

Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic

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Abstract. Theory states that both the spatial complexity of landscapes and the strength of interactions between consumers and their resources are important for maintaining biodiversity and the balance of nature. Spatial complexity is hypothesized to promote biodiversity by reducing the potential for competitive exclusion; whereas, models show that weak trophic interactions can enhance stability and maintain biodiversity by dampening destabilizing oscillations associated with strong interactions. Here, we show that spatial complexity can reduce the strength of consumer–resource interactions in natural food webs. By sequentially aggregating food webs of individual aquatic habitat patches across a floodplain mosaic, we found that increasing spatial complexity resulted in decreases in the strength of interactions between predators and prey, owing to a greater proportion of weak interactions and a reduced proportion of strong interactions in the meta-food web. The main mechanism behind this pattern was that some patches provided predation refugia for species that were often strongly preyed upon in other patches. If weak trophic interactions do indeed promote stability, then our findings may signal an additional mechanism by which complexity and stability are linked in nature. In turn, this may have implications for how the values of landscape complexity, and the costs of biophysical homogenization, are assessed.

Key words: *aquatic habitat; food web; interaction strength; landscape complexity; meta-food web; predator–prey interactions; river floodplains.*

INTRODUCTION

The idea that spatial complexity in nature sets the stage for the maintenance of biodiversity is treated as axiomatic, yet the ecological mechanisms underlying this relationship are not fully understood. In essence, the paradigm holds that greater spatial complexity, including heterogeneity at multiple scales, translates into more ecological niche-space, less potential for competitive exclusion, and, thus, greater diversity (Gause 1934, Hutchinson 1953, Levin 2000). Along a related line, the hypothesis that more diverse ecological communities are more stable has been a focus of study and debate for decades (MacArthur 1955, McCann 2000), and, though an array of empirical (McNaughton 1985, Tilman et al. 2006) and theoretical (McCann et al. 1998, McCann 2000) evidence lends it support, the processes responsible are unresolved (Hooper et al. 2005). Food web modeling efforts suggest diversity enhances stability if it is accompanied by more weak consumer–resource interactions (McCann et al. 1998, Kokkoris et al. 2002) that dampen destabilizing oscillations associated with strong interactions. Indeed, a suite of empirical

studies point to the prevalence of such weak trophic interactions in natural food webs (de Ruiter et al. 1995, Hall et al. 2000, Sala and Graham 2002) and their potential to confer stability (Cross et al. 2013). At the intersection between these two lines of inquiry lies a largely unexplored possibility, that increasing spatial complexity contributes to maintenance of biodiversity by reducing interaction strengths in food webs.

Spatial heterogeneity has long been recognized as important in terms of its effects on populations (Hanski 1998), the coexistence of predators and prey (Huffaker 1958), and structuring of communities (Holyoak et al. 2005), yet most studies of interactions in food webs have been conducted at small spatial scales or have not made spatial heterogeneity an explicit focus. Therefore, food web studies may not have adequately characterized natural communities, which are typically embedded in complex, multi-scale, landscape mosaics (Levin 2000, Holyoak et al. 2005, Bellmore et al. 2013). Although models have been used to incorporate the effects of landscape heterogeneity and metacommunity dynamics into food webs (Guichard 2005, Gravel et al. 2011), empirical studies of food webs and interaction strengths have yet to catch up (but see Grabowski 2004, Vucic-Pestic et al. 2010). Though the importance of heterogeneity has been recognized across ecological disciplines, and homogenization of landscapes is acknowledged as a

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major agent of global environmental change (Steffen et al. 2011), we are aware of no investigation that has explicitly evaluated how the distribution of interaction strengths in food webs changes with spatial scale or habitat complexity.

River floodplains are among the most biophysically complex and diverse landscapes on earth (Bayley 1995). Floods create a dynamic mosaic of habitat features within these landscapes that support diverse communities and complex food webs (Winemiller 1990, Stanford et al. 2005, Bellmore et al. 2013). Here, we report the results of a study in which we utilized the natural complexity and diversity of a river-floodplain ecosystem to investigate aquatic food webs aggregated at multiple scales in a heterogeneous landscape mosaic. Based on the rationale described above, our goal was to test the overarching working hypothesis that spatial complexity reduces trophic interaction strengths. To test this hypothesis, our aims were to calculate strengths of trophic interactions between fish predators and their invertebrate prey for different patches of the floodplain mosaic; evaluate how biodiversity, food web complexity, and predator–prey interaction strengths vary among these patches; and investigate the influence of scaling and landscape heterogeneity (via the aggregation of patch-scale food webs into successively larger, floodplain meta-food webs) on biodiversity, the complexity of food webs, and the distribution of predator–prey interaction strengths.

METHODS

We investigated food webs in six individual aquatic habitats in a floodplain segment of the Methow River (Washington, USA). These six habitats were selected to encompass the different categories of habitat patches present across the floodplain landscape, from patches that are large and highly connected (e.g., the main channel) to those that are small and become relatively isolated at low flows (e.g., orthofluvial channels on the floodplain surface). In other words, we stratified the aquatic floodplain landscape into different general categories or patches, and then, within each of these patch types, we selected a representative habitat for food web sampling. The six habitats that we selected included the main channel (main ch) and five different side channels, which we identify according to their level of surface water connectivity with the main channel during low-flow conditions (July–March). The side channel “con updown” retained both up and downstream connection to the main channel; “con down” had a downstream connection only; “discon lrg” was disconnected from the main channel, but retained a relatively large isolated pool; “discon sml” was a disconnected channel that contained several relatively small, isolated pools; and “discon noscr” was disconnected, with large pools, but, in contrast to the other side channels, its bed was not scoured by high flows during the study period. Although these habitats vary in their level of connection

with the main channel, they are all part of the shifting habitat mosaic (*sensu* Stanford et al. 2005), which we conceptualize as an extension of the “riverscape” (Fausch et al. 2002). Habitats like these contain communities of fishes and their primarily invertebrate prey, and interactions among these organisms are linked across the mosaic at various scales in space and time via dynamics in the connectivity among habitats and movement patterns of organisms (e.g., Winemiller and Jepsen 1998). For example, during the high flow period (April–June), all of these habitats are typically connected to the main channel at both upstream and downstream ends. Moreover, during peak flows, side channels are frequently linked to one another via a network of overflow channels. It is during this high flow period that most inter-patch movement by fishes occurs (Martens and Connolly 2014), and when aquatic invertebrates are known to disperse among habitats via drift (Townsend 1989, Mackay 1992). Even during times of relative hydrologic isolation, however, aquatic insects disperse among patches via their adult life-stages, which are primarily terrestrial. For these reasons, we judged that the metacommunity/meta-food web framework (e.g., Wilson 1992, Leibold et al. 2004) was well suited to the case of the mosaic of food webs in this river floodplain.

To quantify the character of the food webs within each of these habitat patches, we conducted seasonal sampling over a year-long period (four sampling events between summer 2009 and spring 2010) of fishes and aquatic invertebrates. Here, we give a relatively brief account of the methods necessary to generate the metrics analyzed in this study; further methodological details can be found in Bellmore et al. (2013) and Martens and Connolly (2014). Within each habitat, a combination of backpack electro-fishing, and underwater visual surveys were conducted to estimate the abundance and biomass of all the dominant members of the fish assemblage, which included chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), rainbow trout (*O. mykiss*), westslope cutthroat trout (*O. clarkia lewisi*), bull trout (*Salvelinus confluentus*), mountain whitefish (*Prosopium williamsoni*), longnose dace (*Rhinichthys cataractae*), bridgelip sucker (*Catostomus columbianus*), and several species of sculpin (*Cottus* spp.; for a complete list of fish and invertebrate taxa see Bellmore et al. 2013). We estimated population size via electro-fishing surveys using both removal-depletion and mark-recapture approaches. For removal-depletion, subsections of each habitat were blocked off with nets and two or more removal passes (a maximum of six) were conducted until a desired level of precision (coefficient of variation <25%) was met (see Martens and Connolly 2014). In habitats that were too large or deep (e.g., large pools) to effectively sample with the removal method, we conducted mark-recapture surveys, whereby all fish captured (>65 mm) were marked with passive integrated transponder (PIT) tags to allow identification during subsequent recapture events. Underwater visual surveys

were reserved for situations where it was not possible to effectively electro-fish, due to water depth, fast current, or large wood jams. These were conducted by two to four divers, equipped with mask and snorkel, slowly working their way up through channel units, counting and estimating the size of all fish encountered. Variation in underwater estimates was evaluated by conducting repeat surveys in specific channel units. Seasonal fish biomass estimates, calculated using these approaches, were used to estimate annual fish production via the instantaneous growth or size-frequency method (Benke and Huryn 2006, Hayes et al. 2007). To determine the proportion of different prey items in fish diets, gut contents were collected seasonally from a representative sample of fishes in each habitat (approximately five per season–species–habitat combination, or 20 samples per species per habitat). Invertebrate prey items were identified to the family level, and fish found in gut contents were identified to species. Gut content proportions were combined with fish annual production estimates to calculate prey-specific annual consumption using the trophic basis of production approach (Benke and Wallace 1980, Bellmore et al. 2013, Cross et al. 2013).

The composition, abundance, and biomass of aquatic invertebrate prey were determined by seasonally sampling known areas (0.23 m²) of benthic substrate using a modified surber sampler (attached to a shovel handle) whose sample quadrat was three times larger than traditionally sized surber samplers. On each sampling date, we collected three to five replicate benthic samples from each habitat, where each replicate sample was composed of several subsamples ($n = 3\text{--}11$ subsamples) collected in proportion to the different channel unit types present (e.g., riffles, pools, etc.) within the habitat. When subsamples were combined, each replicate sample incorporated the perceived variation within each habitat, for each sampling date. Because surber nets are primarily designed to sample flowing habitats, in low velocity areas (disconnected side channels), we modified the approach by scooping the benthic substrate within the surber frame into the net, assisted by mask and snorkel in deeper water habitats. Following identification in the laboratory, all invertebrates were dried and weighed, and their annual production was estimated via the size-frequency an instantaneous growth methods (Benke and Huryn 2006).

Using these data, we calculated the total richness of invertebrate prey and fish predator taxa in each habitat patch, the total number of predator–prey food web links, and trophic interaction strengths for each predator–prey linkage. Trophic interaction strength (IS) was calculated as:

$$IS_{i(j)} = \frac{C_{i(j)}}{P_i}$$

where $C_{i(j)}$ = annual consumption of prey i (g dry mass·m⁻²·yr⁻¹) by predator j , and P is the annual

production of prey i (Wootton 1997, Woodward et al. 2005, Wootton and Emmerson 2005), such that a value of 1 would indicate that a predator consumed all of that prey's production over a year and, hence, a very strong interaction.

We compared trophic interaction strengths among habitat patches in terms of the means of all IS values within each patch and cumulative distribution plots of IS values for each patch. The latter allowed us to quantify the proportion of interactions in a given habitat that exceeded certain threshold values. Throughout the manuscript, we set the threshold for a weak interaction at 0.1 (i.e., predator consumes 10% of prey annual production), and the threshold for a strong interaction at 0.9. These values are, admittedly, somewhat arbitrary, however, identification of thresholds was necessary for quantifying differences in interaction strength distributions, and previous studies provided a basis for using the values we selected (see Cross et al. 2013). We also calculated total interaction strengths for each prey taxon in each habitat patch (total IS), which we defined as the total annual consumption of each prey type i by all members of the fish assemblage, values that we used to investigate how overall impacts of predators on prey varied among habitat patches. In particular, we used these values to calculate the proportion of instances in which strong total IS values ($IS > 0.9$, and $IS > 0.5$) for a given prey item in one habitat patch were balanced by much weaker total IS values ($IS < 0.1$) in another patch (or patches). The values from these simple analyses were compared to those that would be expected based on chance, assuming that total IS values among the habitat patches were randomly distributed between 0 and 1 (based on an average of 10 randomly drawn distributions).

The contribution of patch scale food webs to characteristics of the meta-food web was evaluated by adding food web elements of different patch types one by one to an aggregate, meta-food web for the floodplain mosaic. Starting with a single, randomly selected habitat patch, we added food web information from one patch type at a time, until all six habitat patches were included. Each time we added another patch to the meta-food web, we recalculated richness, number of links, and IS for each predator–prey combination. For this analysis, IS was weighted by the total area of each patch type, as follows:

$$\text{landscape } IS_{i,j} = \frac{(C_{i,j,1} \times A_1) + (C_{i,j,2} \times A_2) + \dots}{(P_{i,1} \times A_1) + (P_{i,2} \times A_2) + \dots}$$

where $C_{i,j,1}$ is the consumption of prey i by predator j in patch type 1 (e.g., the main channel), and A_1 is the area (m²) of patch type 1. We estimated the total area of each patch type (see Appendix for patch areas) by utilizing digitized maps and associated metadata provided by the U.S. Bureau of Reclamation (Bureau of Reclamation 2010). To eliminate potential bias associated with combining habitat patches in a particular order, we

used a randomization algorithm to produce a systematic set of all the different permutations, or orders, by which the habitat patches could be combined ($n = 720$). This full permutation procedure involved no assumptions regarding the primacy of any one habitat patch in the structure of the meta-food web, based on the fact that organism movement and hydrology connects these habitats in various ways and at different time scales. However, we wanted to evaluate how robust our findings were to assumptions regarding the size and arrangement of habitat patches. In particular, because there was a possibility for the main channel to play a unique role (e.g., due to its size or role in connecting patches), we wanted to investigate any disproportionate effect it might have on the observed pattern of average landscape IS. Therefore, we conducted a separate analysis in which the main channel was always the first patch included in the meta-food web, and then, using the same randomization algorithm, we sequentially added food web elements of side channel patches, one by one.

For both analyses, we summarized landscape IS values at different levels of landscape complexity (i.e., number of patches included) by calculating the mean of all the predator–prey interaction strengths for each level, and plotting cumulative interaction strength distributions for each level. For each level of landscape complexity, the mean values that we report represent the average of all the different unique values produced via the permutation procedure, and error bars represent 95% confidence intervals around this average value. For example, when three habitat patches were included in the landscape, the permutation procedure produced 120 possible combinations, only 20 of which are unique; the reported value is simply the average of those 20 unique values, and the error bars (95% confidence intervals) represent the variation among them. Similarly, for each level of landscape complexity, the cumulative distribution plot represents the average shape of all distributions generated via the permutation procedure; calculated by averaging specific values at several set points (i.e., exceedance probabilities) across the cumulative distributions. Finally, to gauge the contribution of meta-food web structure to the patterns we observed in landscape IS with increasing landscape complexity, we conducted an additional, null-model comparison. We compared the observed landscape IS values associated with each level of landscape (and meta-food web) complexity with those that would be expected if the meta-food web structure had no influence on patterns of IS at the landscape scale. These expected values were the product of another permutation procedure, but one in which we disregarded the identity of individual predator–prey interactions and simply calculated the weighted average of the mean interaction strengths for each patch type, as follows:

$$\text{expected landscape IS} = \frac{(\overline{\text{IS}}_1 \times A_1) + (\overline{\text{IS}}_2 \times A_2) + \dots}{A_1 + A_2 + \dots}$$

where $\overline{\text{IS}}$ represents the mean of all the predator–prey interactions within a given patch type.

RESULTS

At the patch-scale, taxa richness of fishes and invertebrates was generally consistent among habitat patches (range = 31–39; Fig. 1a). The number of food web links was highest in the main channel (140 different predator–prey links; Fig. 1b), and lower, but relatively similar, among side channels (range = 64–84 links). The latter was principally driven by the fact that side channel habitats typically contained fewer fish predators (three to six species) than found in the main channel (seven species). The mean trophic interaction strength (IS) was generally low, but variable; ranging between 0.07 and 0.14 in all habitats except for the disconnected channel that contained several relatively small isolated pools, where it was 0.25 (Fig. 1c).

As food webs associated with each patch were aggregated into successively larger meta-food webs, taxa richness and the number of food web links increased in a linear fashion. Richness increased from 35 when the landscape included only one patch, to 60 when all six patch types were included (Fig. 1d). The number of unique food web links (i.e., links found only in one patch in the landscape) increased from 83 to 238, and the number of repeated links (i.e., links found in two or more patches) increased to a maximum of 267 (Fig. 1e). The increase in richness and the addition of unique links was associated with variation in hydrologic connectivity among patches that encompassed a range of areas with fast current to those with minimal velocity that, in turn, were occupied by distinct suites of invertebrates. For example, the amphipod family, Gammaridae, was principally found in minimal velocity habitats, whereas the stonefly Perlidae was limited to faster water patches. Contrastingly, as richness and linkages increased, mean landscape IS sequentially decreased with the aggregation of food webs from each patch, falling from 0.13 to 0.08, approaching the lowest IS value found in any of the patch types (0.07) and representing a total reduction of 38% (Fig. 1f). The same analysis conducted using median IS values, instead of means, produced a similar, sequential decline in interaction strength. This observed pattern of declining values in mean IS contrasted to “expected” values at each level of landscape complexity (calculated as the weighted average of the mean IS’s from the different patch types), which did not decline with patch aggregation (Fig. 1f). The additional analysis we conducted, in which food web aggregation was started with the main channel, produced a similar pattern of sequential decrease in landscape IS (39% total reduction), indicating that the pattern of declining landscape IS was robust to assumptions regarding the size and arrangement of habitat patches in the meta-food web.

The stepwise reduction in mean landscape IS was a result of a shift in the distribution of interaction

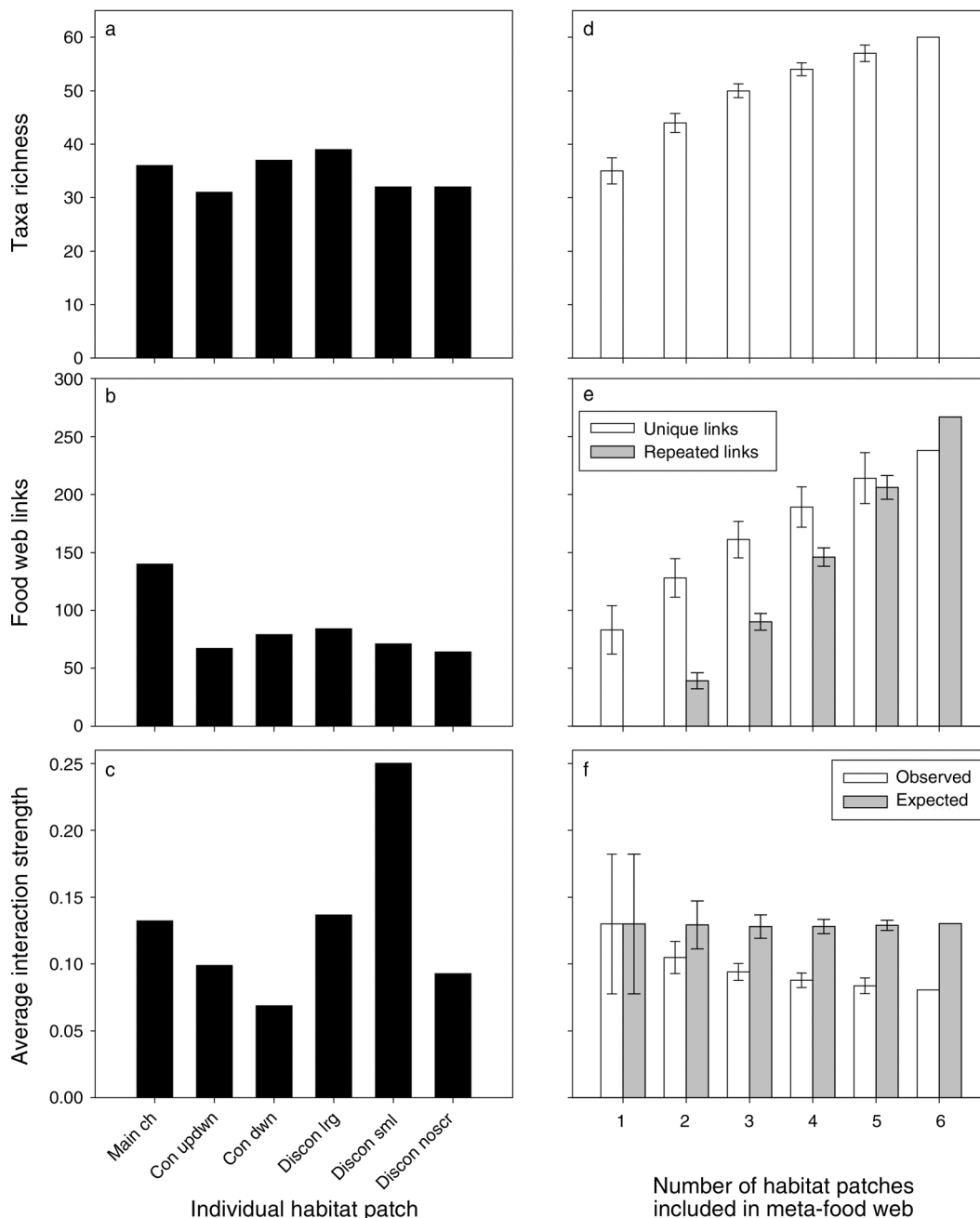


FIG. 1. Effects of increasing spatial complexity on taxa richness, number of food web linkages, and average interaction strengths (IS). Panels are (a) number of prey taxa, (b) number of food web links, and (c) average predator–prey IS, for individual habitat patches; and (d) cumulative number of taxa, (e) cumulative food web links, and (f) cumulative average landscape IS, for the meta-food web, as calculated by sequentially adding patches one by one to the landscape. Unique links are those predator–prey linkages only represented in a single patch type, whereas repeated links are those found in two or more patches. Expected IS values for the landscape were based on a null model (see *Methods* for equations and further description). Error bars are 95% confidence intervals around the mean, and represent variation in the results of the permutation procedure at each level of landscape complexity. There are no confidence intervals associated with the case of six habitats because the permutation procedure produced only one possibility.

strengths, moving toward weaker interactions throughout the distribution with the aggregation of food webs from each habitat patch (Fig. 2). Within individual patches, distributions of interaction strengths were

characterized by a large proportion (61–85%) of weak interactions ($IS \leq -0.1$; Fig. 2); only 15–39% of interaction strengths exceeded 0.1 (–1 on logarithmic scale). As these patches were aggregated, the cumulative

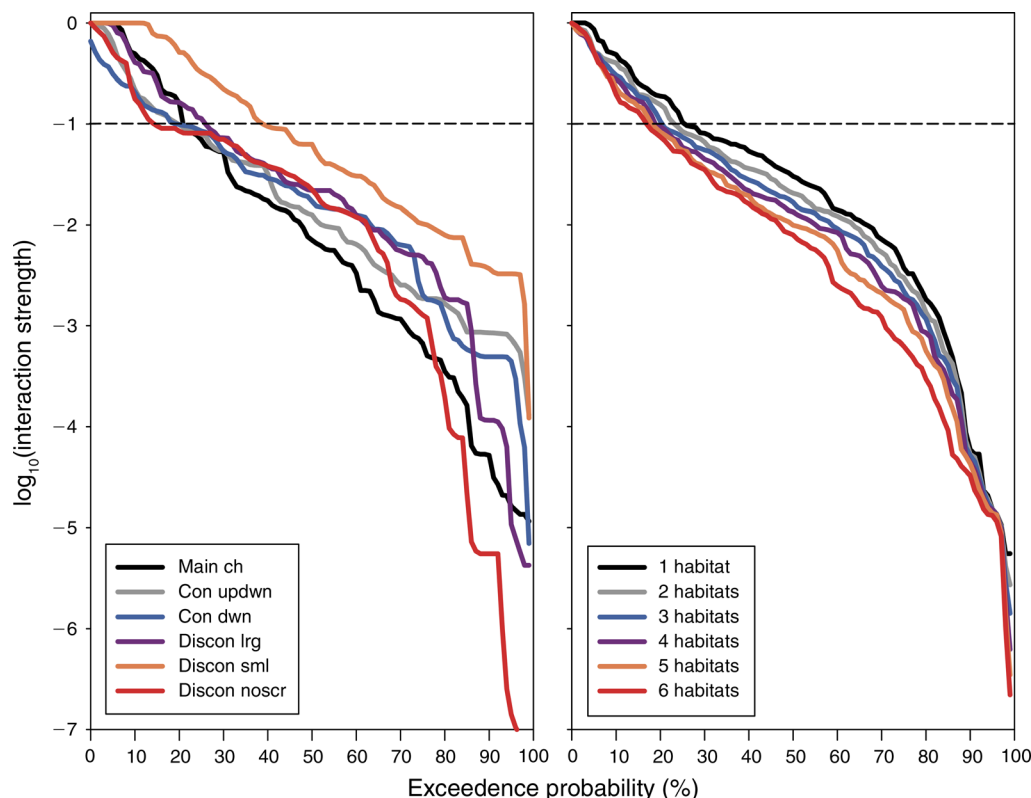


FIG. 2. Cumulative frequency distributions of predator-prey interaction strengths for each habitat patch type (left panel); and for the meta-food webs encompassing increasing levels of landscape complexity (right panel). The cumulative probability distribution of the meta-food web was calculated by sequentially adding habitat patch types one by one to the landscape (i.e., one to six habitats). The dashed line shows the threshold for weak interactions (i.e., interaction strengths of 0.1; -1 on a logarithmic scale).

distribution of interactions in the meta-food web shifted toward weaker interactions, and displayed an associated decrease in stronger interactions (Fig. 2). The occurrence of weak interactions ($IS \leq 0.1$) increased from 75% (average of single patches) to 83% (all patches). Moreover, this shift was observed across the distribution of interaction strengths (Fig. 2), and was even stronger for other domains of the distribution; for instance, the prevalence of interactions less than 0.01 (or -2 on a logarithmic scale) increased from 33% to 53%.

For those prey taxa that were present in two or more habitat patches (i.e., repeated links in the meta-food web), the proportion of their annual production consumed by the entire predator assemblage (total IS) was highly variable among patches (Fig. 3). For example, Brachycentridae and Glossosomatidae caddisflies (order Trichoptera) were strongly preyed upon by fishes in the main channel, but were largely relieved from this predation pressure within side channels (Fig. 3). As a result of such variation, if total IS for a particular prey taxon was strong (e.g., total $IS > 0.9$) in one patch, there was nearly always (14 of 15 cases) another patch in the mosaic where the interaction was weaker (total $IS < 0.9$). In 67% of these cases, strong interactions in one patch were balanced by much weaker interactions (total

$IS < 0.1$) in another (Fig. 3); a much greater percentage than would be expected by chance alone (38%, assuming a uniform random distribution). Because choice of any threshold values for categorizing strong vs. weak interactions might be considered arbitrary, it is important to note that the pattern of balancing interactions was apparent across a range of interaction strengths. For example, over 75% of the time, prey-habitat patch combinations with total IS greater than 0.5 were balanced by much weaker interactions (total $IS < 0.1$) elsewhere in the floodplain, a percentage that was also much greater (46%) than would be expected by chance.

DISCUSSION

We found that sequentially aggregating food webs from individual patches into a larger and increasingly more complex landscape resulted in corresponding decreases in the average strength of trophic interactions between predators and prey, owing to an increase in the proportion of very weak interactions and a decrease in the proportion of strong interactions in the meta-food web. The distribution of trophic interactions in food webs of individual patches was highly skewed toward weak interactions, a finding consistent with results of other empirical food web research (de Ruiter et al. 1995,

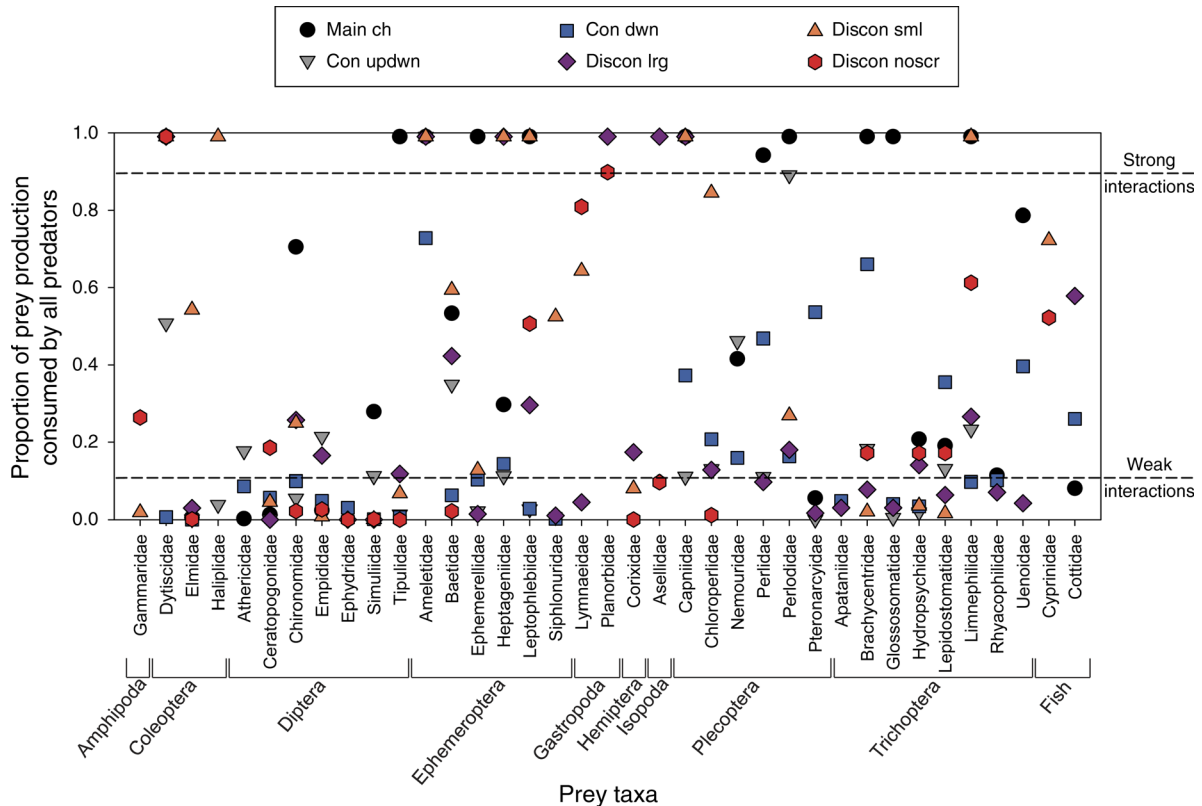


FIG. 3. Variation in the total strength of predation on prey taxa among different habitat patch types. Each point represents the proportion of prey annual production consumed by the entire predator assemblage (total IS), within each habitat patch. Dotted lines are placed at 0.1 and 0.9 to illustrate that patches with strong total IS for certain prey items (total IS ≥ 0.9), are generally balanced by other habitats in the landscape where those interactions are much weaker (total IS ≤ 0.1). Invertebrate prey items are bracketed along the x-axis alphabetically by taxonomic order.

Hall et al. 2000, Sala and Graham 2002, Cross et al. 2013), and one that bolsters the assumptions of modeling studies that have linked these weak interactions to community stability and the maintenance of diversity (McCann et al. 1998b, Kokkoris et al. 2002; but see Allesina and Tang 2012). However, the shift toward a greater proportion of weak consumer–resource interactions with increasing complexity suggests an additional pattern that may be prevalent in real food webs, but which has rarely been investigated. If weak interactions do indeed promote community stability, then this pattern may signal an additional mechanism by which complexity and stability are linked in nature. Regardless, these findings illustrate that new patterns are detected when spatial scale and heterogeneity are made the explicit focus of food web studies, a finding that echoes the tenets of landscape ecology as they have been applied at different levels of ecological organization (Hanski 1998, Levin 2000, Holyoak et al. 2005, Lovett et al. 2005, Yeakel et al. 2014) and as anticipated by those who have called for a spatial ecology of food webs (Polis et al. 2004).

Our findings lead us to identify two related mechanisms by which landscape complexity may contribute to

reduced consumer–resource interaction strengths in meta-food webs (Fig. 4). First, as landscape complexity increases, the number of repeated linkages (i.e., links that occur in two or more patches) increases as well, and this contributes to greater spatial variation in the strength of predator–prey interactions (see Fig. 3). A second, related mechanism is that, with increased complexity come patches that serve as complete refugia for prey; i.e., patches where a prey may escape altogether from a predator that feeds upon them elsewhere. For instance, consistent with their known habitat preferences (Northcote and Ennis 1994, Dunham and Rieman 1999), mountain whitefish and bull trout were absent from side channel patches, whereas, in the main channel, they were abundant and responsible for a large portion of consumption of several invertebrate taxa (Bellmore et al. 2013). Similarly, bridgelip sucker and coho salmon were only observed in side channels that were disconnected at low flows. In fact, only three (of nine total) fish species were found in all six sampled habitats. In combination, then, a strong predator impact on a prey taxon in one patch tended to be balanced by weaker interactions for that same prey in other patches. Such spatial heterogeneity in interac-

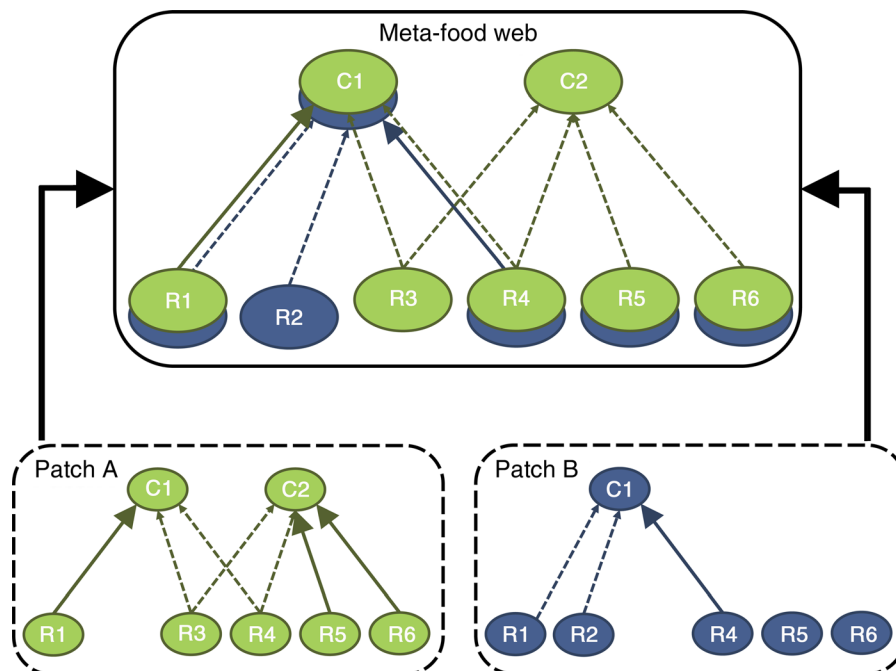


FIG. 4. Food webs to meta-food webs. Meta-food webs consist of an aggregation of linked food webs found in different patches across the landscape. The graphic depicts two related mechanisms by which landscape complexity may contribute to reduced consumer–resource interaction strengths in meta-food webs. First, as landscape complexity increases, the number of repeated linkages (i.e., links that occur in two or more patches) increases, and this contributes to greater spatial variation in the strength of predator–prey interactions (C1–R1 and C1–R4). A second, related mechanism is that, with increased complexity come patches that serve as complete refugia for prey; i.e., patches where a prey may escape altogether from a predator that feeds upon them elsewhere (R5 and R6 in patch A vs. B). C1 and C2 represent predators (consumers); R1–6 represent prey (resources). Solid, bold arrows represent strong IS, whereas dashed arrows represent weak IS.

tion strengths has long been posited to promote coexistence of individual predator–prey combinations (Gause 1934, Huffaker 1958) and contribute to maintenance of community diversity (Menge et al. 1994, Holyoak et al. 2005). However, our results suggest this variation also contributes to the ratcheting down of consumer–resource interaction strengths as scale and landscape complexity increase in meta-food webs. Similarly, reductions in the strength of particular predator–prey interactions with increased complexity have been experimentally demonstrated in the context of oyster reefs (Grabowski 2004) and soil litter (Vucic-Pestic et al. 2010), but studies encompassing a wider array of environments and more complex food webs are needed to evaluate the generality of such findings.

Our approach to characterizing food webs deserves consideration, as it could influence interpretation of these findings. First, we quantified interactions among only a subset of the actual river-floodplain food web, and in most cases, this involved some level of taxonomic aggregation for invertebrates, and, in one case, for fishes as well (sculpin; *Cottus* spp.). We are uncertain what impact including or resolving additional interactions (which might also be accomplished by increased sampling effort of fish diets) might have had on our findings, but speculate that doing either would have

amplified the patterns we observed (e.g., additional resolution would likely identify even more weak interactions; see O’Gorman et al. 2011). Second, we employed an observational approach to estimating the strengths of trophic interactions, each of which represented the proportion of annual production of a specific prey taxon consumed by a given predator (Wootton 1997, Hall et al. 2000, Woodward et al. 2005). This contrasts to an instantaneous, per-capita estimate measured via experimental evaluation of predator impact on a prey population (Paine 1980). The annualized time scale may be seen as both a strength and a weakness of our approach (Cross et al. 2013). Year-round sampling subsumed variation in interactions that occurred at shorter time steps (e.g., due to movements among habitats by fishes), and thus provided a generalized depiction of the food web. A growing array of studies have shown that such observation-based estimates of interaction strength may help explain food web dynamics (Novak 2010, Novak and Wootton 2011, Cross et al. 2013). Yet, the food web flows we measured are themselves products of species interactions occurring at shorter time scales (DeAngelis 1992, Polis 1994) and do not address potentially important indirect or non-trophic interactions (Yodzis 1988, Menge 1995, Kéfi et al. 2012). On the other hand, we characterized a much

wider array of interactions than would have been possible experimentally (Wootton and Emmerson 2005). Evaluations of alignment between experimentally derived and observation based interaction strength estimates are scarce (Wootton 1997), but are generally needed to better link theory and empirical study of food webs (Berlow et al. 2004, Wootton and Emmerson 2005).

Whereas landscape heterogeneity has long been thought to sustain biodiversity via the maintenance of more multidimensional niche-space (Gause 1934, Hutchinson 1953, Levin 2000), the findings of this study suggest a related mechanism, that spatial complexity contributes to proportionally more weak trophic interactions in meta-food webs. If food webs dominated by weak interactions promote stability (McCann et al. 1998, McCann 2000, Kokkoris et al. 2002), then our findings may affect how the values of landscape complexity, and conversely the costs of biophysical homogenization, are assessed. When landscapes are homogenized, among the unforeseen sacrifices may be lost complexity of meta-food webs, which, in turn, may feed back to degrade community stability and biodiversity. The potential for such loss provides added impetus for conserving and restoring ecological processes that create and maintain spatial complexity, and amplifies the need for scientific understanding of the role of complexity in an increasingly homogenized world.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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