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Title:

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

Date:

2017-03-01

Citation:

Sievers, M., Hale, R. & Morrongiello, J. R. (2017). Do trout respond to riparian change? A meta-analysis with implications for restoration and management. *Freshwater Biology*, 62 (3), pp.445-457. <https://doi.org/10.1111/fwb.12888>.

Persistent Link:

<https://hdl.handle.net/11343/292301>

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5 Received Date : 18-May-2016

6 Revised Date : 21-Nov-2016

7 Accepted Date : 23-Nov-2016

8 Article type : Review

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

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20 Running title: Trout responses to riparian change

21 **Keywords**

22 *Restoration, salmonid, woody debris, land-use change, monitoring*

23 **Summary**

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

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/fwb.12888

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

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

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

18 4. Most studies were undertaken in North America using control-impact designs. We
19 found little evidence for species-specific responses to riparian change, and
20 surprisingly, many drivers deemed important in the literature (e.g. revegetation,
21 managed canopy removal, grazing, and forestry clearing) did not consistently
22 influence trout population- or individual-level metrics. Nonetheless, trout populations
23 did respond positively to increasing woody debris and livestock exclusion (+87.7%
24 and +66.6% respectively), and negatively to bushfire and afforestation (-67.4% and -
25 88.2%, respectively). We found some evidence that positive riparian changes may just
26 attract fish (i.e. increased abundance or density) rather than enhance actual population
27 production (i.e. individual size and growth). Whilst this conclusion necessarily needs
28 to be interpreted with caution, it does suggest that targeted research on the
29 'production vs. attraction' hypothesis would be beneficial.

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

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

5 **Introduction**

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

18 Human population expansion and associated intensification of land clearing,
19 forestry and agriculture have all impacted on waterways and their riparian zones with
20 resultant serious consequences for freshwater fishes (Meyer & Turner, 1992; Tilman,
21 1999; Jones *et al.*, 2010). For example, increases in stream sedimentation and
22 turbidity can affect in-stream primary and secondary productivity, and when coupled
23 with reductions in terrestrial food inputs due to lost riparian vegetation, can severely
24 limit food resources for stream fishes (Meehan, 1991; Saunders & Fausch, 2012;
25 Wipfli, 1997). In addition, the riparian canopy plays an important role in regulating
26 the temperature of lotic systems and its removal may result in increased water
27 temperatures beyond levels fish can tolerate (Broadmeadow *et al.*, 2011). Conversely,
28 for cold-climate streams the removal of riparian shading may have positive impacts
29 on fish assemblages through increasing solar radiation and thus water temperature,
30 primary and secondary productivity, and increasing feeding efficiency (Riley *et al.*,
31 2009; Wilzbach *et al.*, 2005; Bilby & Bisson, 1992; Wipfli, 1995). As these
32 examples demonstrate, there is a strong conceptual basis for predicting that fish are
33 likely to respond to riparian restoration.

1 Efforts have increasingly been directed towards management activities that
2 attempt to restore the ecological function of damaged riparian zones (Naiman &
3 Latterell, 2005). Most commonly, these activities involve adding woody debris,
4 replanting riparian vegetation, or erecting fences to exclude livestock (Lehane *et al.*,
5 2002; Ryder *et al.*, 2011; Summers, Giles & Stubbing, 2008). Many of these
6 activities are implemented on the presumption they will lead to desired ecological
7 outcomes. However, concurrent monitoring to assess progress towards these
8 outcomes is generally lacking, as is the empirical research necessary to understand the
9 potential pathways of effect (Palmer *et al.*, 2005). Without this information, it is
10 impossible to evaluate the efficacy of different riparian management activities in
11 meeting their desired outcomes.

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

21 Trout declines across their native range have been linked to pollution, exotic
22 species introductions, forestry and agricultural practices, catchment modification,
23 river regulation, over-exploitation, and climate change-related temperature and
24 hydrological changes (Clews *et al.*, 2010; Marschall & Crowder, 1996; Kovach *et al.*,
25 2016). Many of these factors directly impact riparian zones and have prompted
26 targeted riparian rehabilitation and restoration programs, along with in-channel
27 focussed restoration efforts (Whiteway *et al.*, 2010). For example, managing grazing
28 regimes and constructing fences to exclude livestock from streams can enhance trout
29 populations through the preservation and regrowth of riparian vegetation, a reduction
30 in bank erosion, and the promotion of terrestrial invertebrates inputs (Summers, Giles
31 & Stubbing, 2008; Saunders & Fausch, 2012). Despite widespread implementation of
32 riparian management activities based on our conceptual understanding of fish-riparian
33 linkages, we still lack a broad quantitative and comparative assessment of how trout
34 respond to changes to riparian zones. Such an assessment would help us better

1 understand the links between trout and riparian zones, and more specifically how
2 riparian management might affect trout.

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

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

28

29 **Methods**

30 *Literature search*

31 We conducted literature searches using ISI Web of Science and Google
32 Scholar on 3rd August 2016 (see Table S1 in Supporting Information). Google Scholar
33 results were restricted to the first 50 papers for each of the search terms. In addition,

1 we examined the available grey-literature and reference lists of selected papers,
2 including related meta-analyses and reviews for additional studies. It should be noted
3 that our grey literature search was not exhaustive due to the complexities of finding
4 and obtaining unpublished government and consultancy reports. Nonetheless, our
5 focus was primarily on understanding research efforts rather than monitoring more
6 generally which is often the focus of grey literature studies. Excluding duplicates,
7 6514 papers were systematically screened for inclusion in the meta-analysis (Figure
8 1). Four criteria determined study inclusion: (i) focused on the following species of
9 ‘trout’ (and their variants; family Salmonidae): brook trout/charr (*Salvelinus*
10 *fontinalis*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarkii*), or
11 rainbow or steelhead trout (*Oncorhynchus mykiss*), (ii) published quantitative data on
12 trout responses to riparian change, (iii) utilised a before-after (BA), control-impact
13 (CI) or before-after control-impact (BACI) design, and (iv) the effects of individual
14 drivers of riparian change could be isolated from other changes that may have taken
15 place.

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

27 *Data extraction, classification and effect-size calculation*

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

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

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

14 We extracted treatment and control group data from the text, tables or figures
15 (using graphical digitiser software) of each paper, allowing the calculation of log
16 response ratios following published methods (Hedges, Gurevitch & Curtis, 1999). For
17 BA and CI studies: $RR = \ln[I \text{ or } A] - \ln[C \text{ or } B]$, and for BACI studies: $RR = \ln[I_A /$
18 $C_A] - \ln[I_B / C_B]$, where RR is the response ratio, I is the impacted site mean, C is the
19 control site mean, A is the after mean, and B is the before mean.

20 Response ratios greater than zero, thus, indicate a positive individual- or
21 population-level response within impacted/altered sites compared to control/reference
22 sites (CI studies), or for post-alteration compared to pre-alteration (BA studies). A log
23 response ratio cannot be defined for situations when the numerator or denominator is
24 zero (Hedges, Gurevitch & Curtis, 1999). Adding a constant to these values can
25 induce serious bias (Rosenberg, Rothstein & Gurevitch, 2013), so we took the more
26 conservative approach of excluding these data from further analysis. This resulted in
27 35 site or time observations of trout response to riparian change to be excluded from
28 our analysis (5.8% of the total data).

29 If papers recorded data for multiple years, log response ratios were calculated
30 for each year. Similarly, if papers recorded data from multiple experimental sites or
31 species, we calculated separate response ratios for each. In some circumstances, we
32 swapped the sign of the response ratio to ensure that its interpretation was consistent
33 with all studies in a category (i.e. drivers are operating in the same direction). This
34 was only done for one driver (woody debris addition) where the negative impacts of

1 'woody debris removal' were reversed so that they reflect the benefit of 'woody
2 debris addition'. There was no significant difference in response ratio values between
3 these two types of woody debris study ($p=0.691$). We exponentiated response ratios
4 throughout to provide more easily interpretable percentage differences.

5 *Data analysis*

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

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

26 In our first suite of models we fit a complex random effect structure to the
27 combined-species data for individual and population level responses. 'Species' (7
28 levels based on lowest possible taxonomic resolution: brown, rainbow, brook,
29 cutthroat, steelhead, *Oncorhynchus* combined, undefined trout) was nested within
30 'site' (unique identifier), which in turn was nested within 'study' (i.e. paper).
31 'Species' nested within 'site' induced a correlation amongst RRs from the same
32 species collected at the same time and site (e.g. between rainbow trout size and
33 density) or through time at a site (i.e. repeated surveys). 'Site' nested within 'study'
34 induced a correlation amongst all observations (across species) at a given site and

1 accounted for common local environmental or contextual effects. The ‘study’ random
2 effect accounted for any systematic differences due to, for example, common regional
3 environmental conditions or study-specific methodologies or biases. In our second
4 suite of species-specific models, we used the same random effect structure illustrated
5 above but dropped the redundant ‘species’ random effect. Overall, our model
6 structures allowed us to analyse the specific response ratio data from each species,
7 site or time point within a given study rather than having to simplify data to a single
8 mean value per study, removing the need to weight response ratio estimates by
9 sample size as is commonly done in other aggregate-based methods of meta-analysis.

10 Where appropriate, competing models with different fixed effects structures
11 were fit using maximum likelihood (ML) and compared using Akaike’s Information
12 Criterion corrected for small sample sizes (AIC_c; Burnham & Anderson, 2002). These
13 values were rescaled as the difference between each model and the model with the
14 lowest AIC_c (ΔAIC_c) for a given data set. The optimal response ratio model as
15 selected by ΔAIC_c was then re-fit using REML to produce unbiased parameter
16 estimates. Analyses were performed using the lme4 package (Bates *et al.*, 2013) in
17 3.3.1 (R Development Core Team, 2016).

18 19 **Results**

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

27 *Study design*

28 The primary experimental design used was control-impact comparisons (CI:
29 64%), followed by before-after control-impact (BACI: 20%) and before-after (BA:
30 16%). The overall average time after the riparian alteration when trout monitoring
31 was conducted (based on all RR) was 8.28 years (± 0.57 SE, range: 0.08-65 years),
32 although there was considerable variation among the primary drivers analysed (Table
33 1). Grazing studies had the longest (22.9 years) and revegetation studies the shortest
34 (1.5 years) average interval between riparian change and fish monitoring.

1 *Overall responses to drivers of riparian change*

2 Our models showed that overall alterations to the riparian zone strongly
3 affected population-level trout responses (AIC_c null model (no driver effect, $k=5$):
4 955.3 vs. AIC_c driver model ($k=12$): 931.1; ΔAIC_c : 24.2), but had little effect on
5 individual level responses (AIC_c null model (no driver effect $k=5$): 156.8 vs. AIC_c
6 driver model ($k=10$): 160.4; ΔAIC_c : 3.6; Figure 3). At a population level, trout
7 responded positively to increases in the amount of large woody debris and livestock
8 exclusion (average increase of 87.7% and 66.6%, respectively) and responded
9 negatively to bushfire and afforestation (average decrease of 67.4% and 88.2%,
10 respectively). Despite reasonable sample sizes (≥ 20 RRs), we detected no significant
11 directional effect (95% CI overlapping zero) of forestry clearing, grazing, or managed
12 canopy removal on trout populations (Figure 3). Limited data was available for
13 studies investigating the effects of revegetation (11), making it difficult to draw
14 conclusions on the effects of this driver. There was no clear effect of any riparian
15 driver on individual level responses, despite large sample sizes being present for
16 woody debris addition (20 RRs) and forestry clearing (72 RRs).

17 *Species-specific responses*

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

27

28 **Discussion**

29 *Overall responses to drivers of riparian change*

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

34 Adding instream woody debris is a common strategy to enhance fish

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

8 We found that trout responded positively to livestock exclusion, likely due to
9 subsequent improvements in instream habitat condition. Bank erosion and bare
10 ground are typically higher in grazed riparian zones, which often also have less
11 woody vegetation, and fewer shrubs and groundcover plants (Kauffman & Krueger,
12 1984; Robertson & Rowling, 2000). Habitat conditions adjacent to grazed riparian
13 zones can be worse for trout (e.g. less nutrient filtration, less shading) and reduce fish
14 growth and abundance (Saunders & Fausch, 2012; Summers, Giles & Stubbing,
15 2005). Removing livestock may also alter channel geomorphology, improve water
16 quality and increase terrestrial food supply (Opperman & Merenlender, 2004;
17 Kauffman, 2002; Saunders & Fausch, 2012). These changes may consequently lead
18 to an overall improvement in the condition of instream habitat for trout..

19 Trout responded positively to livestock removal, but interestingly we did not
20 observe a logical negative response to grazing. One possibility is that trout respond
21 differently to alternative grazing practices, for example, some less intense methods
22 (e.g. rotational grazing) may even increase trout biomass relative to more intensively
23 grazed, or even ungrazed sites (see Saunders & Fausch, 2007; Saunders & Fausch,
24 2012). Alternatively, the pathways describing degradation and recovery from
25 livestock may be different (Sarr, 2002). For example, trout responses may be more
26 rapid following livestock removal relative to the negative impacts of grazing. Our
27 results provide some support for this notion, given that stock exclusion and grazing
28 studies differed considerably in their length (9.1 vs 22.9 years, respectively; Table 1),
29 and several studies have shown short-term (<5 years) responses at stock exclusion
30 sites (Keller & Burnham, 1982; Stuber, 1985; Bayley & Li, 2008). However, more
31 work is needed to why this difference in responses was observed.

32 Trout populations responded negatively to afforestation, which typically
33 involved streams surrounded by coniferous plantations within the riparian zone. This
34 result was based on only three studies, but demonstrates that trout biomass and

1 density may be lower at afforested sites both shortly after afforestation (Smith, 1980),
2 and over longer time frames (> 40 years; Laura Miserendino *et al.*, 2011; Rees &
3 Ribbens, 1995). Short-term responses may be caused by the indirect effects of
4 reduced incident radiation on primary productivity, and reductions in terrestrial prey
5 from (often exotic) monocultures relative to native vegetation (Smith, 1980; Tierney,
6 Kelly-Quinn & Bracken, 1998). In the longer-term, acidification may occur in streams
7 with coniferous afforested riparian zones lowering instream productivity and
8 impacting trout (Rees & Ribbens, 1995).

9 Trout populations responded negatively to bushfires, which have the capacity
10 to dramatically modify habitat conditions for fish (Lyon & O'Connor, 2008; Burton,
11 2005). Bushfires initially alter water temperature, chemistry and dissolved oxygen
12 levels, and in the longer-term reduce woody debris input and riparian cover, and
13 increase the input of sediments (Arkle, Pilliod & Strickler, 2010; Gresswell, 1999;
14 Bisson *et al.*, 2003). Interestingly, trout populations may recover in the several years
15 following fire-induced hydrological events that cause debris flows and short-term
16 reductions in dissolved oxygen (Burton, 2005; Lyons *et al.*, 2000). Following fire,
17 these disturbance-induced debris flows may stimulate primary productivity and
18 subsequently enhance invertebrate biomass, with benefits for higher-trophic taxa such
19 as fish (Harris, Baxter & Davis, 2015). Our bushfire dataset comprised just three
20 studies (1, 2 and 6 years post fire) but these provide anecdotal support for relatively
21 rapid population recovery. The largest change in average response ratio was between
22 1 and 2 years post fire (-2.355 to -0.664), with a more gradual recovery between 2 and
23 6 years post fire (-0.664 to 0.272). Longer term monitoring is necessary to better
24 assess how trout respond to extensive bushfires.

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

1 of responses to these changes reflects the complex, multi-directional ways that
2 riparian vegetation influences instream habitat conditions for trout

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

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

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

33 *Species-specific responses*

34 In general, the trout species we studied responded similarly to each driver of

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

13 *Management implications*

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

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

32 Second, the long-term data necessary to fully evaluate the impacts of riparian
33 change are largely unavailable for even the most well-studied drivers. Longer-term
34 datasets allow the temporal trajectories of degradation, and potentially recovery

1 following interventions, to be documented (i.e. ‘degradation-recovery’ pathways;
2 Sarr, 2002; Lake, Bond & Reich, 2007). Ideally, these long-term studies should be
3 implemented using replicated Before-After Control-Impact designs. Currently, most
4 (64%) of the studies made comparisons between control and restored sites without
5 sampling prior conditions, raising the potential that differences between these sites
6 simply reflect intrinsic between-site variability.

7 Our study has provided an important summary of how trout, an economically
8 and ecologically important group of freshwater fish, respond to alterations to riparian
9 zones. We show that there are some significant knowledge and data gaps that hinder
10 our ability to properly assess trout-riparian zone links. These gaps would no doubt be
11 even more pronounced for other less charismatic and studied freshwater fish species.
12 While fish have clear conceptual links to riparian zones (Pusey & Arthington, 2003),
13 many of these links, and how they might change following restoration/rehabilitation
14 efforts, are assumed rather than tested. Further work is needed to explore how fish
15 respond to changes in the riparian zone, especially given that riparian restoration is
16 amongst the most common forms of stream remediation globally (Brooks & Lake,
17 2007), and that human pressures on riparian zones are likely to increase as climate
18 change progresses (Capon *et al.*, 2013).

19 20 **Acknowledgments**

21 We thank two anonymous reviewers for comments on an earlier draft that greatly
22 improved this manuscript. This project was funded by Fisheries Victoria and the
23 Victorian Government’s Department of Environment, Land, Water and Planning
24 (DELWP). We thank Paul Reich and the Riparian Working Group (DELWP) for
25 constructive comments on earlier versions of this work. M. Sievers was supported by
26 an Australian Postgraduate Award and R. Hale the Australian Research Council
27 (LP140100343).

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20

21 **Table legends**

22

23 Table 1: Descriptions of the eight drivers of riparian change including the type of
24 control and impact sites used to calculate the response ratios, the number of papers
25 (N_{papers}) and response ratios (N_{RRs}) for each driver, and the average length of time
26 ($\text{Mean}_{\text{years}}$) and range ($\text{Range}_{\text{years}}$) since the change occurred.

27

28 **Figures legends**

29

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

32

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

10

11 Figure 3. Forest plot of trout individual and population-level response ratios (and their
12 95% CIs on log scale) for eight drivers of riparian change. Numbers in brackets next
13 to each driver indicate the number of response ratio estimates for individuals and
14 populations included in each model (observations within studies, not individual
15 papers). Percentages are exponentiated response ratios to aid interpretation. See
16 methods for explanation of response ratio calculation.

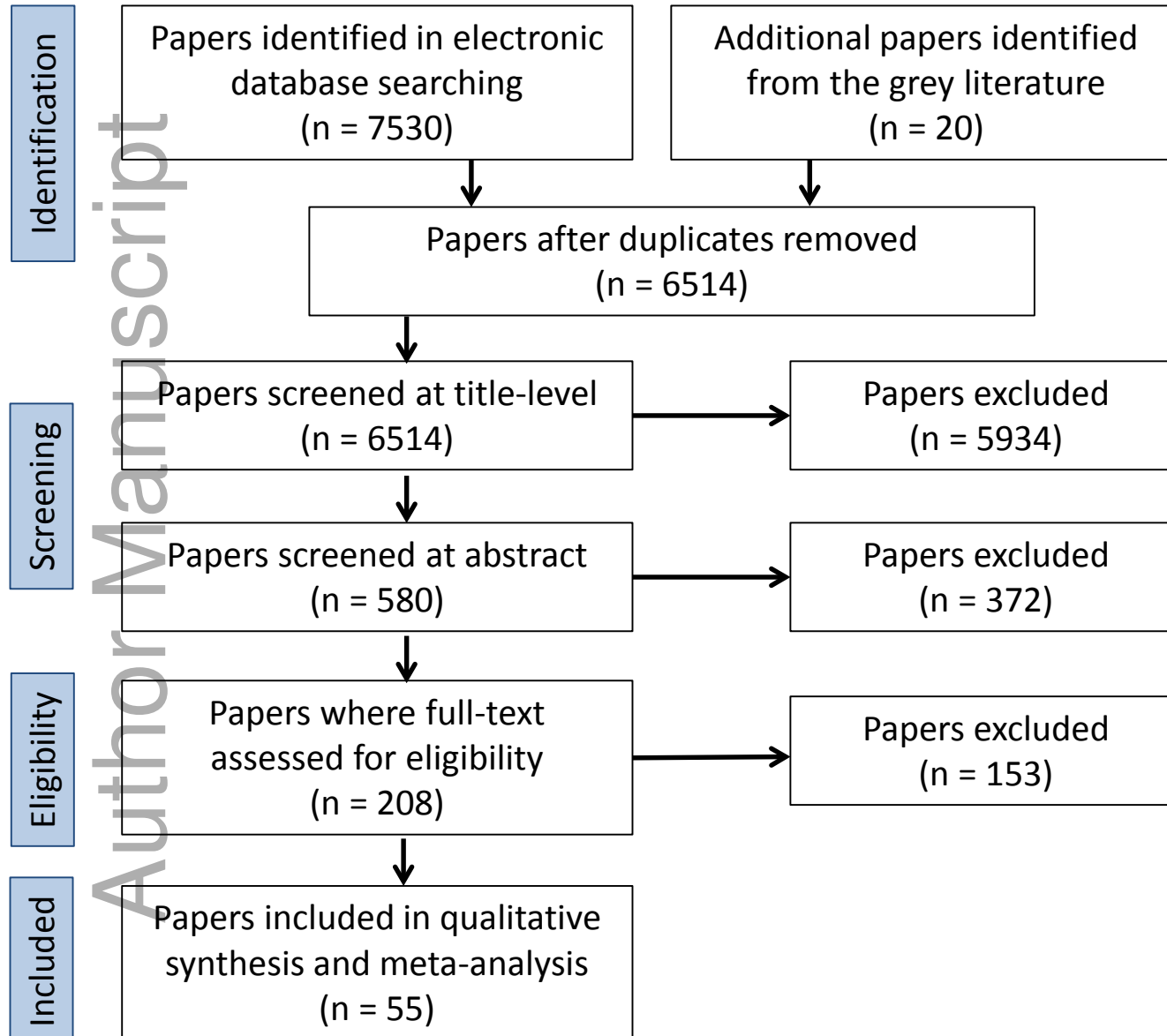
17

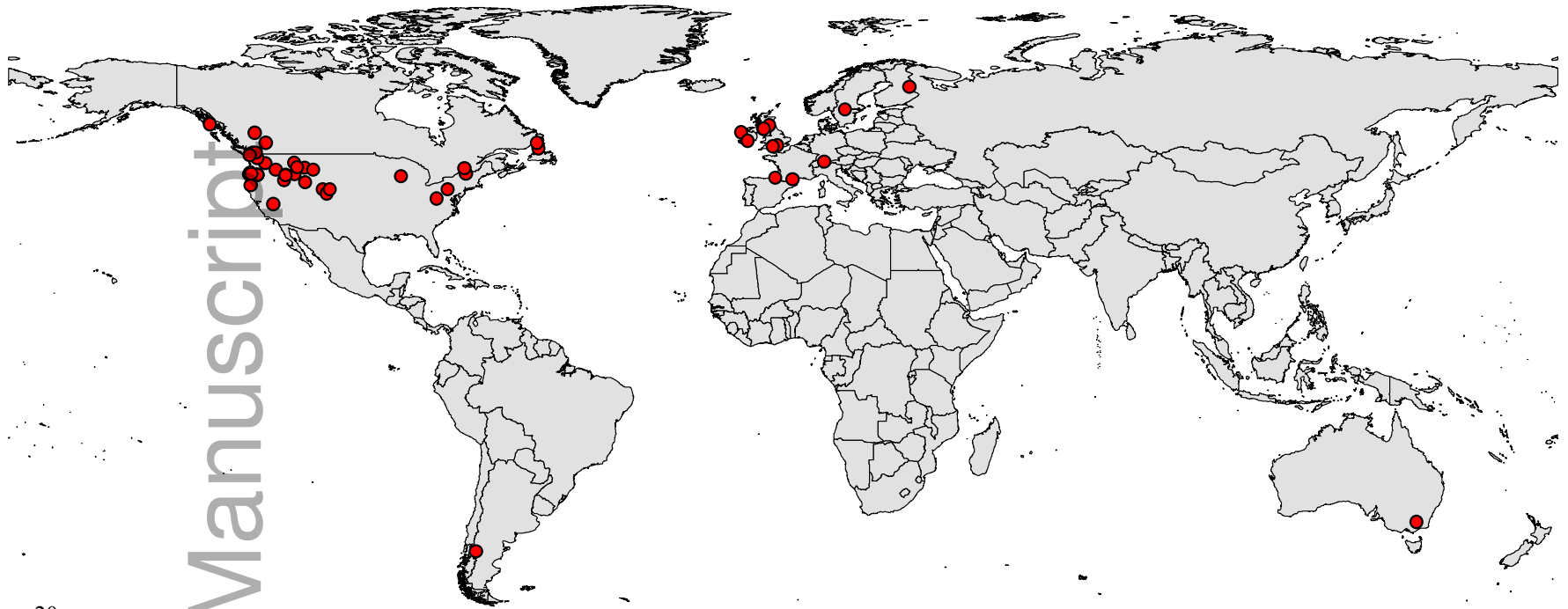
18 Figure 4: Forest plot of species-specific response ratios (and their 95% CIs on log
19 scale) for eight drivers of riparian change for (a) individual level responses (survival,
20 growth and size) and (b) population level responses (abundance, biomass and
21 density). Species: brook trout (*Salvelinus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

Table 1.

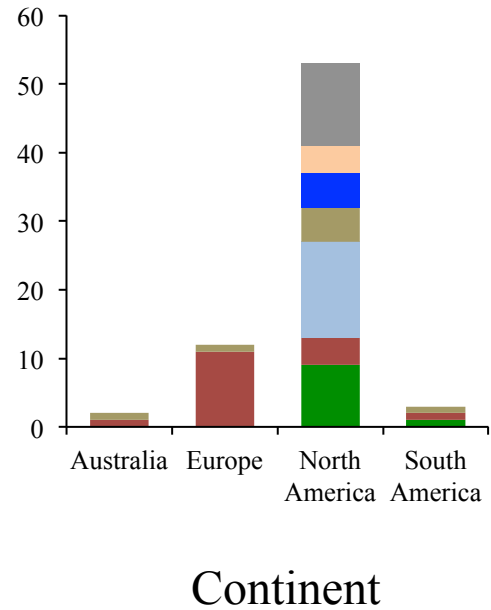
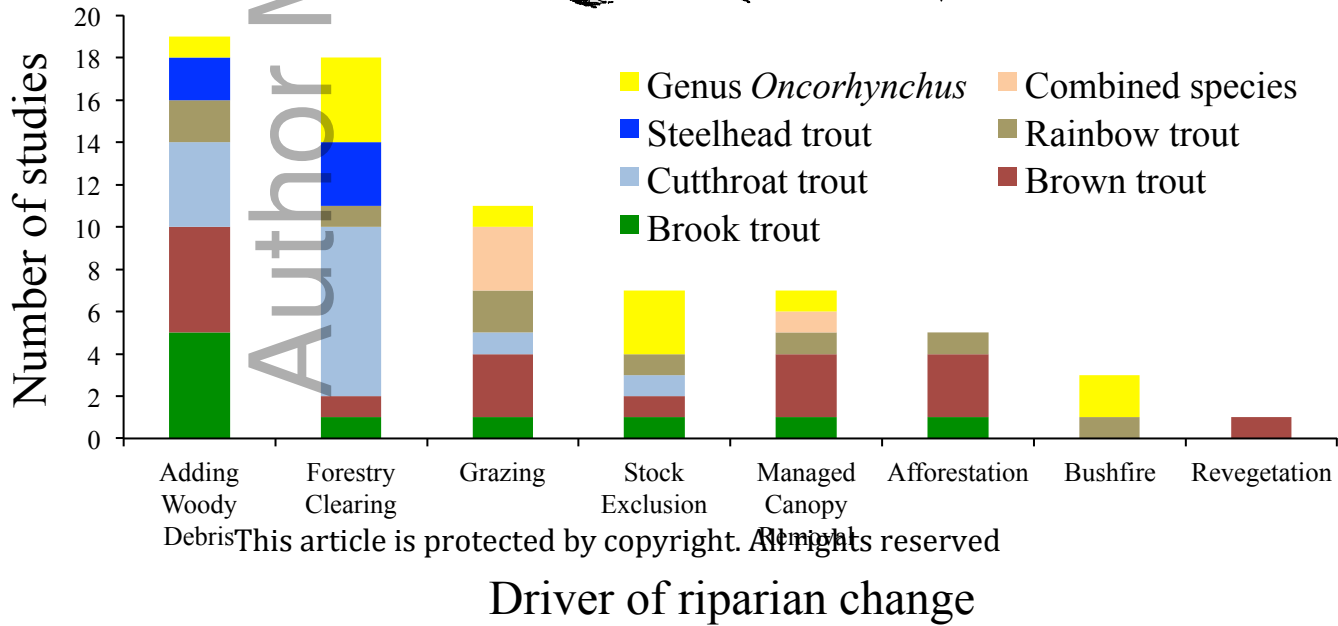
Driver	Description	Control site	Impact site	N _{papers}	N _{RRs}	Mean _{years}	Range _{years}
Afforestation	Afforested plantation (often coniferous) that includes the riparian zone.	Natural forests and meadows	Afforested sites	3	10	17.9 ± 6.5	1–43.5
Bushfire	Bushfire that burnt the riparian zone.	Before	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

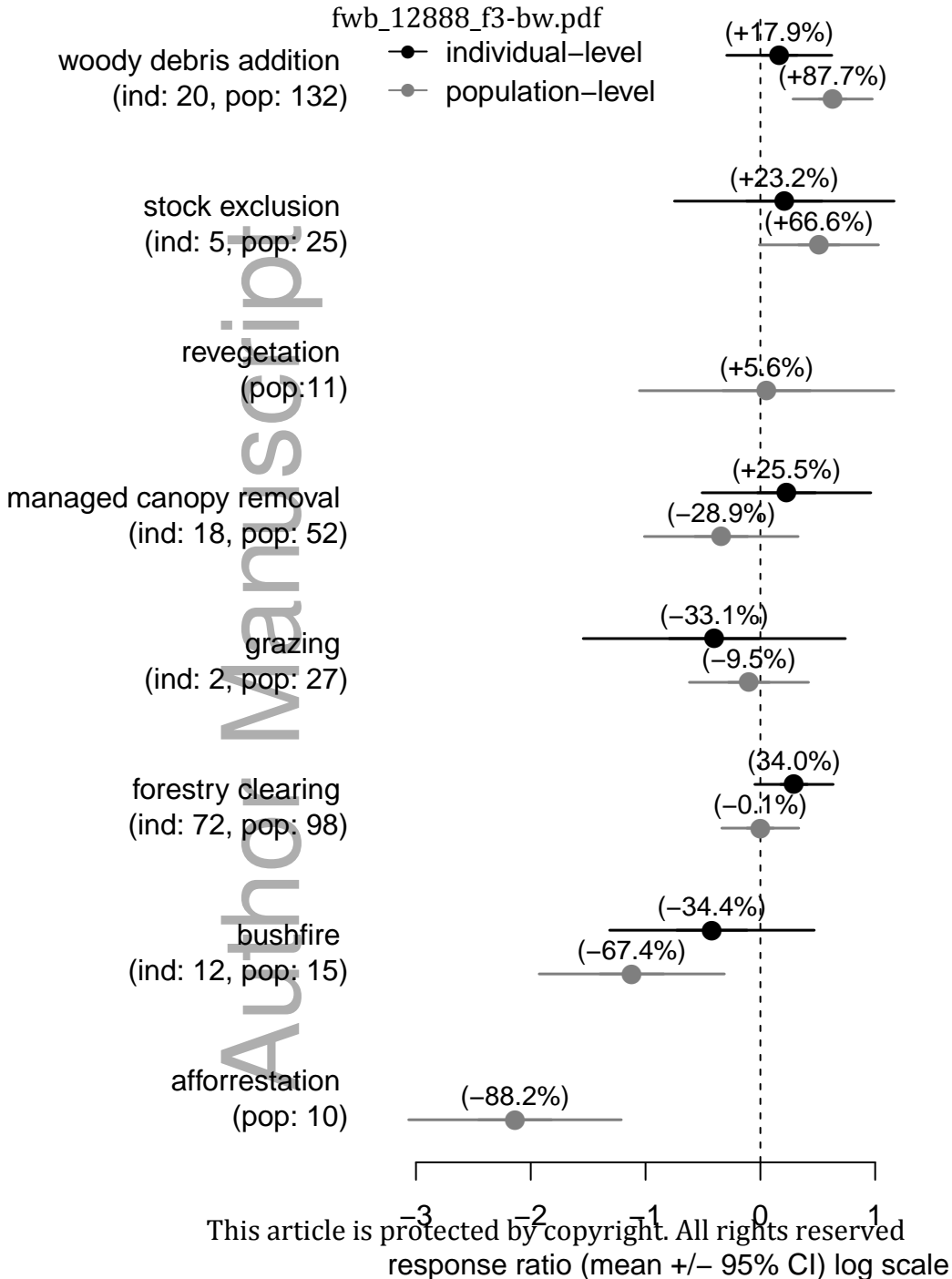




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—●— individual-level

—●— population-level

woody debris addition
(ind: 20, pop: 132)

(+17.9%)

(+87.7%)

stock exclusion
(ind: 5, pop: 25)

(+23.2%)

(+66.6%)

revegetation
(pop: 11)

(+5.6%)

managed canopy removal
(ind: 18, pop: 52)

(+25.5%)

(-28.9%)

grazing
(ind: 2, pop: 27)

(-33.1%)

(-9.5%)

forestry clearing
(ind: 72, pop: 98)

(34.0%)

(-0.1%)

bushfire
(ind: 12, pop: 15)

(-34.4%)

(-67.4%)

afforestation
(pop: 10)

(-88.2%)

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response ratio (mean \pm 95% CI) log scale

-3 -2 -1 0 1

managed canopy removal

fwb_12888_f4-bw.pdf

woody debris addition

stock exclusion

forestry clearing

bushfire

revegetation

woody debris addition

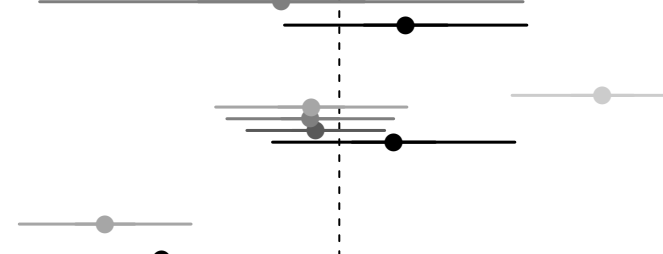
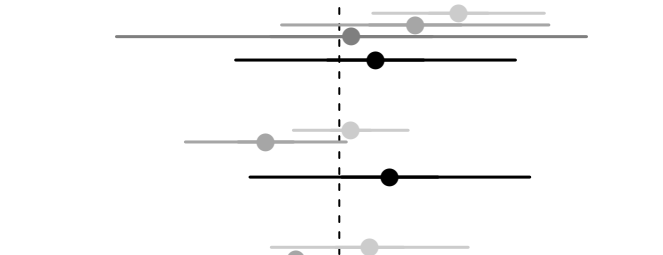
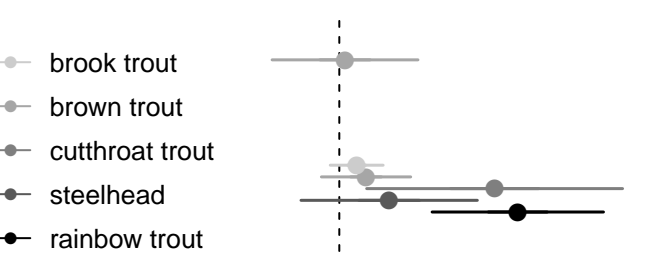
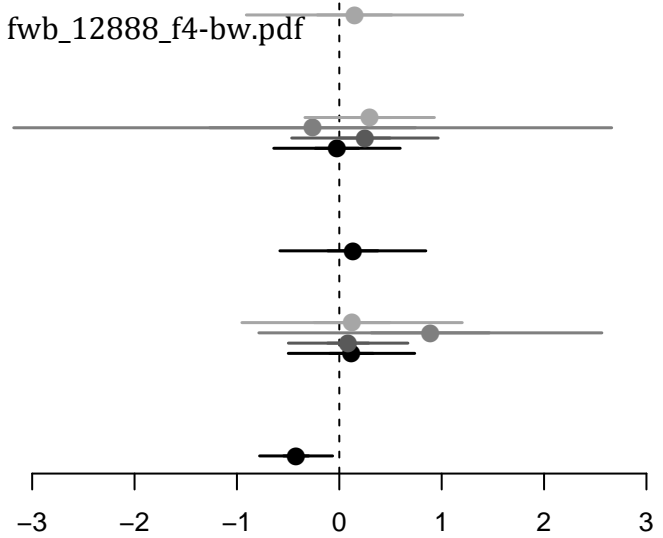
stock exclusion

managed canopy removal

grazing

forestry clearing

afforestation



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- response ratio (mean \pm 95% CI) log scale

managed canopy removal

fwb_12888_f4.pdf

a)

woody debris addition

stock exclusion

forestry clearing

bushfire

-3 -2 -1 0 1 2 3

b)

revegetation

woody debris addition

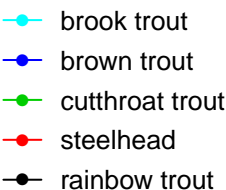
stock exclusion

managed canopy removal

grazing

forestry clearing

afforestation



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-3 -2 -1 0 1 2 3

response ratio (mean \pm 95% CI) log scale