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SPECIAL FEATURE Trends in isotope ecology

Gaku Takimoto · David M. Post

Environmental determinants of food-chain length: a meta-analysis

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Abstract Food-chain length is an important character of ecological communities that affects many of their functional aspects. Recently, an increasing number of studies have tested the effects of productivity, disturbance, or ecosystem size on food-chain length in a variety of natural systems. Here we conduct a formal meta-analysis to summarize findings from these empirical studies. We found significant positive mean effects of productivity and ecosystem size but no significant mean effect of disturbance on food-chain length. The strength of mean effect sizes was not significantly different between productivity and ecosystem size. These results lend general support to previous theories predicting the effect of productivity and ecosystem size, but fail to support the prediction that disturbance shortens food chains. In addition, our meta-analysis found that the effect sizes of primary studies were significantly heterogeneous for ecosystem size and disturbance, but not for productivity. This pattern might reflect that ecosystem size and disturbance can affect food-chain length through multiple different mechanisms, while productivity influences food-chain length in a simple manner through energy limitation.

Keywords Disturbance · Ecosystem size · Food-chain length · Random-effects meta-analysis · Productivity

G. Takimoto (✉)
Department of Biology, Faculty of Science, Toho University, Funabashi, Chiba 274-8510, Japan
E-mail: gaku@bio.sci.toho-u.ac.jp
Tel.: +81-47-4725228
Fax: +81-47-4725228

D. M. Post
Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA

Introduction

Food-chain length is an important property of ecological communities, affecting a variety of ecosystem functions, such as primary and secondary production, rates and stability of material cycling, and persistence of higher-order predators under human-exploitation (Post 2002). Ecologists have long asked which environmental factors, such as productivity and disturbance, determine food-chain length (Elton 1927; Hutchinson 1959; Slobodkin 1961; Pimm 1982; Lawton 1989; Schoener 1989). Productivity is thought to limit food-chain length because limited efficiency in trophic conversion necessarily diminishes energy available at higher trophic levels (Hutchinson 1959; Slobodkin 1961; Oksanen et al. 1981). Disturbance is predicted to shorten food-chain length because mathematical models predict that long chains are dynamically fragile in environments subjects to frequent and/or intense perturbations (Pimm and Lawton 1977).

Early approaches to test the effects of productivity and disturbance on food-chain length used microcosm experiments and compiled data sets of various kinds of food webs (Briand and Cohen 1987; Jenkins et al. 1992; Lawler and Morin 1993; Kaunzinger and Morin 1998). More recently, theory and evidence suggest ecosystem size (e.g., lake volume, island area, and watershed area) is an important determinant of food-chain length, because larger ecosystems may have larger total resources available at the base of food webs (Schoener 1989) and foster functional trophic diversity and spatial processes to maintain longer food chains (Cohen and Newman 1991; Holt 1993, 2002; Spencer and Warren 1996; Wilson et al. 1998; Post et al. 2000). Currently, a growing number of empirical works, often taking advantage of stable isotope analysis, compare a large number of natural food webs under standardized methods to evaluate the influences of productivity, disturbance, and ecosystem size on food-chain length.

There have been a few attempts to summarize recent findings from an increasing number of empirical tests (Post 2002; Vander Zanden and Fetzer 2007; Sabo et al. 2009). A review by Post (2002) suggested that productivity would ultimately limit food-chain length only in systems with low resource availability, and found little evidence that disturbance was an important determinant of food-chain length. Vander Zanden and Fetzer (2007) collected estimates of food-chain length in aquatic systems across the world, and found that stream food chains are significantly shorter than lake and marine food chains. They also found a weak positive relationship between ecosystem size and food-chain length of lakes at the global scale. Sabo et al. (2009) surveyed studies testing the effects of environmental determinants on freshwater food chains, and counted the number of tests that found significant effects. They found that most studies found significantly positive effects in the tests of productivity and ecosystem size, and many studies found significantly negative effects in the tests of disturbance. There are now a sufficient number of empirical studies to take the next step and quantify the effect sizes of productivity, disturbance and ecosystem size on food-chain length.

In this paper, we employ a formal meta-analysis to summarize the effects of productivity, disturbance, and ecosystem size on food-chain length from 13 empirical studies. We test the following three fundamental hypotheses: (1) productivity increases food-chain length, (2) disturbance decreases food-chain length, and (3) ecosystem size increases food-chain length. We view that potential environmental determinants act on the processes of food-web assembly from regional species pools (Kitching 2000; Post 2002), and variation in environmental determinants drives variation in food-chain length among food webs of the same ecosystem types within the same region. We thus collect primary studies, each of which tested one or more of the above hypotheses with food webs of the same ecosystem types in a single region. We extract information necessary to calculate effect sizes from each study. In addition to testing the above hypotheses, we examine how much variability exists among the effect sizes of primary studies, in order to understand the consistency of the effect of each potential environmental determinant across different systems.

Methods

Data sources

We gathered studies that explicitly tested the relationships between food-chain length and one or more potential environmental determinants (productivity, disturbance, and ecosystem size). To collect data sources, we started with the literature that we had already known, then examined the studies cited in this literature, and also searched those citing this literature using databases (the ISI Web of Knowledge and Google Scholar). We did not include studies that used experimental microcosms (e.g., Jenkins et al. 1992; Lawler and Morin 1993; Spencer and Warren 1996; Kaunzinger and Morin 1998) because we intended to evaluate the effect sizes of potential determinants in natural systems. We focused on studies that examined realized food-chain length (sensu Post 2002) or mean chain length estimated from connectance webs, and did not include those studying functional food-chain length (sensu Post 2002) or those evaluating food-chain length only by the presence or absence of top or intermediate predators. We found 13 studies in total, many of which tested more than one potential determinant (Table 1). Among these, eight studies tested the effect of productivity, six studies tested the effect of disturbance, and nine studies tested the effect of ecosystem size. All but one study was from freshwater systems, but of a variety of ecosystems, such as streams, lakes, ponds, wetlands, and pitcher plants. The non-freshwater study is from a terrestrial insular ecosystem. There were no studies from marine ecosystems.

Effect sizes

We used the simple correlation coefficient, r, as the effect size index (Borenstein et al. 2009). From each primary study, we obtained correlation coefficient and sample size. Correlation coefficients were obtained using the following methods (in order of preference): (1) direct reporting of r or R^2, (2) test statistics (F or t values) converted to r using methods in Rosenthal and Dimatteo (2001), (3) simple correlation using original data when available, (4) simple correlation using data obtained from image analysis of published figures, and (5) assigning r of zero when a study reported only that there was no significant effect (Rosenthal and Dimatteo 2001). When primary studies used univariate mixed-effects models and report F values of potential determinants as fixed-effects, we converted the F values into r and used residual degree of freedom as sample size. All analyses were performed after converting r onto the Fisher's z scale.

Our meta-analysis tests for the raw effect of each potential determinant, rather than the effect of one determinant after the effects of others are controlled. Throughout the analysis, we thus use effect sizes calculated from simple correlations between one determinant and food-chain length, rather than from partial correlations gained from multiple regressions. This means that the effect of one determinant in a single primary study is not necessarily the independent effect of this determinant if it correlates with other determinants in this study. We took this approach because we were not able to obtain correlation relationships among multiple potential determinants from all primary studies.

Table 1 Primary studies used in meta-analysis

Study	Ecosystem	Potential determinant[a]	Sample size	Effect size
Townsend et al. (1998)[b]	Streams	D	10	−0.33
Vander Zanden et al. (1999)[c]	Lakes	P, E	16 (P), 20 (E)	0.60 (P), 0.45 (E)
Post et al. (2000)	Lakes	P, E	25	0.12 (P), 0.88 (E)
Thompson and Townsend (2005)	Streams	P, E	18	0.73 (P), 0.51 (E)
Williams and Trexler (2006)	Wetlands	P, D	18	0.62 (P), 0.00 (D)
Hoeinghaus et al. (2008)	Rivers	P	10	0.73
Takimoto et al. (2008)	Islands	D, E	33 (D), 36 (E)	−0.051 (D), 0.72 (E)
Walters and Post (2008)[d]	Streams	D	6	0.47
Doi et al. (2009)	Ponds	P, E	15	0.58 (P), 0.57 (E)
McHugh et al. (2010)	Streams	P, D, E	16	0.39 (P), −0.6 (D), 0.62 (E)
Sabo et al. (2010)[e]	Streams	P, D, E	20 (P), 29 (D), 30 (E)	0.25 (P), −0.61 (D), 0.52 (E)
Baiser et al. (2011)[d]	Picher plants	E	740	0.21
Reid et al. (2011)	Lakes	E	10	0.67

[a] Potential environmental determinants examined in each study are denoted by P (productivity), D (disturbance), and E (ecosystem size)

[b] Effect of productivity was studied, but the data was a subset from Thompson and Townsend (2005). Not included in meta-analysis

[c] Data retrieved from image analysis

[d] The effect size was calculated from the difference in lower reaches between with and without diversion. Data retrieved from image analysis

[e] Residual degree of freedom from a mixed-effects model was used as sample size

We assumed that each primary test in a specific study system evaluated a true effect of a focal potential determinant in this system. Thus we chose to use a random-effects meta-analysis (Borenstein et al. 2009), because a random-effects meta-analysis assumes that each primary study has its true effect, which is distributed randomly around the population mean value of effect sizes of primary studies. To test the hypotheses regarding productivity, disturbance, and ecosystem size, we examined the mean effect size of each potential determinant. For each potential determinant, we evaluated the mean effect size as the weighted mean of effect sizes of primary studies, calculated its 95 % confidence interval, and performed a two-tailed test of the null hypothesis that the mean effect is zero. In order to evaluate how variable the effects of each potential determinant among primary studies, we calculated several measures of heterogeneity, including the Q statistics to test the heterogeneity, the estimated variance T^2 and the estimated standard deviation T of true effects, and the I^2 statistics. These statistics express different aspects of heterogeneity in the effect sizes of primary studies. The Q statistic measures the total variation among primary studies, and is used to test the null hypothesis that all primary studies share a common effect size. The variance T^2 and the standard deviation T describe the distribution of true effects of primary studies. The I^2 statistics measures in percentage what proportion of the observed variation in effect sizes among primary studies represents the dispersion of their true effects. We also obtained a prediction interval of the mean effect of each potential determinant, in order to know how the effect sizes of primary tests would be distributed around the mean effect. To test whether the mean effect sizes differ among productivity, disturbance, and ecosystem size, we performed a Q test followed by multiple comparison with Holm's correction of P values. The Q test is based on the analysis of variance, and computes the weighted sum of squares of the subgroup means (i.e., the mean effect sizes of productivity, disturbance, and ecosystem size) about the grand mean, which would be distributed as Chi-squared with degree of freedom equal to [number of subgroups] − 1. The post hoc multiple comparison used Z tests. We presented the results with forest plots and tables of the above statistics. In a Forest plot, we showed the effect sizes and confidence intervals of primary studies in the order of relative weights, and the size of the mean effect with its confidence and prediction intervals. We did not see any indication of publication bias in the forest plots, which showed even distributions of the effect sizes of primary studies around the mean effects (Fig. 1). Detailed explanations about measures of heterogeneity and statistical tests are found in Borenstein et al. (2009, Chaps. 16, 17, 19).

Results

The direction (sign) of the mean effects of productivity, disturbance, and ecosystem size were all in accord with general predictions from theories (positive for productivity and ecosystem size, and negative for disturbance; Fig. 1; Table 2). However, only the mean effects of productivity and ecosystem size were significantly different from zero, and the mean effect of disturbance was not significantly deviated from zero (Table 2). Mean effect sizes of productivity, disturbance, and ecosystem size were different ($\chi^2 = 41.38$, $P < 0.01$), with significant difference found between productivity and disturbance ($Z = 4.17$, $P < 0.01$) and between disturbance and ecosystem size ($Z = 4.27$, $P < 0.01$), while the mean effect sizes of productivity and ecosystem size were not significantly different ($Z = 0.72$, $P = 0.47$).

Fig. 1 Forest plots of meta-analyses. **a** Effects of productivity; **b** effects of disturbance; **c** effects of ecosystem size. The effect sizes of individual studies are shown by *vertical marks*, with *horizontal bars* representing their 95 % confidence intervals. The mean effect of each determinant is shown by the *lowest vertical mark* of each panel, with *thick horizontal bars* representing its 95 % confidence intervals and *longer horizontal bars* its prediction intervals. Relative weights of individual studies are shown on the *right of each panel*. Studies were named after the first author of primary studies, and the mean effects are labeled as summary effect, shown on the *left of the panels*

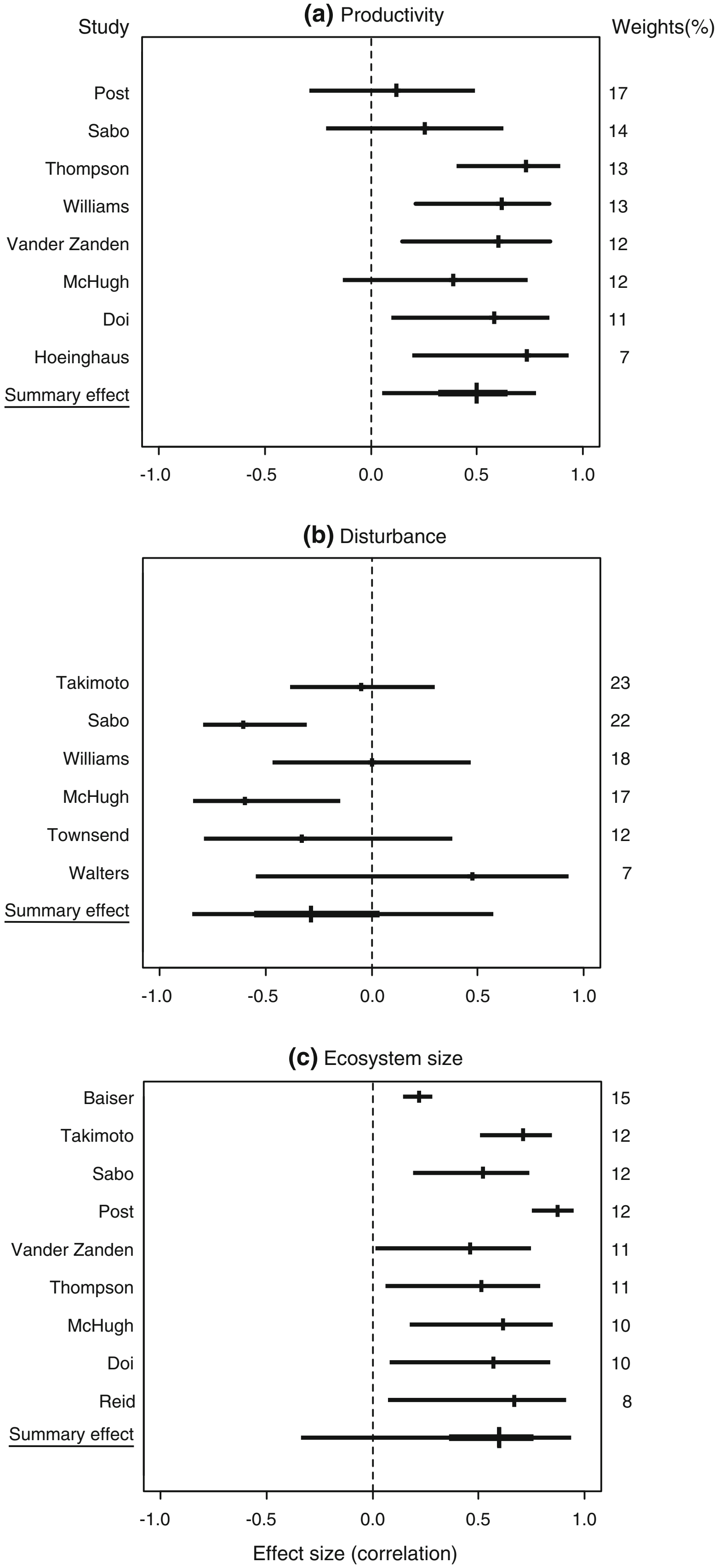

Table 2 Summary of random-effects meta-analyses

	df	Fisher's *z* (SE)[a]	*Z* (*p*)[b]	*Q* (*p*)[c]	T^2 [d]	*T*[d]	I^2 (%)[e]
Productivity	7	0.55 (0.11)	4.90 ($<10^{-6}$)	9.82 (0.20)	0.029	0.17	28.7
Disturbance	5	−0.29 (0.17)	−1.75 (0.080)	11.39 (0.044)	0.088	0.30	56.1
Ecosystem size	8	0.69 (0.16)	4.37 ($<10^{-4}$)	52.48 ($<10^{-7}$)	0.17	0.41	84.6

[a] Fisher's z is transformed back to correlation r by $r = (e^{2z} - 1)/(e^{2z} + 1)$

[b] The Z statistics to test whether Fisher's z is significantly different from zero

[c] The Q statistics for the tests of heterogeneity of effect sizes

[d] Estimated variance (T^2) and standard deviation (T) of true effects

[e] The I^2 statistics of the proportion of true-effect variance in total observed variance, a measure of heterogeneity

The amounts of heterogeneity in primary studies were different among productivity, disturbance, and ecosystem size (Table 2). For productivity, the estimated T value suggested that true-effect variation was small, and the Q statistics showed that true effects were not significantly different among primary studies. The I^2 value indicated that the true-effect variation comprised about one-fourth of total observed variation. This led to a relatively small prediction interval of the productivity effect (Fig. 1a), suggesting that 95 % of primary tests would likely observe positive effects (although it does not necessarily guarantee that the effects would be significant). For disturbance, the true-effect variation among primary studies was large, significantly heterogeneous, and comprised about a half of the total observed variance (Table 2). As a result, the prediction interval of the disturbance effect was large, spanning both positive and negative effects (Fig. 1b). For ecosystem size, the effect size of primary studies were highly and significantly heterogeneous, with the true-effect variance accounting for more than 80 % of total observed variance (Table 2). This broadened the prediction interval of the ecosystem size effect to include zero (Fig. 1c), suggesting that even a negative effect of ecosystem size could potentially be found in a primary test.

Discussion

A number of potential determinants of food-chain length have been proposed (Pimm 1982; Schoener 1989; Post 2002). In this meta-analysis, we summarized recent empirical tests of productivity, disturbance, and ecosystem size. We found that the mean effects of productivity and ecosystem size were significantly positive, matching their corresponding theoretical predictions. On the other hand, the mean effect of disturbance was negative but not significantly different from zero, failing to support the theoretical prediction. The mean effect sizes of productivity and ecosystem size were not significantly different. We also evaluated the degree of heterogeneity among the true effects of individual primary studies. While there was no evidence of heterogeneity in the productivity effect, heterogeneity of the disturbance effect was significant, and the ecosystem size effect showed high heterogeneity.

We did not find statistical support for (1) negative mean effect of disturbance, (2) different mean effect sizes of productivity and ecosystem size, or (3) heterogeneous true effects of productivity. Although these patterns might be true, we caution that these non-significant findings can result from the lack of statistical power and should not be regarded as broad conclusions. Rather, these results call for further tests on the effects of these environmental determinants on food-chain length. For example, all but one study in our meta-analysis are from freshwater systems. More empirical tests from diverse ecosystems would be highly valuable.

The results of our meta-analysis provide important insights about the mechanisms by which productivity, disturbance, and ecosystem size act to influence food-chain length. Productivity showed a positive mean effect size, and true-effect variance of productivity among primary studies was not strong. Low variability among individual effect sizes might reflect that productivity can act as a fundamental necessary condition to remove energetic constraints on lengthening food chains (Pimm and Lawton 1977; Post 2002). Because productivity is a necessary condition, the productivity effect might be expressed with relatively definite strength across different ecosystem types and regions.

The mean effect size of disturbance was not significantly deviated from zero, and individual true effects varied significantly from system to system. Previous studies pointed out that the disturbance effect could be reduced or even reversed because disturbance interacted with species interactions to modify food-web structure (Power et al. 1996; Takimoto et al. 2008; Walters and Post 2008). The heterogeneous effects of disturbance in our meta-analysis seem to agree with this argument.

Ecosystem size had a positive mean effect size, in consistent with existing theories (Schoener 1989; Holt 1996; Post et al. 2000; Takimoto et al. 2012). Interestingly, true effects of ecosystem size were highly variable among primary studies, despite the fact that all primary studies found significant positive effects. Two primary studies best represent this heterogeneity. Baiser et al. (2011) studied a large number of food webs in pitcher plants across North America, finding a weak but significant effect of ecosystem size ($r = 0.21$). On the other hand, Post et al. (2000) found a strong and significant effect of ecosystem size on food-chain length of North

American lakes ($r = 0.88$). High heterogeneity of these individual effect sizes led to a large prediction interval that included zero. This suggests that future field tests of the ecosystem size effect may well find non-positive effects, although all currently available evidence in our meta-analysis detected significant positive effects.

There are several theoretical mechanisms that can lead to the ecosystem size effect. The productive space hypothesis argues that ecosystem size increases food-chain length because greater basal resources are available in larger ecosystems (Schoener 1989). Functional trophic diversity may also be higher in larger ecosystems, contributing to longer food chains (Cohen and Newman 1991; Post et al. 2000). Spatial processes possible in large enough ecosystems may enhance the persistence of locally unstable predator–prey interactions, promoting long food chains (Wilson et al. 1998; Holt 2002; Takimoto et al. 2012). Stochastic extinction of local populations may be more likely to be recovered or rescued in larger ecosystems, because larger ecosystems are likely to contain more viable local populations from which colonization may save other local populations under crisis. A disturbance event and its impacts may be only partial if an ecosystem is large (cf. Sabo et al. 2010), and impacted populations can be re-established or rescued through colonization from intact populations. Such spatial effects may pile up at higher trophic levels, and lengthen food chains in larger ecosystems (Holt 1997).

That multiple theoretical mechanisms can cause the ecosystem size effects might explain the high heterogeneity of its effect sizes among primary studies. Among these multiple mechanisms, the productive space hypothesis seems to explain, at least partially, the positive mean effect of ecosystem size in our meta-analysis. Indeed, three primary studies finding positive ecosystem-size effects also detected positive productivity effects (Vander Zanden et al. 1999; Thompson and Townsend 2005; Doi et al. 2009), indicating that the increase of ecosystem size lengthened food chains in these systems via increasing total available resources. On the other hand, the productive space hypothesis may not be the unique mechanism of the positive mean ecosystem size effect in our meta-analysis. Three primary studies found the ecosystem size effect but not the productivity effect (Post et al. 2000; McHugh et al. 2010; Sabo et al. 2010). In particular, Post et al. (2000) scored the largest effect size of ecosystem size in our meta-analysis, but rejected the productive space hypothesis (Post 2007). Moreover, a microcosm experiment by Spencer and Warren (1996), not included in our meta-analysis, demonstrated that the increase of ecosystem size alone lengthened food chains. In addition, a mathematical model found that increasing ecosystem size, while unchanging total resource availability, can still increase food-chain length (Takimoto et al. 2012). These appear to support that multiple theoretical mechanisms, including the productive space hypothesis, drive the positive mean effect of ecosystem size found in our meta-analysis. Unfortunately, our meta-analysis cannot distinguish which mechanisms may contribute strongly or weakly to the positive mean effect of ecosystem size. However, conceivably, multiple mechanisms underlying the ecosystem size effect may act strongly in some study systems but weakly in others, causing highly heterogeneous effects among different systems.

The results of our meta-analysis are generally in accord with the patterns found in a previous verbal review (Post 2002) and in a vote-counting meta-analysis (Sabo et al. 2009) about environmental influences on food-chain length. On the other hand, our meta-analysis contrasts with an earlier analysis of 113 food webs that found no effect of productivity or disturbance on food-chain length (Briand and Cohen 1987). An important difference is that Briand and Cohen (1987) sought to find the effect of environmental determinants by combining estimates of food-chain length from many ecosystem types and many different regions, while our meta-analysis accumulated the evidence of effects on food chains of the same ecosystem types within the same regions. This reflects the idea that effects of potential environmental determinants, such as productivity, disturbance, and ecosystem size, should act on the processes of food-web assembly from regional species pools (Kitching 2000; Post 2002). Combining estimates of food-chain length from different ecosystem types or different geographic regions into a single analysis will weaken or obscure the importance of underlying mechanisms when the relationship between food-chain length and environmental determinants vary among different study systems, as we found for disturbance and ecosystem size. Without accounting for such regional variation, Vander Zanden and Fetzer (2007) compiled data across the globe, and found a weak effect of ecosystem size on food-chain length in lakes. Its effect size ($r = 0.28$) fell around the lower end of the effect size range of ecosystem size in our meta-analysis (Fig. 1). This result could be because estimates of food-chain length from many biogeographic regions were combined into a single analysis. Diverse relationships between environmental determinants and food-chain length seem to highlight the importance of the history of community organization and biogeographic backgrounds in driving natural variation of food-chain length.

To summarize, our results support predictions from previous theories that productivity and ecosystem size increase food-chain length, but fail to provide strong support to the prediction that disturbance decreasing food-chain length. Interestingly, our meta-analysis found that different environmental determinants have different degree of heterogeneity in effect strength. A recognition of effect strength variation among different environmental variables could be important for ecosystem conservation and management, for example, when one wishes to control these environmental variables to restore historic levels of food-chain length (Vander Zanden et al. 2003). Understanding why there are differences in effect size variation among productivity, disturbance, and ecosystem size, and how these factors may interact one another, will be important challenges for future empirical and theoretical research.

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