kauffman, 2002; Saunders & Fausch, 2012). These changes may consequently lead to an overall improvement in the condition of instream habitat for trout..

Trout responded positively to livestock removal, but interestingly we did not observe a logical negative response to grazing. One possibility is that trout respond differently to alternative grazing practices, for example, some less intense methods (e.g. rotational grazing) may even increase trout biomass relative to more intensively grazed, or even ungrazed sites (see Saunders & Fausch, 2007; Saunders & Fausch, 2012). Alternatively, the pathways describing degradation and recovery from livestock may be different (Sarr, 2002). For example, trout responses may be more rapid following livestock removal relative to the negative impacts of grazing. Our results provide some support for this notion, given that stock exclusion and grazing studies differed considerably in their length (9.1 *vs* 22.9 years, respectively; Table 1), and several studies have shown short-term (<5 years) responses at stock exclusion sites (Keller & Burnham, 1982; Stuber, 1985; Bayley & Li, 2008). However, more work is needed to why this difference in responses was observed.

Trout populations responded negatively to afforestation, which typically involved streams surrounded by coniferous plantations within the riparian zone. This result was based on only three studies, but demonstrates that trout biomass and density may be lower at afforested sites both shortly after afforestation (Smith, 1980), and over longer time frames (> 40 years; Laura Miserendino *et al.*, 2011; Rees & Ribbens, 1995). Short-term responses may be caused by the indirect effects of reduced incident radiation on primary productivity, and reductions in terrestrial prey from (often exotic) monocultures relative to native vegetation (Smith, 1980; Tierney, Kelly-Quinn & Bracken, 1998). In the longer-term, acidification may occur in streams with coniferous afforested riparian zones lowering instream productivity and impacting trout (Rees & Ribbens, 1995).

Trout populations responded negatively to bushfires, which have the capacity to dramatically modify habitat conditions for fish (Lyon & O'Connor, 2008; Burton, 2005). Bushfires initially alter water temperature, chemistry and dissolved oxygen levels, and in the longer-term reduce woody debris input and riparian cover, and increase the input of sediments (Arkle, Pilliod & Strickler, 2010; Gresswell, 1999; Bisson *et al.*, 2003). Interestingly, trout populations may recover in the several years following fire-induced hydrological events that cause debris flows and short-term reductions in dissolved oxygen (Burton, 2005; Lyons *et al.*, 2000). Following fire, these disturbance-induced debris flows may stimulate primary productivity and subsequently enhance invertebrate biomass, with benefits for higher-trophic taxa such as fish (Harris, Baxter & Davis, 2015). Our bushfire dataset comprised just three studies (1, 2 and 6 years post fire) but these provide anecdotal support for relatively rapid population recovery. The largest change in average response ratio was between 1 and 2 years post fire (-2.355 to -0.664), with a more gradual recovery between 2 and 6 years post fire (-0.664 to 0.272). Longer term monitoring is necessary to better assess how trout respond to extensive bushfires.

No significant responses to managed canopy removal or forestry clearing were detected. Conceptually, these actions may modify instream conditions via increases in light penetration, water temperature or food availability (Johnson & Jones, 2000; Wilzbach *et al.*, 2005). In the short-term, these drivers might be expected to have some negative effects, for example, by reducing terrestrial food resource inputs (Dineen, Harrison & Giller, 2007; Kawaguchi & Nakano, 2001). However, managed canopy removal is also used to enhance primary and secondary productivity, and subsequently fish abundance (e.g. Wootton, 2012). In addition, an opened canopy can enhance foraging efficiency (Wilzbach, Cummins & Hall, 1986) and the quantity of aquatic invertebrate food sources (Riley *et al.*, 2009). It is likely that the overall lack of responses to these changes reflects the complex, multi-directional ways that riparian vegetation influences instream habitat conditions for trout

Although we assessed the responses of trout to revegetation in our models, the small number of available studies needs to be considered when interpreting these results. Restoring the function of riparian zones is important (Naiman, Decamps & McClain, 2010), and such efforts generally involve replanting vegetation. However, the lack of available data to assess the relationship between these efforts and responses by trout most likely reflects that fact that stream and riparian restoration projects are often not monitored (Palmer *et al.*, 2005; Brooks & Lake, 2007).

Overall, we did not detect individual-level responses of trout to riparian drivers. For several, there was only limited data available, potentially due to the relative difficulty of quantifying individual-level responses (e.g. survival and growth) compared to population-level responses (e.g. abundance). However, even for those drivers with adequate data, none significantly influenced individual responses. For drivers that enhanced trout populations, it is possible that individual responses may be negated via density dependent growth/size and survival (Jenkins *et al.*, 1999). It is also possible that drivers of riparian alteration do not influence trout fitness, and any changes to populations are due to fish moving into areas of new habitat or away from areas where habitat has become unsuitable.

It has traditionally been assumed that habitat is a major limit on fish population growth and that restoring habitats will increase population size. However, restoration could simply attract fish from elsewhere, leading to a redistribution of individuals rather than an increase in net population abundance. This ‘production vs. attraction’ debate has received attention in the marine artificial reef literature (e.g. Lindberg, 1997; Brickhill, Lee & Connolly, 2005). Our results provide some indication that, at least in the short-term, fish productivity is likely to be unaffected by woody debris addition and stock exclusion, and thus, the observed population enhancement may be a direct result of migration and movement. However, the responses (almost exclusively size and growth) we assessed may be poor indicators of population productivity, and more work is needed, especially incorporating the collection of data on survival and reproduction, to examine if trout productivity can be enhanced by changes to riparian zones.

Species-specific responses

In general, the trout species we studied responded similarly to each driver of riparian change, but we did detect some species-specific variability. The most notable of these responses involved brook trout populations responding very strongly to forestry clearing, whilst all other species showed no response. This result comes from one study (Shepard, 2004), and the observed positive response may be due to three factors. Firstly, the impacted site received more instream large woody debris; an alteration we have shown enhances trout populations. Secondly, temperatures in the cleared streams were 1-2 °C higher, potentially advantaging brook trout over native cutthroat trout that are weaker competitors at higher temperatures (see De Staso III & Rahel, 1994). Thirdly, and arguably most importantly, in this study area brook trout are highly invasive and displace native cutthroat trout. Therefore, both the increase in brook trout and concurrent decrease in cutthroat trout within this region may have less to do with forestry practices and more to do with these species' interactions.

Management implications

While efforts to restore or rehabilitate habitats for aquatic animals are now commonplace, success stories in terms of changes in biodiversity are rare, even when habitat conditions are improved (Palmer, Hondula & Koch, 2014; Roni, Hanson & Beechie, 2008). Current evidence suggests that trout respond positively to some management practices associated with the condition of riparian zones, especially livestock exclusion and the addition of in-stream woody debris. Documenting when restoration fails can still be considered a form of success, if these failures enable us to understand what went wrong and why, and use this to guide future efforts (Palmer *et al.*, 2005). Our meta-analysis highlights data limitations that hamper our ability to properly assess trout responses to riparian management, but which can be used to guide future efforts.

First, the paucity of experimental data for many of the key drivers of riparian change makes it hard to properly assess change and make clear conclusions and recommendations. While our results suggest consistency among species, life cycle stages and response-type variables, greater research effort and replication will allow this to be tested more specifically. Indeed, if observed trends hold true, our results provide valuable evidence for the generality of trout responses to riparian change and management activities.

Second, the long-term data necessary to fully evaluate the impacts of riparian change are largely unavailable for even the most well-studied drivers. Longer-term datasets allow the temporal trajectories of degradation, and potentially recovery following interventions, to be documented (i.e. 'degradation-recovery' pathways; Sarr, 2002; Lake, Bond & Reich, 2007). Ideally, these long-term studies should be implemented using replicated Before-After Control-Impact designs. Currently, most (64%) of the studies made comparisons between control and restored sites without sampling prior conditions, raising the potential that differences between these sites simply reflect intrinsic between-site variability.

Our study has provided an important summary of how trout, an economically and ecologically important group of freshwater fish, respond to alterations to riparian zones. We show that there are some significant knowledge and data gaps that hinder our ability to properly assess trout-riparian zone links. These gaps would no doubt be even more pronounced for other less charismatic and studied freshwater fish species. While fish have clear conceptual links to riparian zones (Pusey & Arthington, 2003), many of these links, and how they might change following restoration/rehabilitation efforts, are assumed rather than tested. Further work is needed to explore how fish respond to changes in the riparian zone, especially given that riparian restoration is amongst the most common forms of stream remediation globally (Brooks & Lake, 2007), and that human pressures on riparian zones are likely to increase as climate change progresses (Capon *et al.*, 2013).

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Table legends

Table 1: Descriptions of the eight drivers of riparian change including the type of control and impact sites used to calculate the response ratios, the number of papers (N_{papers}) and response ratios (N_{RRs}) for each driver, and the average length of time ($Mean_{years}$) and range ($Range_{years}$) since the change occurred.

Figures legends

Figure 1. Flow diagram showing study selection for systematic review of studies on the impact of riparian change on trout.

Figure 2. Worldwide distribution of the location of studies examining trout responses to changes in riparian zones. The number of papers investigating each driver of riparian change based on the focal trout species, and the continent were the research took place. Brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarkii*), rainbow or steelhead trout (*Oncorhynchus mykiss*) and multiple species (any combination of the previous species or unidentified fry). Note: many studies focused on multiple (yet independent) drivers or multiple species, so totals based on the columns will not equal the total number of studies in the systematic review/meta-analysis.

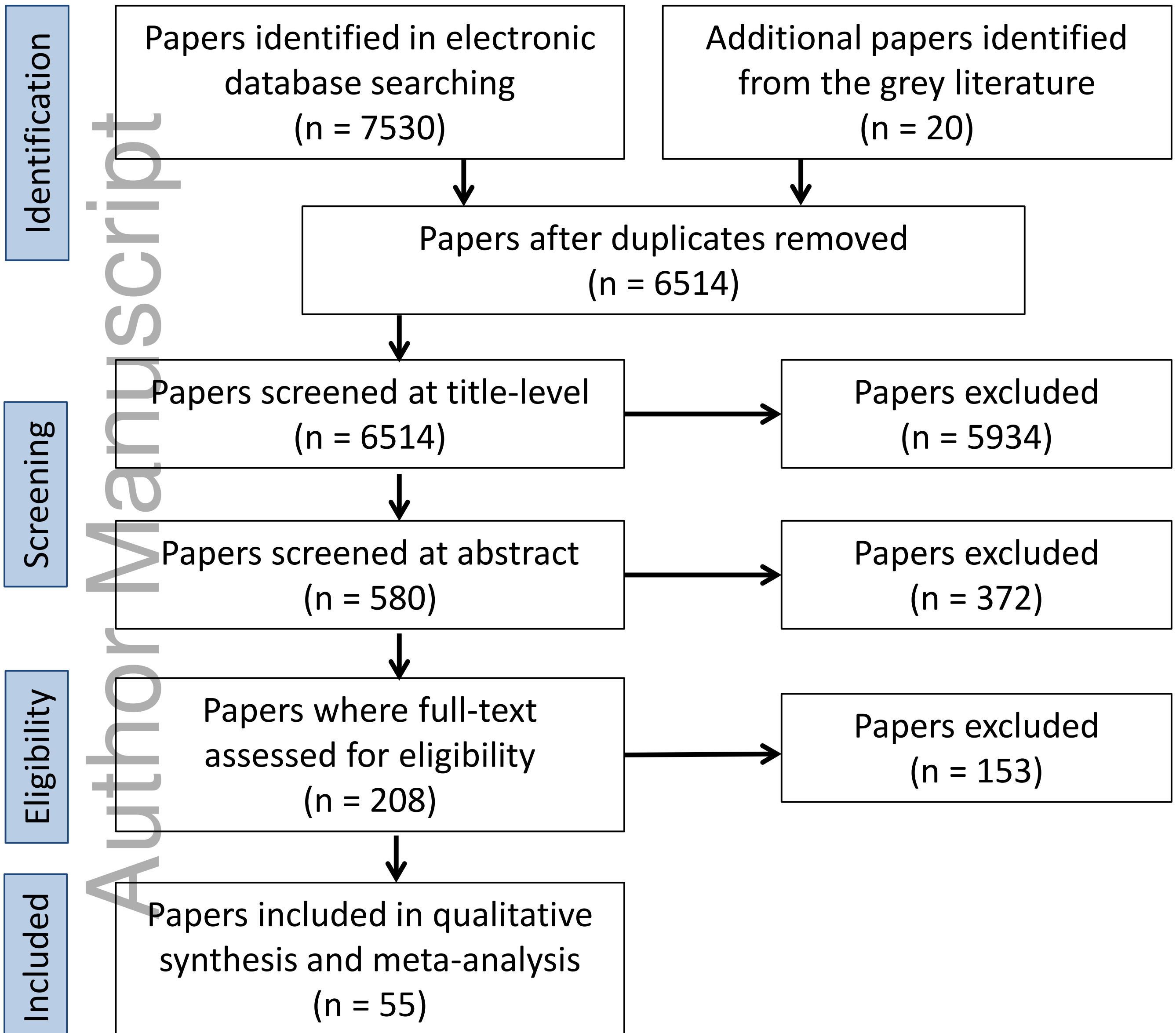
Figure 3. Forest plot of trout individual and population-level response ratios (and their 95% CIs on log scale) for eight drivers of riparian change. Numbers in brackets next to each driver indicate the number of response ratio estimates for individuals and populations included in each model (observations within studies, not individual papers). Percentages are exponentiated response ratios to aid interpretation. See methods for explanation of response ratio calculation.

Figure 4: Forest plot of species-specific response ratios (and their 95% CIs on log scale) for eight drivers of riparian change for (a) individual level responses (survival, growth and size) and (b) population level responses (abundance, biomass and density). Species: brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarkii*), steelhead trout (*Oncorhynchus mykiss*) and rainbow trout (*Oncorhynchus mykiss*), Note, not all drivers are included under each response type category, as data was often not differentiated to species. See Table S1 for breakdown of sample size per species by driver combination.

Table 1.

Driver	Description	Control site	Impact site	N_{papers}	N_{RRs}	$Mean_{years}$	$Range_{years}$
Afforestation	Afforested plantation (often coniferous) that includes the riparian zone.	Natural forests and meadows	Afforested sites	3	10	17.9 ± 6.5	1–43.5
Bushfire	Bushfire that burnt the riparian zone.	Before	After	3	27	3.9 ± 0.4	1–6
Forestry clearing	Forestry practices that included harvesting up to and including the riparian zone.	Old growth / natural forest	Logged / cleared	15	170	13.8 ± 1.2	0.1–50
Grazing	Streams and riparian zones currently impacted by livestock (primarily sheep and cattle).	Sites not grazed	Sites grazed	8	29	22.9 ± 3.9	1–65
Woody debris addition	The addition of coarse/large wood to streams.	No wood added	Wood added	15	152	2.4 ± 0.3	0.1–20
Managed canopy removal	The removal of the riparian canopy, including weed control for willows.	Canopy intact	Canopy removed	5	70	2.5 ± 0.2	0.5–7.5

Revegetation	The planting of vegetation in the riparian zone, including riparian buffer zones.	Before	After	1	11	1.5 ± 0.1	1–2
Stock exclusion	Fencing to exclude livestock (primarily sheep and cattle) from the bank.	Sites grazed	Fenced sites to exclude grazing (were grazed)	6	30	9.1 ± 1.7	1–36.5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Papers identified in electronic database searching (n = 7530)
Additional papers identified from the grey literature (n = 20)
Papers after duplicates removed (n = 6514)
Screening
Papers screened at title-level (n = 6514)
Papers excluded (n = 5934)
Papers screened at abstract (n = 580)
Papers excluded (n = 372)
Eligibility
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Included
Papers included in qualitative synthesis and meta-analysis (n = 55)

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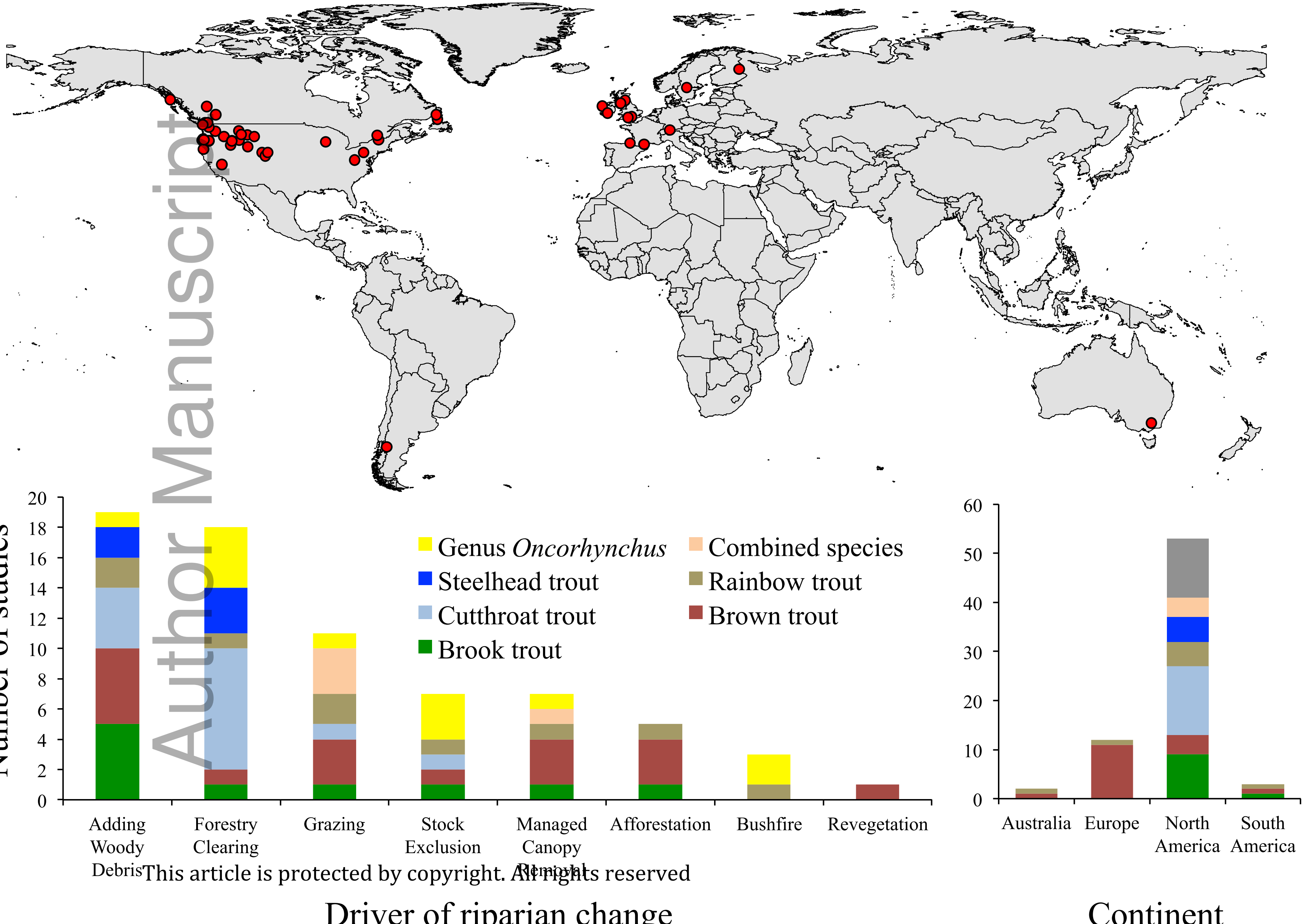

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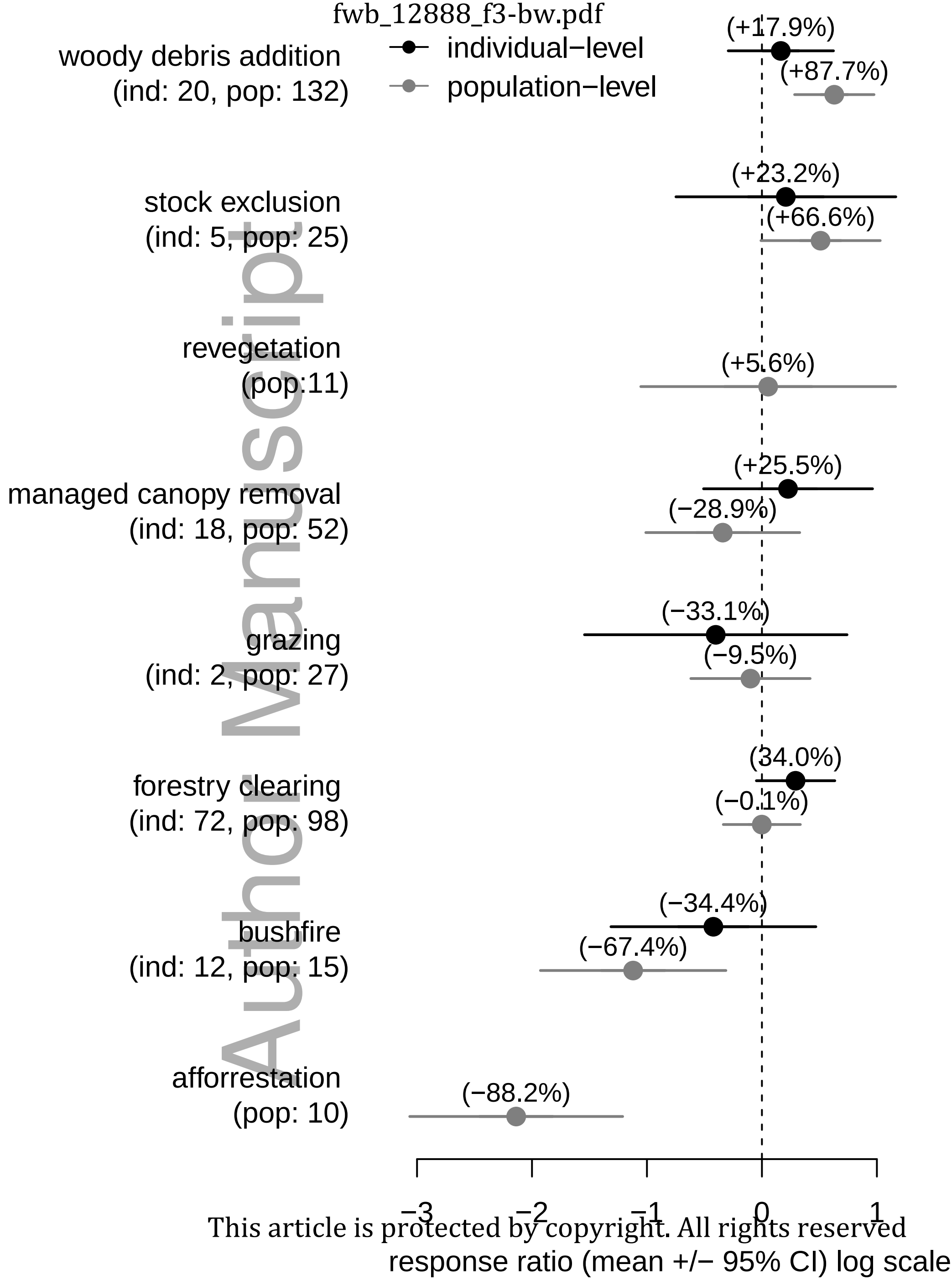

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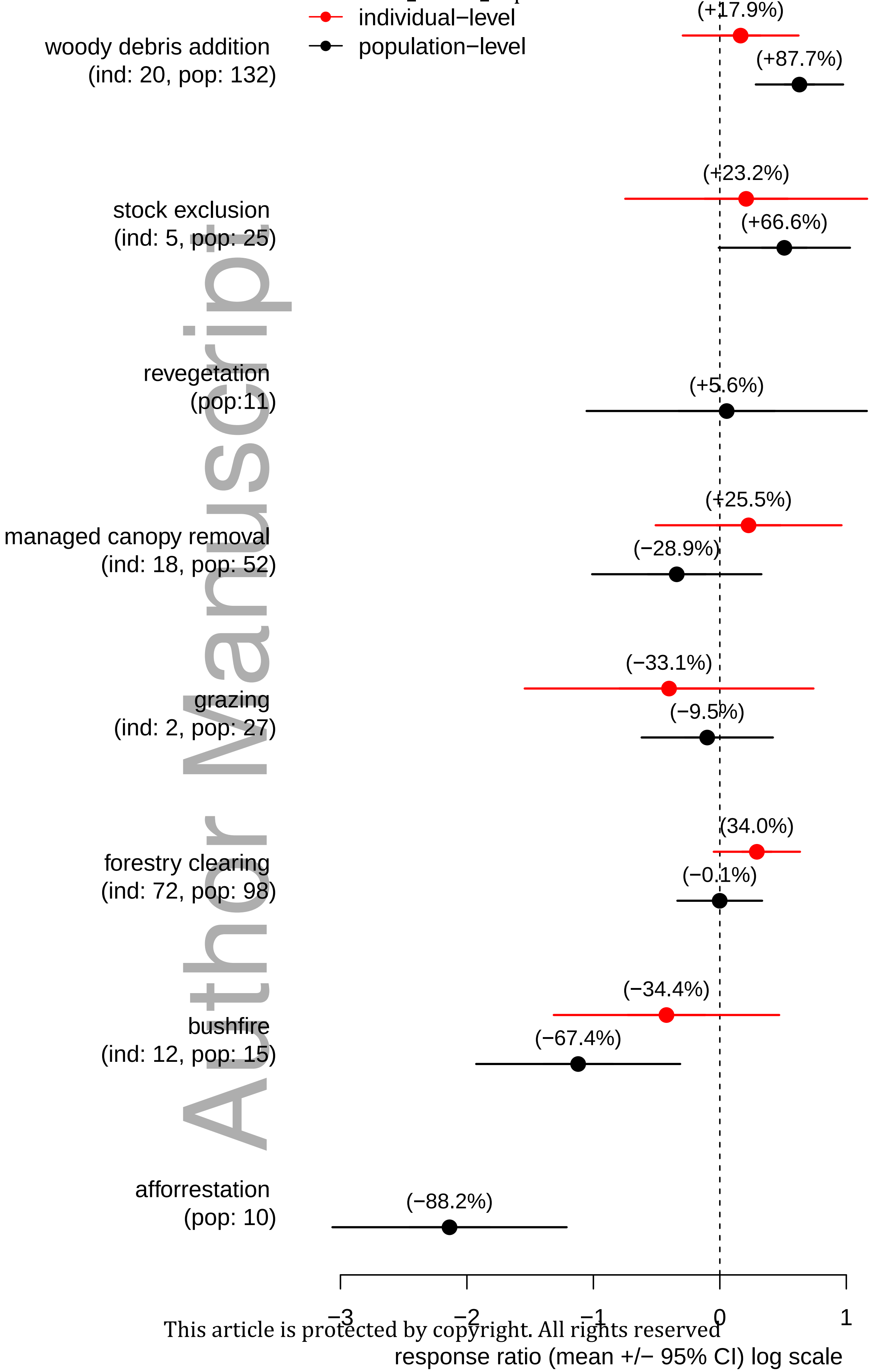

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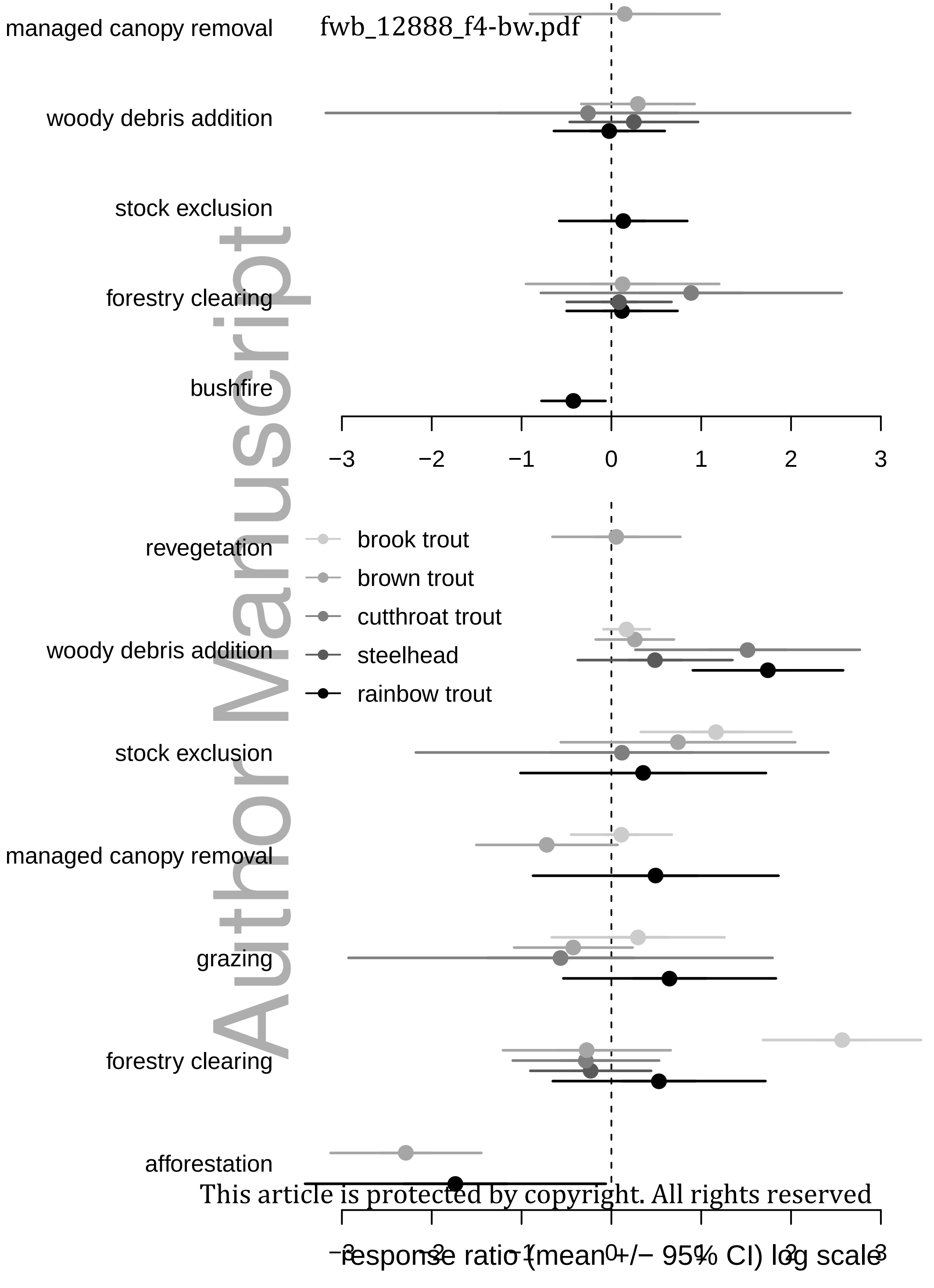

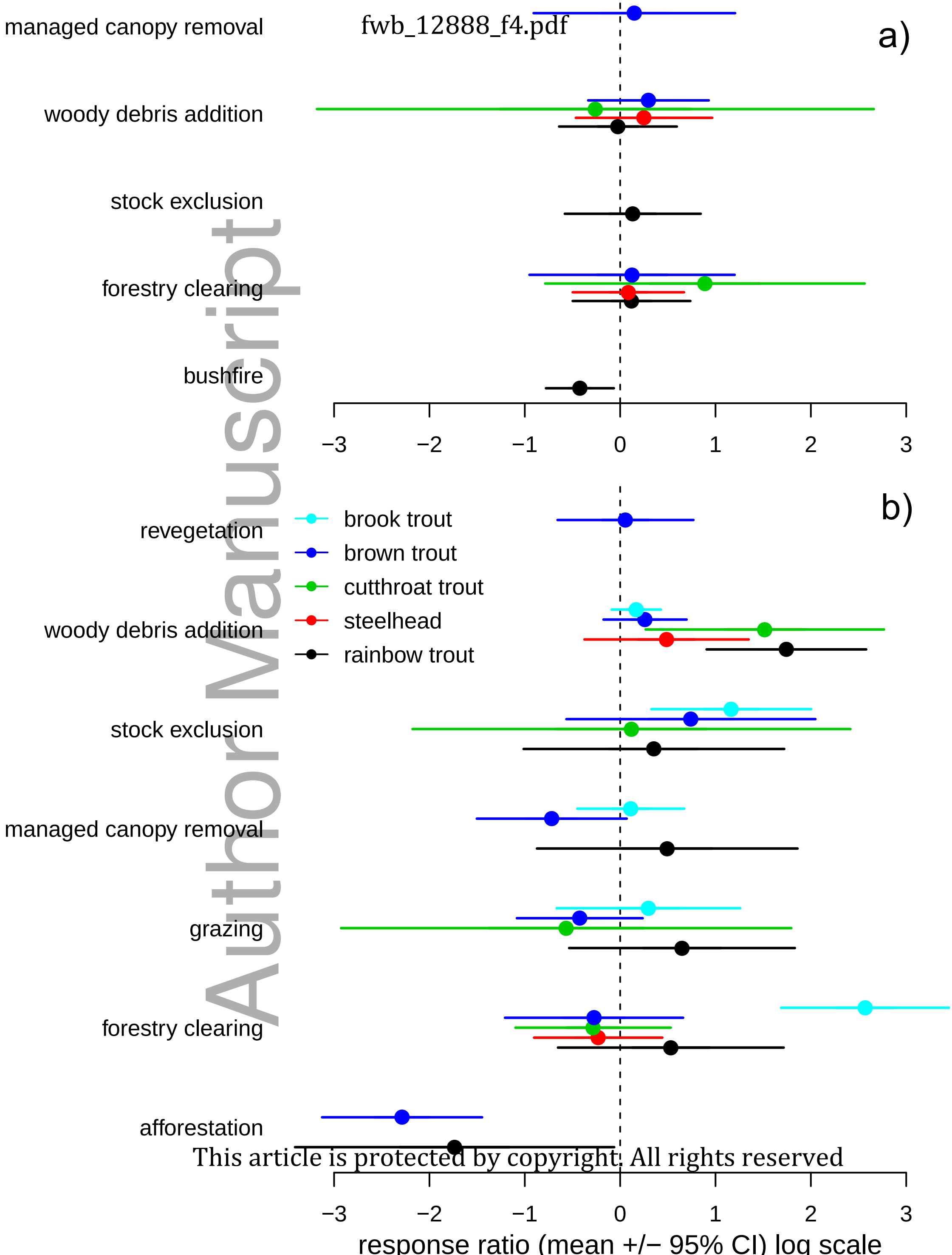
a)
managed canopy removal
woody debris addition
stock exclusion
forestry clearing
bushfire
−3
−2
−1
0
1
2
3
b)
brook trout
brown trout
cutthroat trout
steelhead
rainbow trout
revegetation
woody debris addition
stock exclusion
managed canopy removal
grazing
forestry clearing
afforestation
−3
−2
−1
0
1
2
3
response ratio (mean +/− 95% CI) log scale