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Quantifying invertebrate resistance to floods: a global-scale meta-analysis

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Abstract. Floods are a key component of the ecology and management of riverine ecosystems around the globe, but it is not clear whether floods have predictable effects on organisms that can allow us to generalize across regions and continents. To address this, we conducted a global-scale meta-analysis to investigate effects of natural and managed floods on invertebrate resistance, the ability of invertebrates to survive flood events. We considered 994 studies for inclusion in the analysis, and after evaluation based on a priori criteria, narrowed our analysis to 41 studies spanning six of the seven continents. We used the natural-log-ratio of invertebrate abundance before and within 10 days after flood events because this measure of effect size can be directly converted to estimates of percent survival. We conducted categorical and continuous analyses that examined the contribution of environmental and study design variables to effect size heterogeneity, and examined differences in effect size among taxonomic groups. We found that invertebrate abundance was lowered by at least one-half after flood events. While natural vs. managed floods were similar in their effect, effect size differed among habitat and substrate types, with pools, sand, and boulders experiencing the strongest effect. Although sample sizes were not sufficient to examine all taxonomic groups, floods had a significant, negative effect on densities of Coleoptera, Eumalacostraca, Annelida, Ephemeroptera, Diptera, Plecoptera, and Trichoptera. Results from this study provide guidance for river flow regime prescriptions that will be applicable across continents and climate types, as well as baseline expectations for future empirical studies of freshwater disturbance.

Key words: disturbance ecology; environmental flows; quantitative synthesis; river management.

INTRODUCTION

Freshwater is becoming an increasingly important and scarce resource around the world (Yeston et al. 2006). While humans have altered freshwater ecosystems through damming in the majority of large-river systems in the world (Nilsson et al. 2005), there is a trend to bring flows back to a more natural regime and to recognize rivers themselves as legitimate users of water (Naiman et al. 2002). Environmental flows are one paradigm used to manage rivers across the world, with over 200 different methodologies having been developed (Tharme 2003). Under this broad framework, elements of the natural flow regime are mimicked to produce desired ecological outcomes, such as increased biodiversity or habitat creation for target species.

Despite the diversity of methods that have been developed at various scales to prescribe environmental flows to rivers (Jowett 1997, Arthington et al. 2006), there is little quantitative information regarding how flood events affect specific biota and ecosystem processes (Bunn and Arthington 2002). This quantitative information is necessary for accurate parameterization of predictive models of ecological effects of managed flow regimes, and can aid in forming useful hypotheses for further scientific studies on freshwater ecology.

Overall, while there are many case studies investigating effects of floods on aquatic organisms, differences in river type, regional climate, and continental setting make it difficult to draw general conclusions (Resh et al. 1988, Death 2010). A quantitative understanding of how aquatic organism populations immediately respond to disturbance events would lead to better predictions of post-flood population sizes, simpler interpretation of post-flood monitoring data, and a better understanding of organisms' responses to disturbance events (Poff and Zimmerman 2010).

In this study, we used a global-scale meta-analytic study to examine the quantitative relationships between flood events and change in invertebrate abundance (resistance). We focused on aquatic invertebrates because they encompass a wide array of life-history and behavioral characteristics that can inform studies of other aquatic taxa. Specifically, our goals were to (1) determine whether effects of natural vs. prescribed flood events differ and to what degree, (2) investigate differences in effects of floods among riverine habitat types and study designs, (3) determine whether a flood's relative magnitude affects organism resistance, and (4)

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explore differences in response to flooding across taxonomic groups.

Methods

Literature search

We searched the literature with a priori criteria for appropriate primary case studies concerning effects of floods on aquatic invertebrate abundance immediately after flood events. We used the electronic database Web of Science (including papers from 1970–2010) to identify potential studies for inclusion. We used the terms *spate* or *flood*, *macroinvertebrate* or *macro-invertebrate* or *insect* or *invertebrate*, and *benthic* or *aquatic* or *stream* as keywords, resulting in 994 potential studies. We evaluated each study for inclusion with the following criteria. Studies were required to be primary research papers, and needed to contain information on independent flood events in rivers, streams, or artificial stream channels, with both pre and post data on aquatic invertebrate density in relation to floods (e.g., invertebrate abundance per square meter, or abundance per cage, artificial substrate, or rock). We excluded studies that only reported correlation coefficients or significance values concerning flood effects on invertebrates. We also excluded studies that had confounding treatments such as insecticide application. We included both natural and managed floods. The pre-flood samples must have occurred within 60 days of the flood event, and the post-flood samples within 10 days of the flood event. If other papers were cited that could contain needed, missing information, we included data from those papers as well. With these criteria in place, we obtained 41 studies for analysis (Table 1).

We collated data from these studies in two ways, each intended to test different questions about invertebrate response to flood events (Table 2):

1) General data set. Total abundance of all invertebrates per unit area, without respect to taxonomy, was used as the sample unit. This conservative approach avoids the issue of independence among taxa at a given site, but fails to identify taxon-specific differences in flooding response.
2) Taxon-specific data set. Abundance of different taxonomic groups of invertebrates per unit area, broken down by lowest taxonomic level reported in studies, represents the sample unit. Within a study, taxonomic groups were weighted equally. This approach allowed us to identify potential taxon-specific differences in flooding response.

For example, a study could have reported abundance before and after a flood event for five taxa. For the general data set, we would sum the abundances of the five taxa and consider this a sample unit. For the taxon-specific data set, the abundance before and after the flood event for each of the five taxa was considered a sample unit. In this scenario, we would have obtained one sample unit for the general data set, and five sample units for the taxon-specific data set. These alternative replication schemes have different implications for the interpretation of results.

For the general data set, the cumulative effect size (Rosenberg et al. 2000) of floods on total invertebrate abundance could be biased towards taxa that generally occur in higher abundance. For the taxon-specific data set, the cumulative effect size is representative of the overall magnitude of the effect of floods on all taxa treated as individual units of replication in all the studies in the data set. Besides calculating a cumulative effect size of floods on overall invertebrate abundance from the taxon-specific data set (and using this value in categorical and continuous analyses), we were also able to compare effect of floods among different taxonomic groups.

For the general data set, if a study reported the total invertebrate densities before and after the flood event, these numbers were used. If a study only reported densities for specific taxa, densities of individual taxa were aggregated so long as data for three or more orders of invertebrates were reported (Table 2). For the taxon-specific data set, we first recorded invertebrate data at the finest taxonomic level reported in each study, and then standardized to higher taxonomic levels where appropriate. We considered different taxonomic groups within a study independently. For taxon-specific analyses, we also included studies in which data were reported as a percent change from pre to post-flood.

Within the taxon-specific data set, data were standardized to different taxonomic levels depending on the analysis being performed. For analyses that were performed using both the general data set and the taxon-specific data set, sample units consisted of abundances for each insect order (and other levels for non-insects). Thus, data were standardized to this level by summation of lower taxonomic levels (if the data were reported as density data) or by averaging (if the data were reported as a percent change). A categorical analysis among groups of taxa at these higher-level taxonomic groupings was also performed.

A second set of taxon-specific analyses were conducted at the family level. All groups of taxa determined in the first set of taxon-specific analyses were analyzed for inclusion in this next step of analysis. For a group of invertebrates to be included, it had to have subgroup data for at least two disparate groups at the next classification level with $n \geq 5$ for each, and with data derived from at least three separate studies for each subgroup. The goal of this set of analyses was to determine whether significant differences in resistance to flooding can be detected among groups at finer classification levels.

We included data only for flood events at least 60 days apart, with no significant floods within 60 days prior to the flood event, for each river in each study. We included data for multiple sites per river per study, if data were

TABLE 1. Characteristics of all included studies.

Reference	Country	River(s)
Angradi (1997)	United States (West Virginia)	Wilson Hollow Stream
Baumgartner and Waringer (1997)	Austria	Mauerbach
Bond and Downes (2000)	Australia	Steavenson
Boulton et al. (1992)	United States (Arizona)	Sycamore Creek
Brewin et al. (2000)	Nepal	Likhu Khola streams
Brown (2007)	United States (New Hampshire)	Alder Brook
Chantha et al. (2000)	Canada (Quebec)	Ruisseau Epinette
Cobb et al. (1992)	Canada (Manitoba)	Wilson Creek
Collier (2002)	New Zealand	Tongagiro
Effenberger et al. (2008)	Germany	Eyach stream
Effenberger et al. (2006)	New Zealand and Germany	Kye Burn and Schmiedlaine
Fritz and Dodds (2004)	United States (Kansas)	Kings Creek tributaries
Hax and Golladay (1998)	United States (Texas)	Sister Grove Creek
Holomuzki and Biggs (2000)	New Zealand	Laboratory flume
Imbert et al. (2005)	Spain	Cuchillo and Salderrey streams
Kilbane and Holomuzki (2004)	United States (Ohio)	Rocky Fork River tributary
Lancaster (1992)	Canada (BC)	Streamside channels at Mayfly Creek
Lytle (2000)	United States (Arizona)	North Fork Cave Creek
Maier (2001)	Switzerland	Kalte Sense
Matthaei et al. (2000)	New Zealand	Kye Burn
Matthaei et al. (1997)	Switzerland	Necker River
Matthaei and Huber (2002)	Germany	Schmiedlaine
Miller and Golladay (1996)	United States (Oklahoma)	Buncombe and Brier Creeks
Negishi et al. (2002)	Japan	Nukanan Stream
Negishi and Richardson (2006)	Canada (BC)	Spring Creek
Olsen and Townsend (2004)	New Zealand	Kye Burn
Orr et al. (2008)	United States (Wisconsin)	Boulder Creek
Ortiz and Puig (2007)	Spain	La Tordera
Palmer et al. (1996)	United States (Virginia)	Goose Creek
Palmer et al. (1992)	United States (Virginia)	Goose Creek
Rader et al. (2008)	United States (Colorado)	Colorado River
Robinson et al. (2004)	Switzerland	Spol River
Robinson and Uehlinger (2008)	Switzerland	Spol River
Robson (1996)	Tasmania	Mountain River
Scrimgeour and Winterbourn (1989)	New Zealand	Ashley River
Shafroth et al. (2010)	United States (Arizona)	Bill Williams River
Silver et al. (2004)	United States (Virginia)	Goose Creek
Stock and Schlosser (1991)	United States (Minnesota)	Gould Creek
Thiere and Schulz (2004)	South Africa	Lourens River
Thomson (2002)	Australia	Cumberland River
Wantzen (1998)	Brazil	Corrego Tenente Amaral

reported for multiple longitudinal sites. Although including multiple flood events and longitudinal river sites from a single study in the analysis could cause a lack of spatial or temporal independence, this is a common problem in meta-analysis, and we concluded that exclusion of these data would be too great of an information loss. If data from multiple rivers were reported in a study, we included data from all rivers in the analyses. When needed, we used Data Thief III software (Tummers 2006) to extract data from graphs.

Examining resistance via effect size

Resistance can be defined as the ability of a population or community to withstand a disturbance event (sensu Grimm and Fisher 1989) so we calculated effect size of floods on aquatic invertebrate taxa within 10 days after the flood event. The primary response variable of interest was density of invertebrate taxa per unit area. We used natural-log response ratio (R) as the measure of effect size in this study: ln([density of invertebrates post-flood]/[density of invertebrates pre-flood]). Thus, a negative effect size indicated a reduction in density of individuals following a flood event. Taking the natural log of the response ratio linearizes the results by equally accounting for the numerator and denominator, and normalizes the sampling distribution of the response ratio (Hedges et al. 1999).

Meta-analytic techniques

We performed an unweighted analysis, as seven studies did not report variance and would have been excluded from the analysis. Additionally, summation of invertebrate data from lower to higher taxonomic levels for standardization disallowed accounting for variance. We used an unstructured and unweighted random effects model in MetaWin (Rosenberg et al. 2000) to evaluate overall effect size of floods on aquatic invertebrates. Effect sizes, in the case of ln response ratio, are considered significant if their 95% confidence intervals do not overlap zero (Rosenberg et al. 2000, Shurin et al. 2002).

TABLE 1. Extended.

Invertebrates	Collection method	Flood type	Multiple sites?
most abundant	Surber	natural	no
overall abundance	Surber	natural	yes
hydropsychid caddisflies	Surber	natural	no
common taxa	core	natural	no
together >90%	Surber	natural	no
overall abundance	metal frame	natural	yes
abundance overall	Hess	natural	no
main groups	Hess	natural	yes
Deleatidium and *Cricotopus*	Surber	managed	yes
five most common	tile	natural	no
most common	Surber	natural	no
>1 mm total body length	stovepipe	natural	no
dominant taxa	D-net	managed	yes
tested taxa	visual	managed	no
10 predominant	multiple	natural	no
two numerically dominant caddisflies	Surber	natural	yes
Baetis	Surber	managed	no
all	box	natural	no
five dominant insects	Surber	natural	no
common taxa	stones	natural	no
common	Surber	natural	no
common	Stones	natural	no
common	Hess	natural	no/yes
overall abundance	Surber	natural	yes
numerically dominant	cages	natural	no
select taxa	multiple	natural	no
major groups and trichopterans	Hess	managed (dam removal)	no
overall abundance	Surber	natural	no
copepods and chironomids	core	natural	no
meiofauna	core	natural	no
overall abundance	Surber	natural	no
common	Hess	managed	yes
common	Hess	managed	no
all	quadrat	natural	yes
most common	Surber	natural	no
three representative groups	D-net	managed	yes
chironomids	leafpacks	natural	yes
insects overall	Surber	natural (beaver dam)	yes
common taxa	rocks	natural	no
common predators	electric pump	natural	no
common	artificial substrate	natural	yes

Using both the general data set and the highest-aggregated level of the taxon-specific data set, we examined resistance of overall invertebrate density to flood events, and also explored potential effects of natural vs. managed floods, habitat type, substrate type, collection method, and whether the flood happened in a month with higher or lower average rainfall with categorical analyses. We also performed an analysis of resistance of invertebrates as a function of the number of days since the flood event, and as a function of the relative flood magnitude (peak discharge/mean discharge or mean baseflow). Continuous analyses were performed as unweighted linear regressions.

We reported all statistics at the $\alpha = 0.05$ significance level. We performed the majority of analyses using MetaWin (Rosenberg et al. 2000), and we also used

TABLE 2. Characteristics of the two separate primary data sets used in meta-analyses.

Parameter	General data set	Taxon-specific data set
Sample unit	before/after flood abundance of total invertebrate count	before/after flood abundance of specific taxonomic units
Benefit	minimize pseudoreplication within each study	all taxonomic groups from each study contribute equally to results
Bias to results	taxa of highest abundance in each study have more influence	higher in-study replication
Study inclusion criteria	either: 1) report total invertebrate abundance before/after flood; or 2) report abundance before/ after flood for at least three orders of invertebrates (data will be aggregated)	report abundance before/after flood for at least one specific taxonomic group at any taxonomic level

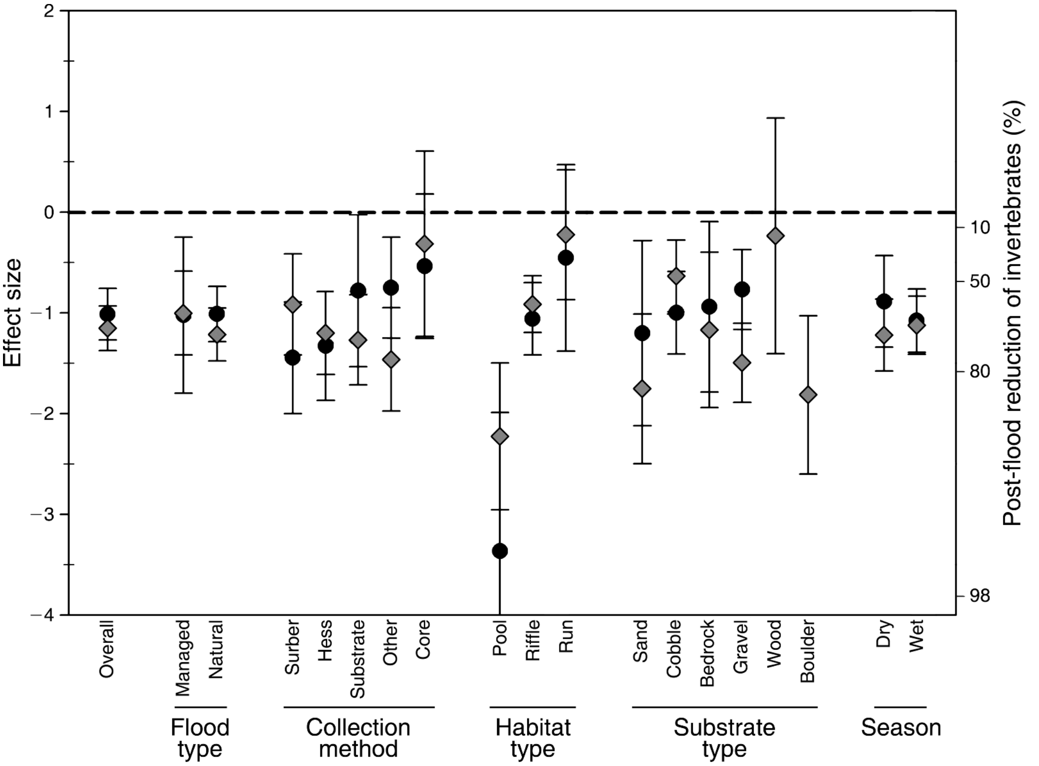

FIG. 1. Effect size (ln[invertebrate density post-floods/invertebrate density pre-floods]) of floods on aquatic invertebrate density and 95% confidence intervals. A scale for effect sizes as converted to percent reduction of invertebrates is on the right side of the figure. The black circles are effect sizes for sample units derived from the general data set, and the gray diamonds are effect sizes for sample units derived from the taxon-specific data set. The dashed line at 0 indicates which effect size results are significant ($P \leq 0.05$); those with confidence intervals overlapping the dotted line are not significant. The overall (cumulative) effect size is shown, as well as effect sizes estimated from categorical analyses of flood type, collection method, habitat type, substrate type, and whether the flood happened in a "wet" or "dry" month.

SigmaPlot (SigmaPlot 2004) for data visualization and some analyses. For categorical analyses, we included categories only if the number of sample units in a given category ≥5, and if the sample units were derived from at least three separate studies. When we detected a significant difference between categories, unplanned comparisons of means were conducted using the Tukey-Kramer method (Sokal and Rohlf 2000).

We examined a funnel plot of effect size vs. sample size to detect publication bias, such as underreporting of nonsignificant studies. Assuming no publication bias, smaller sample sizes are expected to have greater error spread, the cumulative effect size is expected to be independent of sample size, and normal distribution of individual studies is expected at all sample sizes (Palmer 1999).

RESULTS

The 41 studies included in the analyses spanned 13 countries and 37 rivers, streams, or stream systems (Table 1). There appeared to be slight asymmetry in the funnel plots of both the general and taxon-specific data sets, indicating that there could be a relationship between treatment effect and sample size, but there is not enough evidence to indicate strong publication bias. Smaller samples sizes had greater error spread as expected. Especially for the taxon-specific data set, distribution of effect sizes seemed to have a longer left (negative) than right tail. This could be because floods generally have a negative effect on invertebrate abundance, and thus the left tail of the distribution was more prominent. However, it could be due to some underreporting of studies where floods had positive effects on invertebrate abundance, and these different potential underlying reasons cannot be teased apart.

Overall effect

Using the general data set, there was a significant, negative effect of floods on the overall density of invertebrates within 10 days of a flood event (cumulative effect size −1.01, 95% CI −1.27 to −0.76, $n = 90$; Fig. 1). This is equivalent to a reduction of 53–72% of overall density of invertebrates within 10 days of a flood event. To check for independence, we ran the same analysis on a data set with one sample unit randomly selected from each study and found a significant, negative effect that is not significantly different from the effect calculated from the full data set (cumulative effect size −0.8506, 95% CI −1.1074 to −0.5938, $n = 34$).

For the taxon specific data set, there was also a significant, negative effect of floods on the overall density of invertebrates within 10 days of a flood event (cumulative effect size −1.15, 95% CI −1.37 to −0.93, $n = 340$). This is equivalent to a reduction of 61 to 75% of individuals in all groups of invertebrates within 10 days of a flood event.

Categorical analyses

Using the general data set, effect size of floods on invertebrate density did significantly differ between habitat types ($P < 0.01$, groups = 3, Fig. 1, Table 3). Invertebrates were most severely reduced by floods in pool habitats, which differed significantly in effect size from run or riffle habitats (Table 3). Using the taxon specific data set, invertebrates were again most severely reduced by floods in pool habitats, while they were least reduced in run habitats ($P = 0.003$, groups = 3, Fig. 1, Table 3), and in this case all three habitats had significantly different effect sizes from each other (Table 3).

There was no significant difference found between effect size of natural vs. managed floods on invertebrate density using the general data set ($P = 0.98$, groups = 2) or the taxon specific data set ($P = 0.4$, groups = 2; Fig. 1, Table 3). There also was no significant difference in effect size between collection methods using the general data set ($P = 0.12$, groups = 5; Table 3) or the taxon specific data set ($P = 0.17$, groups = 5; Fig. 1, Table 3).

Using the general data set no significant difference in effect size between invertebrate densities collected from different substrate types was detected ($P = 0.63$, groups = 6; Fig. 1, Table 3). However, using the taxon specific data set, complex differences in effect size among substrate types were found ($P = 0.003$, groups = 6; Fig. 1, Table 3), with invertebrate density being most reduced in sandy substrates and least reduced on wood. There was also no significant difference in effect size between floods that happened in a typical "wet" month (higher than mean annual rainfall) or "dry" month (lower than mean annual rainfall) using the general data set ($P = 0.51$, groups = 2; Table 3) or the taxon specific data set ($P = 0.68$, groups = 2; Fig. 1, Table 3).

Continuous analyses

A continuous model analysis showed that effect size became smaller in magnitude (closer to zero) with days since flood event (slope $P = 0.02$, $n = 89$; Fig. 2). However, with removal of the outlier with the largest effect size at 10 days post-flood, the relationship was no longer significant (slope $P = 0.11$, $n = 88$). A continuous model analysis using the taxon-specific data set showed no significant effect of days since flood on effect size within 10 days of a flood event (slope $P = 0.9$, $n = 339$).

When including all data from all river and habitat types in a continuous model analysis of effect size vs. relative flood magnitude, there was no significant trend detected. However, when a continuous model analysis was performed using only samples from riffle or run habitats composed of primarily cobble or gravel substrate (generalized habitat types that were most commonly reported on in primary studies), effect size became greater with increasing relative flood magnitude (slope $P < 0.01$, $n = 49$; Fig. 3). As with the general data set, when including all data there was no significant effect of relative flood magnitude on effect size. There was a significant increase in effect size with relative flood magnitude when examining only riffle or run habitats dominated by cobble or gravel substrate (slope $P < 0.0001$, $n = 202$). It is possible that there is a threshold at a relative flood magnitude of approximately 40–50, where the response to flooding is suddenly much stronger.

Taxon-specific analyses of resistance

Floods had a significant, negative effect on densities of Coleoptera, Eumalacostraca, Annelida, Ephemeroptera, Diptera, Plecoptera, and Trichoptera (95% confidence intervals did not overlap zero; Fig. 4). Floods did not have a significant effect on densities of Acari, Mollusca, or Platyhelminthes (95% confidence intervals did overlap zero; Fig. 4). However, there were no significant categorical differences between groups, since all of their confidence intervals overlapped ($P = 0.26$; Table 3).

Application of selection criteria for categorical analyses at finer taxonomic levels narrowed the groups for further analysis to Diptera, Ephemeroptera, Plecoptera, and Trichoptera. Of these groups, categorical analyses only found significant differences among families within each order for the Diptera, with Chironomidae experiencing significantly greater post-flood reduction than Tipulidae or Simuliidae ($P = 0.049$, $n = 4$; Fig. 4, Table 3). All mayfly families experienced significant reduction following flood events.

DISCUSSION

This meta-analysis found a significant reduction in overall invertebrate abundance and a reduction in abundance of major groups of invertebrates immediately after flood events in rivers. This relationship was apparent despite large differences in river type (parent geology, gradient, catchment size), regional climate, and continental setting. While a number of case studies exist concerning prescribed high-flow releases and ecosystem effects, and other papers have published information on natural floods and effects on invertebrates, there is a paucity of among-stream studies of flood effects on aquatic invertebrates (Death 2007). This is the first calculation of values for immediate invertebrate reduction after floods across studies at a global scale.

There is a need for increased ability to predict outcomes of river flow management on aquatic biota (Death 2007, Souchon et al. 2008, Poff 2009). While

TABLE 3. *P* values for categorical comparisons, sample sizes for all groups used in categorical comparisons, and results of Tukey-Kramer test (T-K) for unplanned comparisons of group mean effect sizes for all categorical comparisons that exhibited significant differences among groups.

	General data set			Taxon-specific data set		
Group	*P*	*n*	T-K	*P*	*n*	T-K
Flood type	0.98			0.40		
Natural		78			242	
Managed		12			98	
Collection method	0.12			0.17		
Surber		20			68	
Hess		21			85	
Substrate		12			65	
Other		24			100	
Core		13			22	
Habitat	<0.01			0.003		
Pool		5	a		24	c
Riffle		39	b		146	d
Run		8	b		30	e
Substrate	0.63			0.003		
Gravel		32			105	f
Cobble		30			127	g
Boulder		na			28	f
Sand		8			31	f
Wood		na			14	g
Bedrock		9			29	f,g
Dry vs. wet	0.512			0.675		
Dry		30			134	
Wet		60			203	
Invertebrates, ordinal or higher	na			0.26		
Coleoptera					20	
Eumalacostraca					15	
Annelida					22	
Ephemeroptera					70	
Diptera					76	
Trichoptera					49	
Plecoptera					46	
Acari					7	
Mollusca					8	
Platyhelminthes					9	
Ephemeroptera	na			0.72		
Baetidae					34	
Heptageniidae					21	
Leptophlebiidae					32	
Diptera	na			0.049		
Ceratopogonidae					20	j,k
Chironomidae					83	k
Tipulidae					12	j
Simuliidae					24	j
Trichoptera	na			0.705		
Hydropsychidae					11	
Lepidostomatidae					5	
Limnephilidae					10	
Plecoptera				0.324		
Nemouridae					20	
Leuctridae					18	

Notes: Sample size is *n*, T-K stands for Tukey-Kramer, and na stands for not applicable (i.e., sample size was below the cutoff for inclusion in the analysis). For the T-K results, groups with the same letter are not significantly different from each other ($P > 0.05$).

some studies have considered quantitative, cross-system effects of river flow management on aquatic organisms and communities (Bickford and Skalski 2000, Monk et al. 2006, Haxton and Findlay 2008, Stewart et al. 2009), this study contributes new information to our growing synthetic knowledge.

One purpose of meta-analyses is to generate predictive hypotheses for further experimentation and evaluation

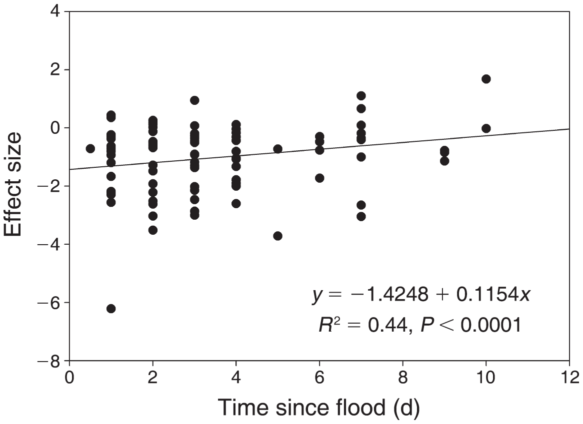

FIG. 2. Effect size of floods on overall aquatic invertebrate density vs. time since the flood event, within the first 10 days of a flood event.

(Osenberg et al. 1999, Lajeunesse 2010). Because log response-ratios may be easily translated into percent reductions, the overall effect size of density change of invertebrates due to floods, and other quantitative data regarding effect sizes in this study, may be used directly for modeling or quantitative prediction of management outcomes. The results of this meta-analysis can therefore be used to predict responses of biota to flood events and to parameterize general models of flood effects on aquatic organism abundance.

What is the overall estimate of reduction of invertebrates post-floods, and does this differ among natural vs. managed floods?

The overall values of resistance from both data sets are in concordance and show that invertebrates are generally reduced in numbers by at least half immediately after flood events, and we found no evidence for differing effects of natural vs. managed floods on invertebrate resistance. While lack of evidence for a statistical relationship does not necessarily mean that a relationship does not exist, our results indicate that as far as we know, general inferences drawn from mensurative (natural) flood experiments may be applied to development of manipulative flood experiments (Konrad et al. 2012). While mensurative flow experiments do not have true replication, pre-condition standardization, or control of treatment size (Konrad et al. 2012), they are useful in the context of synthesis of data from multiple, observable, quantified studies. However, managed floods can sometimes differ from natural floods in ways that can affect the response of organisms. For example, some aquatic invertebrates use proximate cues such as rainfall or flow to escape from floods or return to the stream post-flood (Lytle and White 2007, Lytle et al. 2008). If a managed flood lacks these proximate cues, or follows a hydrograph pattern that is not typical of natural floods (e.g., abrupt increases or decreases in flow), the organisms could be negatively affected.

How do environmental variables influence heterogeneity in effect of floods on invertebrate resistance?

Categorical analysis of both data sets demonstrated significant differences in effect of floods on invertebrate resistance among different general habitat types. While one data set showed differences among all three habitat types—riffle, run, and pool—the other showed that only pool habitats differed from riffle and run habitats. In general, pool invertebrates were reduced in density to a greater degree than invertebrates in riffles or runs. There is evidence that substrates in pools are more easily scoured by spates than substrates in riffles or runs (Scarsbrook and Townsend 1993, Lapointe et al. 2000, Harrison and Keller 2007). This could also affect the egg or larval stages of other aquatic organisms, such as salmon redds. Eggs in riffles or run likely have a higher chance of withstanding high flow events than those in pool habitats. Aquatic macrophytes in riffle or run habitats may also be less susceptible to flow events. These are hypotheses worth testing further.

Substrate type was a significant factor when categorically examining differences in effect sizes from the taxon-specific data set, but not when using the general data set. Differences among groups demonstrated by the taxon-specific data set were complex, with invertebrates reduced to the greatest degree on boulder and sand substrates, and least reduced on wood substrates. Wood and cobble can act as a refuge for invertebrates during flood events by providing greater structural complexity (Palmer et al. 1996, Hax and Golladay 1998). Sand, the smallest-diameter substrate evaluated here, would be moved by the least force and thus be the most easily disturbed of these substrates. Boulders, one of the larger substrates analyzed, also showed very low resistance of invertebrates. This may be due to the lack of interstitial spaces on boulders to act as refuges (Lancaster 1992), or

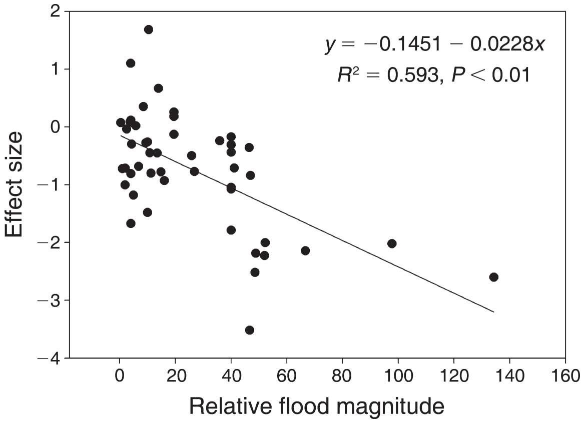

FIG. 3. Effect size of floods on overall aquatic invertebrate density vs. relative flood magnitude for riffle or run habitats composed of primarily cobble or gravel substrate.

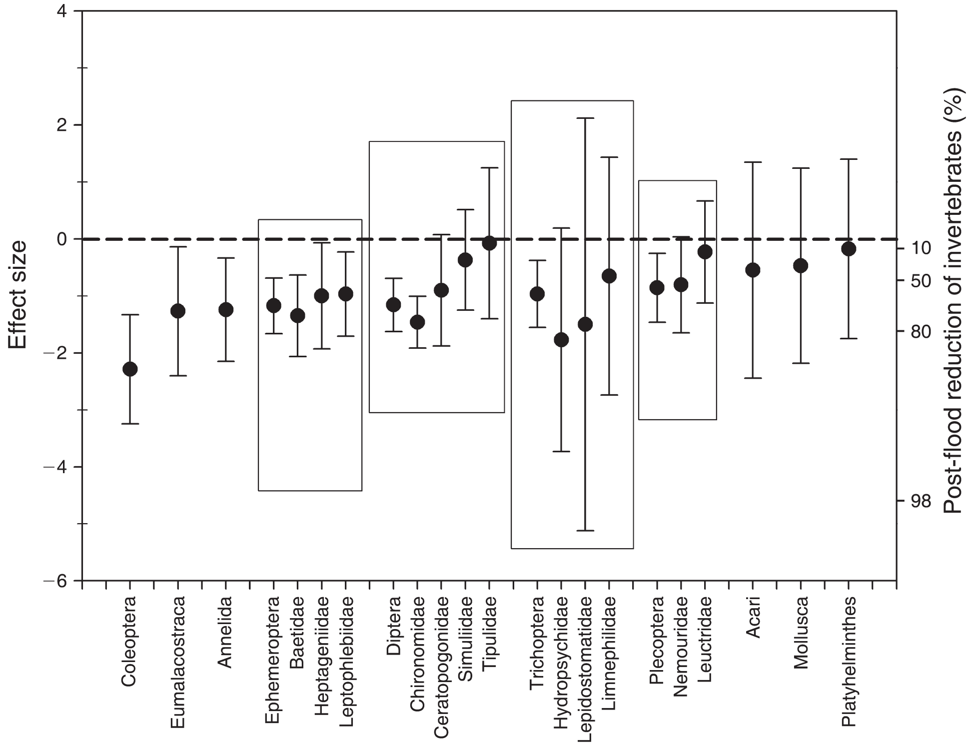

FIG. 4. Effect size of floods on aquatic invertebrate density of different taxonomic groups and 95% confidence intervals. A scale for effect sizes as converted to percentage reduction of invertebrates is on the right side of the figure. The dashed line at 0 indicates which effect size results are significant (the effect of floods on density of these groups was significant [$P \leq 0.05$]); those that have confidence intervals overlapping the dotted line were not significant. Results from categorical analyses that were conducted at lower taxonomic levels are boxed along with the effect size estimated for their parent group.

the frequent covering of boulders with silt and associated algae or macrophytes that may be easily disturbed by floods. Intermediate-sized substrates may provide the most protection for invertebrates from flood events. These results are also important for egg and larval stages of other aquatic organisms (fish, amphibians) and small adult fish or amphibians, which may also withstand flood events best on intermediate substrate. The specific habitat sampled, its constituent substrate, and how it was sampled must be taken into account when predicting flood effects on organisms, due to the great differences in resistance these variables confer on the organisms.

Is there evidence for "hidden resistance," or a short-term increase in invertebrate abundance post-flood?

Analysis of the general data set showed that invertebrates significantly increased in numbers within 10 days after a flood event, although with removal of an extreme data point this relationship was no longer significant. Although succession via recolonization and recruitment may begin immediately after flooding, the evident increase in resistance of invertebrates within 10 days of a flood event may encompass "hidden survival" since the majority of stream-dwelling organisms have life-cycles greater than 10 days. Organisms may be displaced by the flood into marginal habitats (side channels, deep pools) or buried by substrates. Indeed, invertebrates in several groups have the ability to return to the active stream channel if displaced by a flood (Lytle et al. 2008), and still other taxa are known to abandon streams prior to flooding and eventually return (Lytle 2000, Lytle and White 2007). Thus, we cannot assume that low incidence of organisms directly after flood events is always indicative of mortality. Examining short-term recovery of longer-lived aquatic organisms, including fish and amphibians, directly after flood events might provide more evidence for hidden survival. This has important implications for monitoring events after floods, as monitoring too quickly after a flood event could over-estimate mortality.

Analysis of the taxon-specific data set showed no relationship between effect size and days since event in a continuous model analysis. With such varied life-history patterns and overall lifespans in aquatic invertebrates, what is defined as "resistance" vs. "resilience" may vary between groups. For example, fast life-cycled mayflies such as *Fallceon quilleri* (Ephemeroptera: Baetidae) may transform from egg to reproductive aerial adult in as fast as 7 days (Gray 1981), and their aerial stage can escape river-bed flood events. Measuring resistance of this species to floods may need to happen within a day or two of a flood event, as their populations may immediately rebound immediately after flood events. For longer-lived organisms, and those without aerial stages, the effects of flood disturbance may be evident for a much longer time period.

How does flood magnitude influence invertebrate resistance?

When including all data, both for the general data set and the taxon-specific data set, there were no significant changes in effect sizes with relative flood magnitude. However, for some specific habitats (riffles, runs, cobble or gravel substrates) we did find an effect. We believe that flood magnitude does play an important role in shaping the effect of floods on invertebrates and other aquatic organisms, and that the effect of flood magnitude on invertebrates was masked in our full data set because it spanned such a wide array of habitats that differed in response to flooding. Thus, any broad generalizations about the effect of floods on invertebrates must still account for differences in response due to habitat and substrate type.

Does resistance to floods differ among taxonomic groups?

While there was no significant categorical difference between groups at the level of Order (insects) and higher (non-insects), some groups were significantly affected by flood events (95% confidence intervals not overlapping zero), while others were not (95% confidence intervals overlapping zero). All insect groups were significantly affected by flood events. The only groups not shown to be significantly affected were water mites (Acari), molluscs (Mollusca), and flatworms (Platyhelminthes). However, variance in effect size within these groups was also very large, and sample sizes were low, so this may be an issue of statistical power rather than biological response. Similar analyses could potentially be performed by trait group instead of by taxonomic categories, which could answer questions about which morphological, life-history, or behavioral traits are most successful at providing organisms defense against flood disturbance events. However, information on lower levels of taxonomic organization for reported invertebrates would likely be needed since traits may vary widely at higher taxonomic levels.

There were not enough data reported on some aquatic insect taxa (and other aquatic invertebrates) to justify including them. These less-commonly reported insect groups included odonates (dragonflies and damselflies), hemipterans (true bugs), megalopterans (alderflies and dobsonflies), collembolans (springtails), and aquatic lepidopterans (moths). Many studies reported only a subset of taxa, generally those found to be most abundant in the system. Greater reporting of data regarding all taxa collected and identified instead of just the most abundant taxa collected would broaden our ability to discern the generalities critical to both basic biological understanding and effective management. Also, there were few available published studies from 1970–2010 quantifying immediate effects of floods on biota from Africa, Asia, and Central and South America. In fact, all together only 13% of rivers and streams reported on in this analysis are drawn from those continents, while 49% were in the United States and Canada. More studies concerning flows in these under-reported countries are needed.

This meta-analysis suggests further studies that would be useful to answer specific questions concerning disturbance effects on aquatic organisms. For example, organisms inhabiting pool vs. riffle or run habitats in rivers could be censused to determine if differences in community structure exist. If so, it could be examined whether these organisms inherently differed in ability to survive floods, regardless of initial habitat preference, or whether organisms in pools are simply more susceptible due to greater scouring. This could be useful in predicting outcomes of direct management of riverine morphology on aquatic populations, i.e., influences of artificial enhancement of pools via additions of boulders or wood. Streamside experiments could be undertaken to closely examine the influence of substrate type on flood effects. Populations of specific taxa could be closely tracked after flood events to elucidate whether resistance measurements may be influenced by short-term "hidden resistance." Also, comprehensive, quantitative evaluation of other aspects of the flow regime (drought, base flows, timing of flow events, etc.) and studies on other organisms would be useful to solidifying a scientific framework on which to base specific prescribed flow events and to predict ecological reactions to climate induced hydrologic changes.

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