

RESEARCH ARTICLE

In-stream habitat and macroinvertebrate responses to riparian corridor length in rangeland streams

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Conservation and restoration of riparian vegetation in agricultural landscapes has had mixed success at protecting in-stream habitat, potentially due to the mismatch between watershed-scale impacts and reach-scale restoration. Prioritizing contiguous placement of small-scale restoration interventions may effectively create larger-scale restoration projects and improve ecological outcomes. We performed a multi-site field study to evaluate whether greater linear length of narrow riparian tree corridors resulted in measurable benefits to in-stream condition. We collected data at 41 sites with varying upstream tree cover nested within 13 groups in rangeland streams in coastal northern California, United States. We evaluated the effect of riparian tree corridor length on benthic macroinvertebrate communities, as well as food resources, water temperature, and substrate size. Sites with longer riparian corridors had higher percentages of invertebrates sensitive to disturbance (including clingers and EPT taxa) as well as lower water temperatures and less fine sediment, two of the most important aquatic stressors. Despite marked improvement, we found no evidence that macroinvertebrate communities fully recovered, suggesting that land use continued to constrain conditions. The restoration of long riparian corridors may be an economically viable and rapidly implementable technique to improve habitat, control sediment, and counter increasing water temperatures expected with climate change within the context of ongoing land use.

Key words: aquatic ecology, benthic macroinvertebrates, biomonitoring, fine sediment, restoration scale, riparian buffer, water temperature

Implications for Practice

- Greater woody riparian corridor lengths can improve habitat conditions in rangeland streams.
- In landscapes where wide corridors are impractical, coordination of the placement of small revegetation projects to produce a long corridor can improve in-stream condition.
- Understanding the influences and constraints imposed by stream setting and surroundings (e.g. soil type and upstream gap in tree cover) can inform restoration goals and expectations.

Introduction

Restoration practitioners frequently seek to reverse land use and land cover change impacts, whether re-planting on forestlands that have been converted to agriculture or limiting the effects of water pollution associated with urban areas. In many cases, efforts to restore ecological process are most effective at large scales, e.g. through removing a dam to restore connectivity and flow in a river (Holl et al. 2003; Beechie et al. 2008). However, opportunities for such large-scale, process-based restoration are frequently constrained by the presence of ongoing competing land use, particularly in mixed-use landscapes. We explore the value of increasing the size of small-scale restoration efforts to better support both ecological condition and ongoing human land use.

Restoration and protection of riparian tree corridors is a common small-scale intervention in working landscapes such as agricultural, forestry, and grazing lands and can provide multiple benefits (Naiman & Decamps 1997). Importantly, riparian revegetation can restore riparian processes with the potential for long-term benefits: tree cover can provide shading and coarse organic matter inputs in the form of leaf litter, as well as slow overland water flow, reduce peak water velocity, limit bank erosion and soil loss, and filter fine sediment and nutrients (Naiman & Decamps 1997; Sweeney & Newbold 2014). However, there are limits to the improvements that are possible without removing ongoing stressors (Roni et al. 2008), and in some cases, small-scale riparian restoration does not improve in-stream conditions (Bernhardt & Palmer 2011; Louhi et al. 2011; Violin et al. 2011; Muller et al. 2016).

Author contributions: BS, EZ, KDH designed the study; BS collected the data, performed the analysis, and wrote the manuscript; all authors interpreted the analysis and edited the manuscript.

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One factor that might increase the effectiveness of such efforts is incremental changes in project size. Recent research has established that a minimum buffer width of 30–50 m is generally required to effectively filter and process nutrients and sediment before they enter the stream (Sweeney & Newbold 2014), but this width is not always achievable where grazing is ongoing and competing land uses make wide corridors impractical or prohibitively expensive. Although there is evidence that spatial positioning of riparian revegetation can influence in-stream conditions (Parkyn et al. 2003; Baker et al. 2006), and that total area of riparian vegetation may be important (Roy et al. 2006), little research has focused on the importance of corridor length.

Here, we examine whether extending the length of narrow riparian corridors can improve stream outcomes. Although narrow corridors do not adequately filter water entering the channel, they may perform other riparian functions, such as moderating extreme flow velocity, trapping fine sediment during overbank flow, lowering stream temperatures, and providing and retaining coarse organic matter (Moore & Palmer 2005; Urban et al. 2006). In addition, even narrow corridors can stabilize banks and trap dead wood, limiting local channel erosion and supporting pool formation and channel complexity (Gurnell et al. 2016; Muller et al. 2016).

We conducted our study in grazed grasslands of west Marin and Sonoma counties, CA, United States, working in a series of restored (planted >7 years prior) and remnant (never cleared or established >40 years prior) strips of riparian tree cover. We focused on in-stream conditions, including the benthic macroinvertebrate community and habitat features likely to affect this community. Macroinvertebrates are useful indicators of in-stream conditions because of their ubiquity, well-studied food preferences, relatively small ranges as larvae, and taxon-specific responses to stressors in agricultural and grazing land uses (Rosenberg & Resh 1993).

We hypothesized that long corridors could result in lower water temperatures, less fine sediment, more pools (due to addition and stabilization of dead wood and increased scour), and a shift in food resources (less algae, more leaf litter). In turn, we predicted that if greater tree corridor lengths improved in-stream conditions, this could be reflected in a shift in the macroinvertebrate community to include more sensitive taxa, as well as a shift from grazers to shredders. In addition, we hypothesized that if tree cover reduces fine sediment, we could observe more clingers, which require substrata not covered by fine sediment. To account for the well-established variation in conditions between streams (due to e.g. varied drainage area, geology, soils, land use) (Herbst & Silldorff 2006; Urban et al. 2006), we compared conditions at different corridor lengths within each stream.

Methods

Study Design

Marin and Sonoma counties have a Mediterranean climate with average annual precipitation of 68 cm (National Centers for Environmental Information 2018). Over the past 20 years,

riparian vegetation has been restored throughout the region to improve water quality and manage erosion, as well as to support listed subpopulations of coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Oncorhynchus mykiss*). Water temperature is a concern for both steelhead and coho in this region; mean weekly temperatures above 14.8°C result in a 10% reduction in coho juvenile growth (Sullivan et al. 2000; Welsh et al. 2001). Restoration techniques included fencing to exclude cattle, planting willow stakes, and planting of other tree species in small grazing exclosures. A prior study (Lennox et al. 2011) in the same region found high survival of woody species, as well as increases in pool depth and in-stream wood following restoration. We build upon this study by evaluating in-stream responses to tree cover. We controlled for the well-documented effect of watershed condition by sampling streams within one land use type in a small geographic area and using a nested design with multiple sampling points on each stream. We also accounted for three factors that represent potential large-scale influences on the effect of corridor length: stream power, length of upstream gap in tree cover, and soil type (which influences substrate size).

Streams were selected based on four criteria: (1) land use/land cover of grazed grasslands; (2) a break in riparian cover coupled with a downstream remnant or restored riparian tree corridor (if restored, established a minimum of 7 years prior); (3) flowing water in April (i.e. not ephemeral); and (4) site access permission. Remnant riparian cover included any corridors that were more than 40 years old and were reported as naturally recruiting or never cleared by the landowner.

Within a stream, we used GoogleEarth aerial imagery to select a site upstream of the riparian corridor (located in a gap in cover >50-m long) and a site at the downstream end of the corridor (Fig. 1). Where available, we sampled up to two additional points with intermediate lengths of upstream corridor (Table S1). Each comparison set along a given stream represents a “stream group.” In three cases, we had two stream groups on a single stream, but these were a minimum of 2 km apart.

Tree corridors in our study area were narrow, with a median width of 10 m on each bank (maximum 30 m, minimum 5 m) and complete canopy closure (Table S1). Dominant tree species included *Salix* spp. (willows), *Quercus* spp. (oak), *Umbellularia californica* (California bay laurel), *Alnus* spp. (alder), and *Aesculus californica* (California buckeye).

Within each site, we identified a sampling riffle and defined a 50-m sampling reach working upstream from the selected riffle. Where possible we sampled from two or three adjacent riffles (<15 m apart). All samples were collected from the riffles; additional data on habitat types, corridor width, and canopy cover were collected throughout the 50-m reach to characterize conditions directly upstream of the sampling riffle(s).

In April 2015, we sampled 25 sites within seven stream groups. In April–May 2016, we resampled those sites and added 14 for a total of 39 sites within 13 stream groups. Five sites (two stream groups) had perennial flow; the 34 others are summer-dry intermittent streams. Most analyses include both years, but in some cases (e.g. food resources quantification, ordination) we rely on only the 2016 data set, which is more complete.

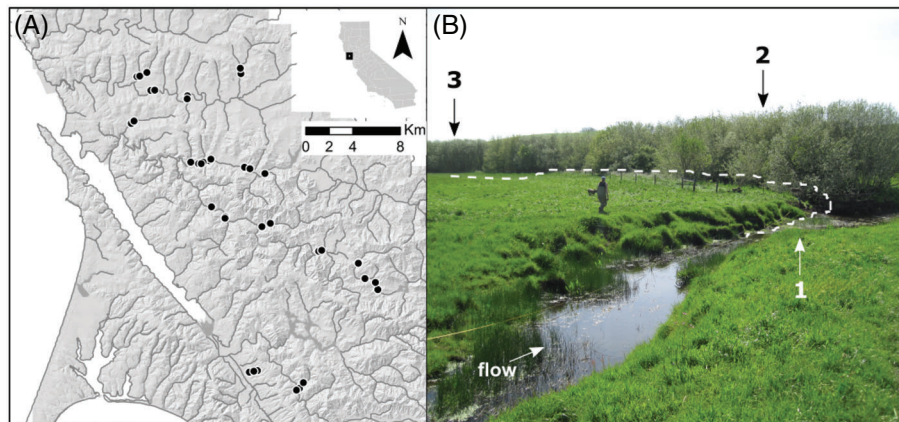


Figure 1. (A) Study area in west Marin and Sonoma counties with sampling sites shown as black dots. (B) The upstream unbuffered site (1) represents the unrestored state, and moving downstream along a restored (or remnant) tree corridor subsequent sampling points (2, 3) capture the effects of progressively longer tree corridors on stream condition.

Invertebrates

We sampled the riffle invertebrate community using a 500- μm D-net. Depending on riffle availability, we sampled from 1 to 3 riffles at the downstream end of the sampling reach. We cleaned cobbles from a 0.09- m^2 area into the net and then disturbed the substrate for 30 seconds. We took three samples per site for a total sampling area of 0.27 m^2 . We combined and elutriated samples in the field and preserved them in 95% ethanol. Our sampling method was based on riffle sampling protocols for California (Ode 2007). In the laboratory, samples with over 600 individuals were split into subsamples with a minimum count of 350 individuals. Invertebrates were sorted from the sample and identified to family for insects and class or order for non-insects using standard keys (Wiggins 1977; McCafferty 1981; Harrington & Born 2000; Cummins et al. 2008).

To assess invertebrate response to riparian tree cover, we used community metrics that have high discrimination and high stability for intermittent streams in this region (SFBRWQCB 2007), are based on relative abundances, and are relatively robust to our limited taxonomic resolution. We calculated mean tolerance value using California Tolerance Values (Ode 2003), assigning each taxon a value from 0 (intolerant or sensitive) to 10 (extremely tolerant) and using an abundance-weighted average to calculate a community tolerance value. Tolerance values were originally developed to detect nutrient pollution, but have since expanded to be used more generally as disturbance indicators in the development of multi-metric indices of ecological integrity (Whittier & Van Sickle 2010; Mazar et al. 2016). We also calculated percent sensitive or intolerant taxa (scores 0–2) and % EPT (Insecta orders Ephemeroptera, Plecoptera, and Trichoptera). EPT orders are typically larger-bodied, diverse, and sensitive to environmental stress (Resh & Jackson 1993). We compared % EPT and tolerance values in our sites to minimally disturbed intermittent streams in the San Francisco Bay Area as a measure of full recovery to reference condition (SFBRWQCB 2007). To assess responses to differences in habitat, we assigned taxa as “clingers” or “other” based on behavioral habit (Poff

et al. 2006) and calculated percent clingers. We calculated rarefied richness, using the R package *vegan* (Oksanen et al. 2017) to rarefy each sample to account for variation in number of individuals across samples. We also considered including functional feeding groups (specifically scrapers and shredders), but the relative abundances of specialist feeding groups were so low in all sites that we could not characterize them accurately and they were removed from the analysis.

Habitat Variables

At the downstream, mid, and upstream points of the reach we measured bankfull width and depth and assessed tree shading using a densiometer (Lemmon 1956). We placed a HOBO Onset pendant continuous temperature logger at each site for 3 weeks. We calculated pool spacing as the number of channel widths per pool within the 50-m reach (50/bankfull channel width/# pools) (Montgomery et al. 1995).

Across each sampling riffle we performed a pebble count of at least 100 pieces of substrate along perpendicular transects placed 0.25–1 m apart, depending on channel width and riffle length (Wolman 1954; Bunte & Abt 2001). Bed material smaller than 2 mm was recorded as “fine sediment.” We calculated median diameter (d_{50}) and % fine sediment. Pebble counts may underestimate fine sediment compared with other methods (Bunte & Abt 2001), but do permit comparison among sites within our study. To minimize variation, one operator performed all pebble counts. Median grain size and % fine sediment were negatively correlated (Pearson’s $r = -0.77$, $p = 9 \times 10^{-14}$).

In 2016, we sampled chlorophyll *a* on three representative cobbles within each riffle. We scrubbed cobbles clean with a nylon brush, captured the algal residue on a glass fiber filter, and measured chlorophyll *a* (corrected for pheophytin *a*) in the lab using a TD-700 fluorometer (Arar & Collins 1997). We then calculated the concentration of corrected chlorophyll *a* per rock area using a spheroid approximation (Bergey & Getty 2006).

In 2016, we sampled riffle coarse particulate organic matter (CPOM, ≥ 1 mm) and fine particulate organic matter (FPOM, < 1 mm and ≥ 500 μm) by collecting an additional 0.27-m² sample using the D-net sampling method outlined above. We repeatedly elutriated the combined sample to remove gravel and sand, and then poured the sample through 1-mm mesh. CPOM was trapped on the net, towel-dried, and weighed in the field to the nearest gram. The sample passing through the mesh was then filtered through a 500- μm net to capture FPOM ≥ 500 μm . We removed macroinvertebrates with forceps and preserved the remainder in formalin. In the lab, FPOM samples were dried, weighed, ashed, and reweighed to calculate the ash-free dry mass (Hutchens et al. 2017).

Landscape Characterization

Using GPS waypoints and Esri ArcGIS, we located each site and manually measured corridor width and upstream corridor length using aerial imagery (DigitalGlobe 2017). We also measured the length of the continuous distance without tree cover upstream of the riparian corridor for each stream group, which we refer to as the upstream gap in cover. We calculated standardized corridor length as corridor length/bankfull stream width, because as stream size increases we expected a longer corridor to be required to impact stream condition (Parkyn et al. 2003). Scaling by width also reduced the influence of a group of points from a few large streams with very long corridors. We re-ran the analyses on unstandardized corridor length, and all significant coefficients were unchanged.

We used a 3-m digital elevation model (USGS 2018) to calculate upstream drainage area and channel slope. We estimated an index of stream power using mean bankfull width and depth multiplied by slope. This index modifies the equation for stream power (stream power = velocity \times width \times depth \times slope) (Bagnold 1966), with the simplifying assumption that stream velocity at all sites was equal. Although not a precise estimate of stream power, this equation does produce an index of power for use within these streams of similar size.

Using the soil map for Marin County (Kashiwagi 1985), we assigned sites to either moderately drained fine coastal soils or well-drained coarser inland soils. All sites within the finer soil type were restored, while 40% of sites within the coarse soil type were restored (the remainder were remnant corridors).

Data Analysis

We completed all analyses in R (R Core Team 2017), and constructed figures using the package *ggplot2* (Wickham 2009). We compared shading, corridor width, and length of upstream gap in cover for remnant and restored corridors using a Wilcoxon rank-sum test.

We modeled six habitat outcomes (% fine sediment, pool spacing, mean water temperature, chlorophyll *a* concentration, FPOM, CPOM), and five invertebrate outcomes (% clingers, % EPT, % sensitive, tolerance value, rarefied richness) separately, constructing a total of 11 models. We define significance at $p \leq 0.05$ and report standard error.

To assess the effect of tree cover on habitat and invertebrate metrics, we performed a series of regressions using the R package *lme4* (Bates et al. 2015). We applied a logit transformation to proportion outcomes (Warton & Hui 2011), adding 0.001 to % sensitive, % EPT, and % fine sediment to avoid zero values. We modeled concentrations and weights (chlorophyll *a*, CPOM, FPOM) and pool spacing using generalized linear mixed effects models (GLMMs) with a gamma distribution and a log link. Other responses were modeled using linear mixed effects models (Table 2). Models included both standardized corridor length and tree presence as predictors, which are nested and collinear; we included both terms to allow for a nonlinear response where the initial effect of tree presence may differ from the marginal effect of increasing corridor length. We log-transformed standardized corridor length (after adding one to remove zeros). To account for temporal autocorrelation in sites sampled in 2 years, year was also included as a fixed effect. All predictors were centered and rescaled prior to analysis (Gelman 2008). To incorporate the nested structure of sites within stream groups and account for spatial autocorrelation, we included stream group as a random intercept (Zuur & Ieno 2016). Parameters for linear models were estimated using restricted maximum likelihood; parameters for GLMMs were estimated using maximum likelihood (Bates et al. 2015).

To assess whether the effect of corridor length varied with larger-scale conditions, we added three covariates in turn, including an interaction between each covariate and corridor length: coarse vs. fine soil type, stream power (log-transformed), and length of the upstream gap in tree cover (log-transformed). We only modeled those relationships for which we had hypotheses (Table 2). We compared each of the resulting models with interactions to the corridor length, (year,) and presence-only model using AICc from the package *glmulti*, and present the interaction where it improved the model ($\Delta\text{AICc} > 2$) (Calcagno 2013). Stream power did not improve any models.

We considered an effect significant where bootstrapped 95% confidence intervals did not cross zero. For models where corridor length did not have a significant relationship with the outcome variable, we performed a paired *t* test comparing sites on the same stream with no tree cover to the nearest downstream site with trees to test for an effect of tree presence. To assess model goodness of fit, we calculated pseudo R^2 for the linear mixed effects models (Nakagawa & Schielzeth 2013) using the package *piecewiseSEM* (Lefcheck 2016). Marginal pseudo R^2 is variance explained by fixed effects only; total pseudo R^2 is variance explained by full model (including random effects). We re-ran all models without influential points, without perennial streams, and with a random effect for stream; results were qualitatively unchanged. To evaluate whether combining remnant and restored corridors was appropriate, we assessed the community variation explained by restored vs. remnant cover using partial redundancy analysis. See Appendix S1 for more details and additional robustness checks.

We evaluated differences in whole community composition in response to watershed and stream condition using non-metric multidimensional scaling (NMDS) ordination and

the R package *vegan* (Oksanen et al. 2017) with our 2016 data (see Appendix S1). For visualization, we created four categories of standardized corridor lengths: no tree cover, short (0–50 m), medium (51–200 m), and long (>200 m), which represent roughly equal proportions of our data.

Results

Comparison of Restored and Remnant Corridors

Restored corridors were on average narrower than remnant corridors: the median difference in mean corridor width between restored and remnant corridors was 7 m ($w = 163$, $p = 0.04$). Both restored and remnant corridors had similar upstream gaps in cover ($w = 108$, $p = 0.9$) and shading ($w = 131$, $p = 0.4$). Invertebrates in restored and remnant corridors were also similar: partial redundancy analysis estimated that 5% of the variation in invertebrate communities was explained by whether the site was restored or remnant, after controlling for the effect of soil type. Based on these results (detailed in Appendix S1), we grouped restored and remnant corridors for the subsequent analyses.

Habitat Response to Tree Corridor Length

The proportion of fine sediment in riffles declined with tree corridor length (Fig. 2A, D). Mean water temperature (over 3 weeks) also declined with corridor length, and declined more strongly where the upstream gap in cover was longer (Fig. 2B, E). Pool spacing did not change with corridor length (Tables 1 and 2).

Food resources did not change consistently with corridor length (Tables 1 and 2). FPOM tended to be higher at sites with long gaps in cover, but the effect was not significant (Fig. 2C, F). When we compared sites with and without trees on the same stream using *t* tests, CPOM was higher at sites with short corridors compared to sites with no tree cover ($p = 0.02$), and chlorophyll *a* decreased ($p = 0.05$) with cover. There was no difference in FPOM with tree presence.

Invertebrate Response to Corridor Length and Tree Presence

Percent EPT, clingers, and sensitive taxa all increased with corridor length (Fig. 3, Tables 1 and 2), although clingers only increased in the fine soil type. Rarefied richness and community tolerance value were not related to tree corridor length or tree presence.

The inclusion of soil type as an interaction term improved predictions. Holding corridor length constant, richness, % EPT, % clingers, and % sensitive taxa were all higher in sites with the coarse soil. Absolute increases in % EPT with corridor length were also greater in streams with higher baseline conditions (coarse soil type and short upstream gaps) (Table 2, Fig. 3). Conversely, proportional increases in % EPT with corridor length were greater in streams with lower baseline conditions (i.e. mean relative abundance changed from 20 to 30% in the coarse soil type and from 1 to 4% in the fine soil type).

Most sites failed to meet the regional reference intermittent stream values for % EPT (Fig. 3B, E) and tolerance value, which we defined as full recovery (SFBRWQCB 2007). Eighty-nine percent of samples (57 of 64) had % EPT values below the minimally disturbed minimum for intermittent streams in the region, and 69% of samples (44 of 64) had a tolerance value above the “minimally disturbed” intermittent stream maximum. The invertebrate community ordination (NMDS) was more strongly influenced by stream group than tree cover treatment (Appendix S1, Fig. S1). Using linear regression, % fines strongly predicted NMDS1 (coefficient 1.4, SE 0.17, adjusted $R^2 = 0.67$; Fig. 4).

Discussion

Long, narrow riparian corridors are an understudied but potentially useful tool for stream conservation. Unlike wide tree corridors, they do not require the removal of large amounts of land from productive use for implementation. We found that narrow corridors can improve downstream habitat with minimal impact on surrounding land use patterns, an important practical consideration in working landscapes. Long riparian corridors were correlated with reduced water temperature and fine sediment loads, two highly limiting stressors in aquatic ecosystems (Cooper et al. 2012; Leps et al. 2015). Corresponding increases in the relative abundances of sensitive invertebrate taxa (including EPT and clingers) with corridor length indicate that the observed reduction in temperature and fine sediment stressors may benefit stream fauna. Stream condition is constrained by large-scale influences (e.g. ongoing land use, gaps in tree cover, soil type), but we found that increasing the length of even small-scale riparian corridors could provide important benefits to stream habitat quality.

Our study focused on small, intermittent streams, which often support aquatic communities distinct from those found in nearby perennial streams (Bonada et al. 2006; Bogan et al. 2013; Tonkin et al. 2017). Taxa in intermittent streams also may have higher tolerance of stressful or variable conditions (Bogan et al. 2017). Moreover, this study was correlative, which is not unusual for stream restoration studies given the challenge of setting up experimental studies in multi-use watersheds. Despite these caveats, we hope this study will inspire others to evaluate the effect of corridor length in other systems. Indeed, many of our findings are broadly consistent with the literature focusing on riparian buffer width, suggesting that they may hold true across a variety of stream types (Palmer et al. 2014; Sweeney & Newbold 2014).

Improvements in Habitat Quality With Corridor Length

Increases in mean water temperatures can severely stress endangered cold water fishes as well as invertebrates (Kroll et al. 2017). Given predicted rising temperatures in the study region (Isaak et al. 2012), and globally (IPCC 2014), maintenance of stable cool water habitats, or cold water refuges, have become a critical area of conservation focus (Isaak et al. 2018). In our study, long corridors predicted reductions in the temperature of

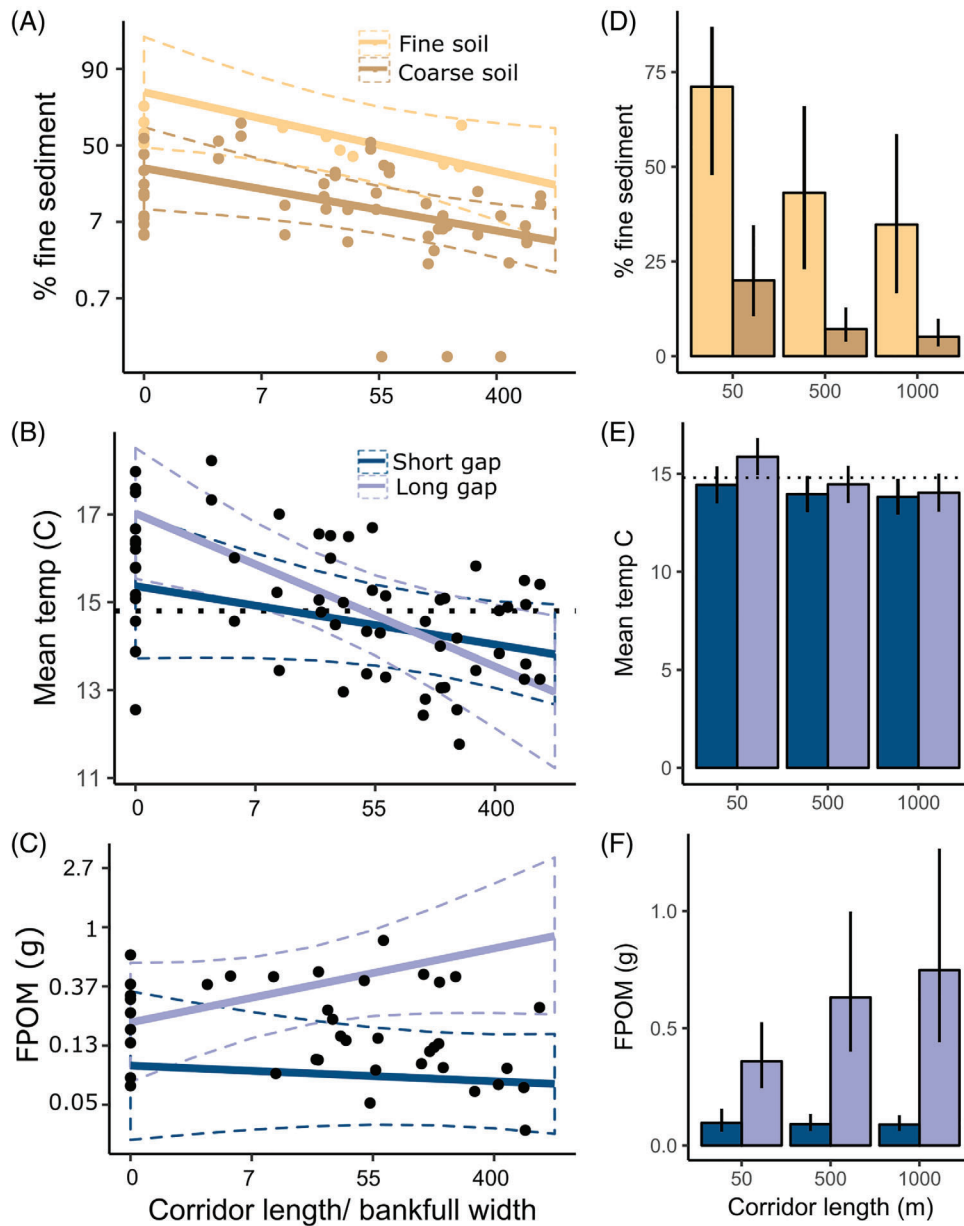


Figure 2. Selected habitat responses to riparian corridor length. (A–C) Solid lines indicate coefficient estimates and dashed lines indicate 95% CI. Dots show observed data. Brown and yellow on A represent sites within the coarse and fine soil type, respectively. Dark and light blue lines in B and C represent short and long unvegetated reaches (gaps) upstream of study area, respectively. Y-axis of A is on a logit scale with units back-transformed; y-axis of C and all x-axes are on a back-transformed log scale (base e). (D–F) Model predictions for the average stream, ± 1 SE; colors match A–C. Dotted line on B and E shows the weekly mean water temperature stressful for coho salmon (Sullivan et al. 2000; SFBRWQCB 2007). A and B include 2 years of data (A: $N = 64$; B: $N = 59$), C is 2016 only ($N = 39$) [Correction added on 15 November 2019, after first online publication: The x axis numbers on the left-hand panel of figures (A–C) have been updated to match the numbers in Figure 3].

water flowing from unshaded upstream reaches within relatively short distances (<1 km), thereby helping to improve current habitat and compensate for higher stream temperatures expected with climate change (Justice et al. 2017). Our study suggests that the restoration of a 1-km corridor could counteract the effects of 1.5°C of warming, and that decreases are more dramatic when initial temperatures are higher (longer upstream gap), consistent with findings of others for small streams (Storey & Cowley 1997; Moore et al. 2005) (although some streams

fail to respond, see Sweeney & Newbold 2014). Temperature reduction, however, is highly dependent on local patterns of subsurface water inputs and microclimate conditions, and is more likely to be consistent in similarly sized streams than much larger systems (Moore et al. 2005; DeWalle 2008). Studies of riparian buffer width suggest that 12–30-m corridors are necessary to provide complete shading and prevent warming, so wider buffers could result in additional cooling (Sweeney & Newbold 2014).

Table 1. Hypothesized and measured responses of habitat and invertebrate outcomes to riparian tree presence and riparian corridor length. For statistics and full results refer to Table 2. Blank indicates test was not performed; dash indicates nonsignificant result (at $p \leq 0.05$; 95% CI overlapped zero). We assessed the effect of corridor length with mixed effects models. We evaluated the effect of corridor presence with paired *t* tests for those outcomes not significantly related to length. The additive and interactive effects of two covariate terms (length of unvegetated reach [gap] upstream of study area and soil type) are presented where they improved the riparian corridor length model.

Outcome	Hypothesis		Findings		Covariate Interaction With Corridor Length	Covariate Additive Effect
	Length	Length	Presence	Presence		
Habitat						
% Fines	↓	↓	–	–	–	Higher in fine soil type
Pool spacing (channel widths per pool)	↓	–	–	–	–	–
3-week mean temperature	↓	↓	–	–	Effect stronger as upstream gap increases	–
CPOM (g)	↑	–	↑	–	–	–
FROM (g)	↑	–	–	–	–	–
Chlorophyll <i>a</i> (µg/L)	↓	–	↓	–	–	–
Invertebrates						
% EPT	↑	↑	–	–	Proportional effect stronger in fine soil type and as upstream gap increases	Lower in fine soil type
% Clingers	↑	↑	–	–	Effect only in fine soil type	Lower in fine soil type
% Sensitive	↑	↑	–	–	–	Lower in fine soil type
Tolerance value	↓	–	–	–	–	–
Rarefied richness	↑	–	–	–	–	Lower in fine soil type

Long corridors were also correlated with less fine sediment. Sediment can be trapped by vegetation during overbank flow (Pluntke & Kozerski 2003; Zong & Nepf 2011) and stored off-channel (Corenblit et al. 2007; Gurnell 2014), which we suggest is the likely mechanism given the density of vegetation we observed along these streams. Vegetation can also filter sediment from overland flow (Sweeney & Newbold 2014), but in streams with fragmented tree corridors (as in this study), some amount of in-stream removal is likely required to reduce fine sediment on riffle habitats. We had hypothesized that tree cover could support increased pool development (as shown by Lennox et al. 2011) and that these pools could store sediment, but we found no relationship of pools and tree cover.

Invertebrate communities in the fine soil type had lower richness and lower relative abundances of sensitive taxa, EPT taxa, and clingers than those in the coarse soil type, generally suggesting lower-quality habitat conditions. Both the strong relationship between invertebrate community composition and % fine sediment (Fig. 4) and the significant effect of soil type on each of these metrics suggests that fine sediment may drive the shifts in community composition with corridor length, in keeping with a large literature showing that fine sediment favors certain life history traits (Larsen et al. 2011; Buendia et al. 2013).

In addition to showing sensitivity to soil type, trait-based invertebrate metrics signaled improved conditions at sites with longer corridors (higher % sensitive, % EPT, % clingers), suggesting that differences in conditions with corridor length were ecologically meaningful. A recent systematic review found that 100% of the 31 riparian restoration projects evaluated showed improvements in % EPT (Palmer et al. 2014), consistent with our findings. Others have found improvements in % EPT with

distance into forested area (600 m, 300 m) (Storey & Cowley 1997; Weigel et al. 2000), although the relationship of tree cover and % EPT has not been consistently supported in the literature (see Parkyn et al. 2003; Richardson & Béraud 2014).

Limits to Improvement

In contrast to the increases in relative abundance of sensitive invertebrate groups with corridor length, taxa richness and tolerance value did not respond to tree cover or corridor length. Both tolerance value and % EPT remained below reference condition at most sites, suggesting a lack of full recovery (McDonald et al. 2016). Specialist functional feeding group taxa were also extremely rare at all sites, which suggests a lack of strong response by these taxa. Although higher taxonomic resolution and the inclusion of smaller instars in our sample may have revealed stronger patterns, others have found a similar lack of response of IBI and richness metrics with riparian cover (Roy et al. 2005; Wahl et al. 2013). The same systematic review recording % EPT improvement in all studies with riparian restoration found improvement in indices of biotic integrity in only 37% of studies (Palmer et al. 2014). These metrics evaluate the entire community, rather than selected traits, and as a result are likely to be less sensitive to trait-specific responses. Similarly, food resources either responded only to tree presence (CPOM, chlorophyll *a*) or had no consistent response to tree cover (FPOM). A recent meta-analysis also found highly variable responses of CPOM (and shredders) to riparian forest cover (Richardson & Béraud 2014).

A high percentage of the variation between sites was unexplained or explained only by stream group. We purposely selected sites within a small geographic area and consistent land

Table 2. Model estimates and standard error for the relationship between corridor length and key habitat and invertebrate variables. All models included an intercept, tree corridor length/channel width, and tree presence, with additional covariates where they improved model fit, and year where sampling spanned 2 years. All predictors were standardized; 2016 and coarse soil type are the reference levels. Stream group is included as a random effect for all models. Tree presence is collinear with corridor length, so tree presence estimates are not meaningful and are included only for completeness. Blanks indicate that we did not perform the test. $\Delta AICc$ shows the change in $AICc$ with the addition of the interaction and covariate to the year, corridor length, and tree presence model. Where $\Delta AICc < 2$, we show the $\Delta AICc$ in italics but do not present or evaluate the model including that covariate term. Bolded terms and * denote $p \leq 0.05$ (using bootstrapped 95% confidence intervals). Paired t tests compare the site with no cover to the nearest downstream site on the same stream, and were only performed where corridor length did not significantly predict the outcome variable.

Outcome	N	Model Type	Corridor			Year 2015	Fine Soil	Length of	Corridor	Random effect		Total R ²	<i>t</i> test:
			Channel	Width (log)	Presence					Intercept	Width (log)		
Habitat—physical													
% Fines	64	Linear, logit transformation	-1.56	-2.43	1.36	0.68	2.29 (0.71)*	$\Delta AICc = 0.2$	-0.52 (0.74) fine soil type	1.04	0.35	0.68	
Pool spacing (channel widths per pool)	39	Gamma family, log link	0.56*	0.39*	0.6*	0.28*	$\Delta AICc = 6.1$			0	n.a.	n.a.	N (t = -0.140, p = 0.99)
Mean temperature	59	Linear	1.55	15.40	-0.12	-1.67	$\Delta AICc = 7.5$	0.59 (0.32); $\Delta AICc = 7.5$	-1.24 (0.41)* upstream gap	0.88	0.54	0.86	
Habitat—food													
CPOM (g)	39	Gamma family, log link	0.66	1.44	-0.51	0.18*	$\Delta AICc = -2.2$	$\Delta AICc = -2.2$	0.82 (0.45) upstream gap	0.69	n.a.	n.a.	Y (t = -3.0, p = 0.02, mean log increase 0.8)
FPOM (g)	39	Gamma family, log link	0.29	-1.76	-0.22	0.18*	$\Delta AICc = 2.5$	1.12 (0.39); $\Delta AICc = 2.5$	0.82 (0.45) upstream gap	0.16	n.a.	n.a.	N (t = -0.005, p = 1)
Chlorophyll <i>a</i> (µg/L)	39	Gamma family, log link	0.66	1.44	-0.51	0.18*	$\Delta AICc = 7.4$			0.14	n.a.	n.a.	Y (t = 2.4, p = 0.05, mean log decrease 0.4)
Invertebrates													
% EPT	64	Linear, logit transformation	1.19	-1.1	-0.96	0.09	-3.48 (0.63)*	$\Delta AICc = 21.0$	1.76 (0.68)* fine soil type	0.78	0.60	0.79	
% Clingers	64	Linear, logit transformation	0.52*	0.34*	0.56	0.26	$\Delta AICc = 3.1$	-0.7 (0.5); $\Delta AICc = 3.1$	1.25 (0.62)* upstream gap	3.76	0.11	0.83	
% Sensitive	64	Linear, logit transformation	0.6*	0.56*	0.64	0.27	$\Delta AICc = 9.8$	$\Delta AICc = -2.3$	1.71 (0.68)* fine soil type	0.61	0.41	0.65	
Tolerance value (0–10)	64	Linear	0.51	0.32*	0.51	-0.19	$\Delta AICc = 7.4$	$\Delta AICc = -2.9$	-0.06 (0.76) fine soil type	2.43	0.43	0.82	
Rarefied richness	64	Linear	0.4	4.98	0.18	0.02	$\Delta AICc = -0.7$	$\Delta AICc = -4.9$		0.28	0.03	0.46	N (t = 0.6, p = 0.5)
	64	Linear	0.7	14.25	0.13	-2.35	$\Delta AICc = 9.6$		1.53 (2.2) fine soil type	5.1	0.28	0.53	N (t = -1.4, p = 0.2)
			1.65	0.95*	1.79	0.85*	$\Delta AICc = 9.6$	-2.52 (1.37); $\Delta AICc = 7.3$	2.96 (1.87) upstream gap	10.1	0.17	0.62	

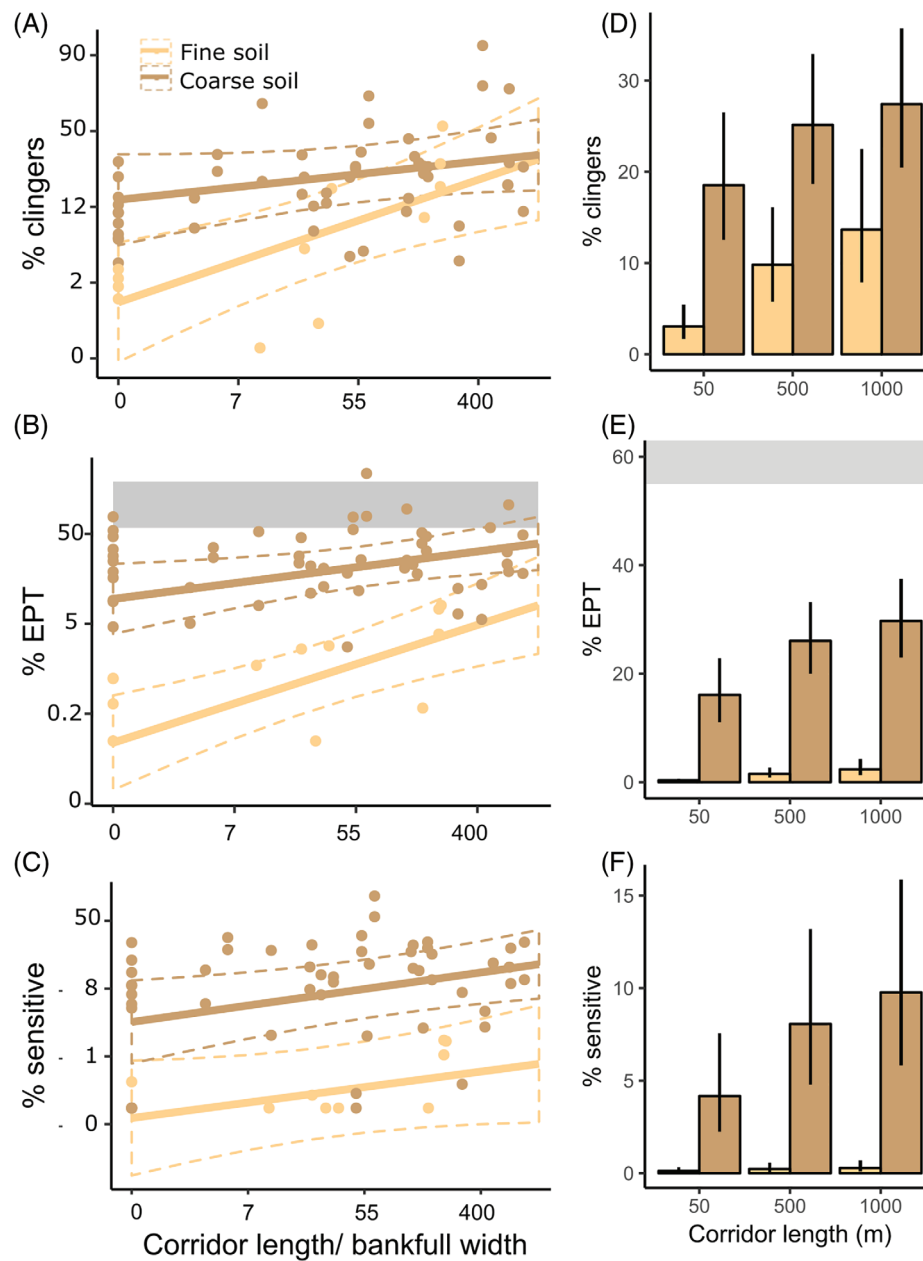


Figure 3. Selected invertebrate responses to riparian corridor length. Brown and yellow represent sites within the coarse and fine soil type, respectively. (A–C) Solid lines indicate coefficient estimates and dashed lines indicate 95% CI. Y-axes are on a logit scale with units back-transformed; x-axes are back-transformed log scale (base e). (D–F) Model predictions at three corridor lengths for the average stream, ± 1 SE. Gray rectangles represent values for least-disturbed intermittent stream reference condition in the region (SFBRWQCB 2007). $N = 64$.

use type to minimize noise due to variable watershed-scale conditions, which can exert a strong influence on stream recovery (Allan et al. 1997; Stanford et al. 2019). Nonetheless, as expected, stream condition and response to riparian corridors was highly variable, likely due to factors such as vegetation characteristics, water quality, proximity of source populations, and hydrology (Sundermann et al. 2011; Lorenz & Feld 2013). The variation in responses by stream highlights the importance of considering site-specific constraints and adjusting expectations accordingly: e.g. sites within the fine soil type

were likely to support a more tolerant invertebrate community than sites within the coarse soil type, regardless of management actions.

Benefits of Long Corridors

The substantial literature that explores minimum riparian corridor widths for effective filtration of overland flow has largely ignored the potential benefits of increasing riparian corridor length to improve stream condition. Even very short corridors

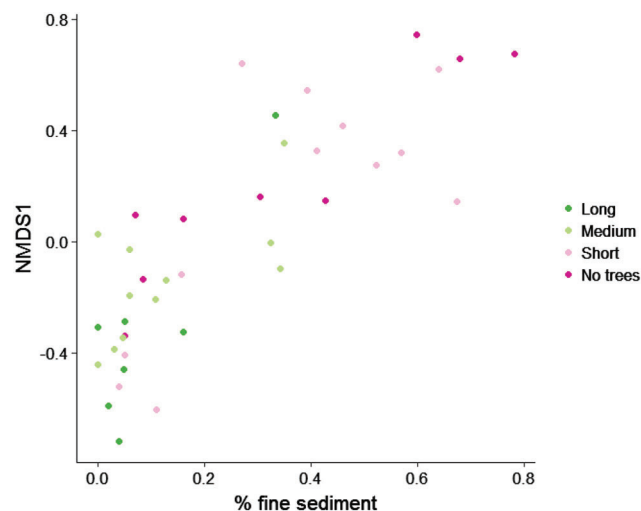


Figure 4. Relationship of 2016 invertebrate community (NMDS1 axis) and % fine sediment on riffles. Colors represent corridor length categories.

result in shifts to food resources, whereas long riparian corridors can support reductions in fine sediment and temperature as well as more sensitive invertebrate communities, with likely effects throughout the aquatic food web. However, we also find evidence that larger-scale land use-related stressors continue to limit improvement. We find strong benefits of long riparian corridors given the degraded starting condition, but most of our long corridor sites still did not support macroinvertebrate communities that met regional reference conditions, suggesting that grazing practices would need to be modified to facilitate full recovery (McDonald et al. 2016). Hence, we caution managers to carefully evaluate existing constraints and expectations for small-scale riparian corridor restoration projects and tailor restoration practices to local conditions.

Given the constraints of land use, extending the length of small restoration projects may enable managers to maximize improvements to stream condition. In landscapes with multiple private landowners, the creation of longer riparian corridors could be accomplished by prioritizing restoration and protection of sites near existing riparian corridors. In addition to the in-stream benefits described in this article, these long corridors can also help improve landscape connectivity for a host of terrestrial species (Fremier et al. 2015). Extending the length of riparian corridors may represent an important tool to improve habitat in agricultural landscapes.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Additional robustness checks and ordination methods.

Figure S1. NMDS plot of sites and environmental variables.

Table S1. Basic attributes and corridor lengths of the 13 stream groups.

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