Lakeshore development and lake food web structure in the Puget Sound lowlands

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A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2024

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Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

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Abstract

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Anthropogenic modification of lake shorelines can eliminate or sharply reduce the elements of shorelines that provide structural diversity in littoral habitats, such as macrophyte and woody debris densities. These changes have been linked to alterations in species abundances, diet patterns, and nearshore food web structure at altered and unaltered shoreline locations within a lake. Few studies, however, have quantitatively examined the association between lakeshore development and food web network structure across lakes with varying levels of lakeshore development. Considering the lake-specific food web networks across multiple lakes could reveal differences in interactions and structural patterns not captured in within-lake studies.

In this study, I quantified community structure and species' positions in food webs across lakes with varying degrees of lakeshore residential development to identify associations between the two. I selected 12 lakes in the Puget Sound lowlands, and for each conducted standardized habitat surveys by measuring littoral and riparian habitat complexity, and recording dock density along the lakeshore, pelagic chlorophyll-a concentration, and lake area. To estimate feeding habits of fish, I employed both stable isotope analysis and stomach content analysis.

Additionally, I used stable isotope analyses to examine diet patterns in aquatic macroinvertebrates. I integrated data from both techniques with preexisting information from the literature within a relatively new analytical framework, EcoDiet, to estimate the proportion of each prey type in the diets of fish and predacious macroinvertebrates within the food web. To quantify species' roles within the food web I calculated diet breadth, diet evenness, and betweenness centrality (relative importance in connecting disparate parts of the food web, hereafter centrality) for each predatory species. I then quantified food web metrics from the estimated lake-specific food webs using network analyses to calculate the connnectance, mean link strength, and mean degree within each food web. Finally, I assessed the correlations among these network metrics and the measured environmental variables using redundancy analysis (RDA), principal component analysis (PCA), and bivariate regressions.

My results suggest that while pelagic chlorophyll-a concentration and the presence of largemouth bass were associated with changes in diet patterns within the food web, lakeshore development had little effect on overall food web connectance. Yellow perch and pumpkinseed exhibited a positive correlation between centrality and both pelagic chlorophyll-a concentrations and the presence of largemouth bass. Thus, both yellow perch and pumpkinseed were more important in connecting basal resources to upper trophic levels when primary production was high and largemouth bass were present in the lakes. Fish species exhibited different associations with lakeshore development and diet breadth and diet evenness. For instance, yellow perch (*Perca flavescens*) diet breadth and diet evenness were positively correlated with lakeshore residential development, whereas largemouth bass (*Micropterus salmoides*) diet breadth was negatively correlated, and pumpkinseed (*Lepomis gibbosus*) displayed little change in diet breadth or diet evenness. The net effect of these species-specific responses was a weak and positive association between food web connectance and both dock density and lake area. Because none of the lakes in this study were undisturbed (the least developed lake having residential development on 25% of its lakeshore), it is possible that changes to food web connectance occur at lower levels of lakeshore residential development than was measured in this study. High network connectance can stabilize food webs, therefore, the weak correlation between connectance and lakeshore residential development suggests that food web stability may be similar among the disturbance levels measured in this study. Future research could directly examine the relationship between lakeshore development, food web network structure, and stability across a wider range of lakeshore development.

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Introduction:

Anthropogenic disturbances have drastically transformed ecosystems across the globe by modifying the landscape, altering nutrient cycles, and changing the biotic community through loss or addition of species (Vitousek et al. 1997; Kaye et al. 2006; Lawler et al. 2014; Haddad et al. 2015; Weyhenmeyer et al. 2024). Urbanization, in particular, has exacerbated these negative impacts by increasing habitat fragmentation, point source pollution, impervious surfaces, and the introduction of invasive species (Grimm et al. 2008). Lakes are especially important because they provide numerous ecosystem services, including access to food and drinking water, water quality regulation, and opportunities for recreation (Carpenter et al. 2011; Jenny et al. 2020). With over 1,950 lakes located within urban watersheds across the continental United States (Costadone and Sytsma 2022), the significance of these ecosystems is evident. However, the health of many lakes has been significantly degraded by urbanization, threatening the provisioning of valuable ecosystem services (Weyhenmeyer et al. 2024).

Residential development can result in elevated nutrient inputs, a major environmental challenge facing lakes globally (Carpenter et al. 2011). Lawn runoff and leaking septic systems increase nutrient loading from the surrounding watershed, especially at the intersection of urban and rural environments (Moore et al. 2003; Morris and Bagby 2008; Withers et al. 2012; Toor et al. 2017). Additional nutrient inputs can alter biogeochemical cycling and lead to cultural eutrophication and harmful algal blooms (Carpenter et al. 1998, 2011; Schindler 2006). Cultural eutrophication can in turn lead to loss of water clarity, reduced oxygen in the water column, and changes in the lake's food web structure (Schindler et al. 1971; NRC 1992). For example, experimental addition of phosphate and nitrogen to Lake 227 in Winnipeg, Manitoba increased blue-green algae which is less digestible by zooplankton than other types of algae, thereby altering the base of the food web (Schindler et al. 1973, 2008). Furthermore, harmful algal blooms can reduce the aesthetic appeal of lakes (NRC 1992) and, more seriously, produce toxins that are dangerous to humans and animals (Kotak et al. 1993; Morris 1999).

In addition to the negative impacts on water quality, residential development alters the physical landscape and habitat around lakes. Residents tend to clear brush and thin riparian forest, which can reduce the amount of coarse woody habitat (CWH) within lakes (Christensen et al. 1996; Francis and Schindler 2006; Sass et al. 2019; Olden et al. 2022). Jennings et al. (2003) examined lakes in Wisconsin and found a negative correlation between residential development at sampling sites within each lake and emergent vegetation, floating vegetation and CWH. Similarly, Francis and Schindler (2006) found that CWH in the Pacific Northwest was also negatively correlated with lakeshore residential development. The loss of aquatic macrophyte and CWH has been linked to numerous negative ecological outcomes, such as decrease littoral and secondary production, leading to a reduction in valuable prey resources (Sass et al. 2006; Pätzig et al. 2018). Furthermore, habitat loss alters relative abundance of fishes (Sass et al. 2006; Helmus and Sass 2008), fish behavior (Ahrenstorff et al. 2009; DeBoom and Wahl 2013), and species interactions in lakes (Crowder and Cooper 1982; French 1988; Persson and Eklov 1995).

This study focuses on three fish species—largemouth bass, pumpkinseed, and yellow perch—that may be impacted by changes to the lake systems described above, as each can play a unique role within lake food webs. All three species were originally introduced to lakes throughout the Pacific Northwest in the 1800s (Cobb 1929; Wydoski and Whitney 2003). As juveniles, largemouth bass consume small crustaceans and insects, and then transition to consuming mainly fish or crayfish, though they remain opportunistic and will consume other readily available prey (Wydoski and Whitney 2003). DeBoom and Wahl (2013) examined the effects of habitat structure on foraging behavior in largemouth bass (*Micropterus salmoides*) by experimentally adding CWH in mesocosms. They found largemouth bass increased their hunting activity in mesocosms with low CWH, which aligns with field observations on the size of largemouth bass hunting ranges (Ahrenstorff et al. 2009). Yellow perch also show ontogenetic shifts in diet from zooplankton to benthic invertebrates to fish as they grow, but being omnivorous, can consume all three if the perch is large enough (Wydoski and Whitney 2003). They potentially occupy an important role in the food web as they rely on both littoral and pelagic resources (Schindler and Scheuerell 2002). In contrast, pumpkinseed are more dependent on benthic invertebrates than largemouth bass and yellow perch (Vander Zanden and Vadeboncoeur 2002; Schindler and Scheuerell 2002), and have been shown to exert top-down pressure on benthic macroinvertebrates in the littoral zone (Bernot and Turner 2001; Mancinelli et al. 2007). Laughlin and Werner (1980) found that the relative abundance of pumpkinseed sunfish (*Lepomis gibbosus*) increased while the relative abundance of longear sunfish (*Lepomis maglotis peltastes*) declined in lakes with high vegetation density, likely due to differences in foraging behavior. These changes in abundances and behaviors have the potential to impact diet patterns within lake ecosystems.

Fishes exhibit varied responses to decreasing macrophyte or CWH presence, which is often correlated with reduced prey abundance (Warfe and Barmuta 2006). For example, European perch (*Perca fluviatilis*) have been observed consuming a greater variety of taxa as macrophyte abundance and prey abundance decrease (Persson and Eklov 1995; Vejříková et al. 2017; Tsunoda and Mitsuo 2018). This behavior is predicted by optimal foraging theory, which suggests that predators select prey to maximize net energy gain, therefore selecting fewer, but more profitable prey items when prey is plentiful, and a wider variety when prey is scarce to compensate for lost energy (Schoener 1974; Hodgson and Kitchell 1987; Perry and Pianka 1997). Similar to European perch, bluegill sunfish (*Lepomis macrochirus*) diet breadth is negatively correlated with macrophyte abundance; however, reduced diet breadth in bluegill is due to their greater foraging efficiency in open water rather than to prey abundance (Crowder and Cooper 1982). In contrast, largemouth bass decrease their diet breadth as habitats become less complex (Anderson 1984). Experimental studies by Sass et al. (2006) and Ahrenstorff et al. (2009) in Little Rock Lake and Camp Lake, Wisconsin demonstrated that when CWH was either removed or added, largemouth bass altered their foraging strategy. In lake basins with high CWH and ample prey, largemouth bass used a sit-and-wait strategy, whereas in lakes with low CWH and less abundant aquatic prey, they adopted a cruising strategy to search for prey. When largemouth bass employed a sit-and-wait strategy in lakes with high habitat complexity they consumed a wider variety of less energetically profitable prey due to reduced energetic demands (Ahrenstorff et al. 2009). Conversely, pumpkinseed in exposed littoral sites, lacking macrophyte cover and soft sediments, and those in vegetated littoral sites within Ashby Lake, Ontario did not differ in their diet composition (Jarvis et al. 2021). These examples demonstrate how reduced habitat complexity due to residential lakeshore development can alter the variety of prey consumed by fishes.

In addition to the variety of prey items, the strength of dietary links can change in response to residential lakeshore development (Tylianakis and Morris 2017). Specifically, as lakeshore residential development increases, yellow perch (*Perca flavescens*) may consume more pelagic resources rather than diversifying their diet within the littoral zone (Twardochleb and Olden 2016a). However, Twardochleb and Olden (2016a) found that in developed lakes with abundant populations of nonnative Chinese mystery snails (*Bellamya chinensis*), yellow perch consumed more benthic invertebrates than in highly developed lakes without mystery snails. Additionally, Nohner et al. (2018) found that largemouth bass consumed more fish prey in highly vegetated in-situ mesocosm environments than sparsely vegetated environments, resulting in a decrease in diet evenness in highly vegetated habitats. Furthermore, strong interactions can create unstable predator-prey dynamics within food webs, while numerous weaker links can lead to greater stability (McCann et al. 1998; McCann 2000). Therefore, the amount of prey consumed has important implications not only for the individual species, but also for food web structure (McCann et al. 1998; Berlow et al. 2004; Rooney and McCann 2012).

Food web structure, which depicts consumptive interactions within a community, allows for the quantification of the aforementioned species-specific responses, and can be used to examine how these changes shape community-wide responses to lakeshore development (Polis and Strong 1996; McCann 2012; Alp and Cucherousset 2022). Lakeshore development can alter food web structure and can cause declines in and extirpations of native species' populations (Twardochleb and Olden 2016b; Start et al. 2020). In addition to species loss, altered basal carbon inputs to lakes can have impacts on the trophic structure of food webs (Holgerson et al. 2018). For instance, Ziegler et al. (2015) found that shallow lakes in Quebec with higher aquatic macrophyte biomass supported longer food chains, even after controlling for ecosystem size and nutrient concentration. They suggested that the increase in refuge and diversity of basal resources within aquatic macrophytes drive these patterns (Ziegler et al. 2015).

Network analysis is one way to quantify species interactions and supports a greater understanding of food web structure within the community by depicting consumptive interactions among species (May 1968; Pimm et al. 1991). Food web networks can be described by the number, arrangement, and weight of consumptive interactions among species, quantifying both the structural roles of individual species and overall community organization (Pimm et al. 1991; McCann 2012). Thus, food web network structure has implications for nutrient cycling, primary production, trophic structure, and ecosystem functioning (Layman et al. 2012; Urrutia-Cordero et al. 2016; Frost et al. 2019; Sullivan and Manning 2019). For example, Sullivan and Manning (2019) created riverine food webs in Ohio across an urban-rural land use gradient based on expert opinion on the presence and absence of feeding interactions to examine changes in terrestrial-aquatic linkages. They found that there were fewer interactions between aquatic and terrestrial subgroups within urban food webs than in rural or forested food webs (Sullivan and

Manning 2019). Additionally, in three north German lowland lakes, Brauns et al. (2011) examined the habitat-specific responses of littoral food webs to residential lakeshore development. They found that at sections of shorelines with residential development, habitat diversity decreased, which was associated with a reduction in the number of trophic links within the macroinvertebrate food web (Brauns et al. 2011).

Previous studies in aquatic systems have primarily examined changes to diet and food web structure using either stomach content analysis (SCA) or stable isotope analysis of carbon (C) and nitrogen (N) (e.g., Francis & Schindler, 2009; Holgerson et al., 2018). However, neither of these methodologies provide a complete picture of the food web on their own (Thompson et al. 2012). SCA provides a snapshot of specific species that fish consume but doesn't provide information on long term diet habits without repeated sampling (Hesslein et al. 1993). For example, Danehy et al. (1991) used stomach content analysis to evaluate the seasonal diet patterns of yellow perch in an eastern bay of Lake Ontario, US. Through repeated sampling events from April to November, they found that yellow perch shifted their diet from fish in early summer to crayfish in mid-June, when crayfish are most abundant, and then back to fish in September. Additionally, Happel et al. (2015) found that stomach content analysis of yellow perch revealed greater variety in diet composition across different sampling sites within Lake Michigan, US than did stable isotope analysis.

Stable isotope analysis (SIA) uses naturally occurring differences in isotopic ratios of carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N) to account for diet assimilation over several months but does not usually reveal specific diet items (Layman et al. 2012). The differences in $\delta^{13}C$ values can stem from distinct forms of photosynthetic pathways, C_3 vs C_4 plants, among other biogeochemical processes and environmental characteristics (Fry 2006; Liu et al. 2012). The difference in $\delta^{13}C$ among plants and organisms can be used to identify the type or location of resource being consumed; within a single lake, pelagic resources have more negative $\delta^{13}C$ values than littoral resources (Vander Zanden and Rasmussen 1999). Additionally, $\delta^{15}N$ increases as trophic position increases because, in general, metabolic processes preferentially select lighter isotopes and the heavier isotopes are left behind as the lighter ones are excreted (Peterson and Fry 1987; Fry 2006). By analyzing the stable isotope ratios within muscle tissues of predators in relation to the ratios of potential prey items, researchers can estimate diet proportions for the predator (Peterson and Fry 1987; Cabana and Rasmussen 1996; Vander Zanden et al. 1997).

The analytical methods used in stable isotope analyses advanced significantly in recent decades by incorporating uncertainty in mixing model inputs (Moore and Semmens 2008; Parnell et al. 2010). Further advances have allowed for the estimation of diet proportions for all consumers in the food web using stable isotope information (Kadoya et al. 2012). However, these models rely on fixed topologies, meaning the probability of a diet link existing is either one or zero. To address this, a recent analytical framework, EcoDiet, combines diet information from existing literature data, SCA, and SIA into a single, Bayesian modeling framework to quantify food web networks (Hernvann et al. 2022). By combining both SCA and SIA to create a food web network, EcoDiet takes advantage of the strengths of both methodologies as well as incorporating pre-existing knowledge of diet proportions (Hernvann et al. 2022).

In this study, I use EcoDiet to examine the impacts of lakeshore residential development on both species' network roles and food web structure. While others have examined changes in relative abundances, diet patterns, and species interactions at altered and unaltered sections of shorelines within a lake (Brauns et al. 2011; Ziegler et al. 2017), I seek to quantitatively examine the association between lakeshore development and food web network structure across lakes with varying levels of lakeshore development. Considering the lake-wide food web across lakes could reveal differences in interactions and structural patterns not captured in studies comparing sites within lakes (Guimarães 2020). Furthermore, I examine the network positions of three fish species common to lakes in the Pacific Northwest, yellow perch, largemouth bass, and pumpkinseed, as well as odonates. Largemouth bass are predicted to decrease their diet breadth and increase diet evenness due to changes in foraging patterns driven by littoral habitat complexity (Anderson 1984; Ahrenstorff et al. 2009; Nohner et al. 2018). Conversely, yellow perch are predicted to decrease their diet breadth but increase diet evenness, potentially because of decreased reliance on zooplankton (Diehl 1992). Pumpkinseed, however, are expected to show limited changes in diet breadth or evenness as habitat complexity decreases and lakeshore residential development increases (Godinho et al. 1997; Jarvis et al. 2021).

Species-specific responses to disturbance collectively influence community responses (Beckerman et al. 2006). As lakeshore residential development reduces habitat complexity and secondary production (Pätzig et al. 2018) optimal foraging theory predicts that, in general, species will increase their diet breadth by consuming a wider variety of items as preferred diet resources become scarce (MacArthur and Pianka 1966; Schoener 1971). Conversely, differences in foraging strategies (e.g., sit and wait vs active searching) and interspecific competition may lead to decreased diet breadths as species adapt to limited prey abundance (Schoener 1974; Eklov 1992; Perry and Pianka 1997). Connectance is the proportion of realized links within the food web compared to the total number of potential links. As species increase their diet breadth, more links are actualized, and connectance increases. Assuming that organisms across the food web typically increase their diet breadths as resources become scarce, following optimal foraging theory (e.g., Dudová et al. 2019), and that macroinvertebrate abundance declines as macrophyte density and CWH decrease (Pätzig et al. 2018), I predict that as lakeshore development increases, there will be an increase in connectance as the proportion of realized links increases.

Methods:

The Puget Sound lowlands in Washington State, United States, present an excellent region to study the consequences of anthropogenic disturbances on lake food webs. Lakes in this area are located within a land-use gradient ranging from undisturbed and infrequently visited lakes to urban lakes whose shores are surrounded by residential housing (Twardochleb and Olden 2016b; Olden et al. 2022). The Puget Sound lowlands contain several lakes with similar sizes (depth and surface area) and fish assemblages, among other characteristics, but which vary in lakeshore development. Thus, this system of lakes can be used to examine spatial variation in community structure in response to lakeshore development. I selected twelve lakes that ranged across a development gradient based on previous estimates of percent lakeshore developed (Twardochleb and Olden 2016b), that were of similar size, contained similar species, and experienced similar pelagic chlorophyll-a concentrations (Figure 1; Table 1)

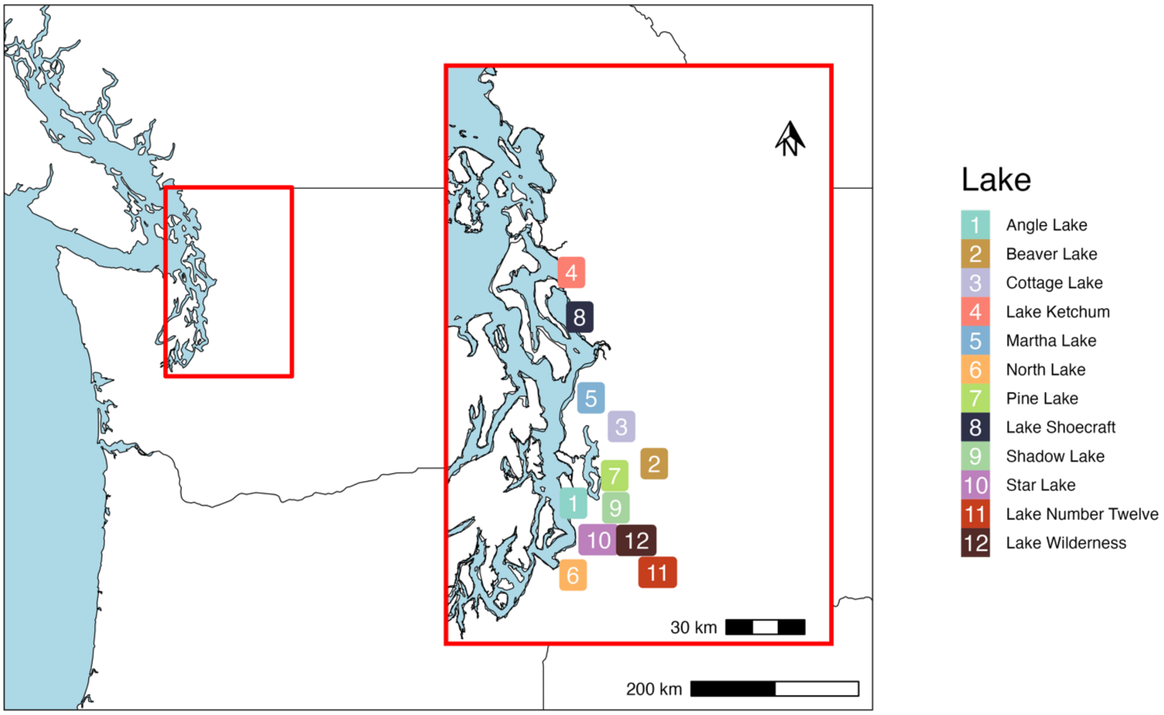

Figure 1: Map of study sites within the Puget Sound Lowlands. Colors and numbers indicate lake name.

Table 1: Lake names, habitat quality variables, environmental variables, dock density and connnectance.

Lake	Abbreviation	Area (km^2)	Pelagic Chl-a ($\mu g L^{-1}$)	Dock Density (km^{-1})	Riparian Complexity	Littoral Complexity	Combined Litt-Rip Complexity
Angle	AGL	0.413	1.25	40.2	0.32	0.26	0.29
Beaver	BVR	0.251	3.23	27.82	0.78	0.32	0.55
Cottage	CTG	0.255	7.73	22.28	0.47	0.33	0.40
Ketchum	KTM	0.105	4.10	20.56	0.47	0.24	0.35
Martha	MTA	0.251	3.13	41.95	0.55	0.56	0.55
North	NTH	0.206	1.42	16.74	0.71	0.48	0.59
Pine	PNE	0.348	2.30	35.68	0.60	0.15	0.37
Shadow	SHW	0.202	5.55	12.74	0.90	0.29	0.59
Shoecraft	SHC	0.538	2.20	29.72	0.61	0.17	0.39
Star	STR	0.138	1.96	36.12	0.60	0.29	0.45
Twelve	TLV	0.166	2.31	17.88	0.90	0.60	0.75
Wilderness	WLD	0.271	4.06	18.72	0.74	0.68	0.71

At each lake I sampled fish, aquatic macroinvertebrates, and aquatic and terrestrial plants. To capture fish, I used a combination of gillnets, hoop nets, and beach seines to target pelagic and littoral fish. Gillnets and hoop nets were set in the late afternoon and collected in the early morning to capture dusk and dawn fish movement. Beach seines were used as necessary to supplement littoral fish samples. All captured fish were identified and a subsample of were euthanized for stable isotope analysis and stomach content analysis. In addition to fish, I used a D-frame net to opportunistically sample for macroinvertebrates in dominant habitat types around the lakeshore to ensure a representative sample of the macroinvertebrate community. Similarly, I collected aquatic and terrestrial leaf samples from terrestrial plants that were common throughout the lake. Finally, I conducted plankton tows using a plankton tow sampling net (150 μm). All collected samples were placed on ice in the field and immediately frozen upon returning to the lab.

To evaluate changes in habitat structure within each lake I conducted littoral and riparian habitat surveys based on the Environmental Protection Agency's National Lake Assessment protocols (USEPA 2017). At ten randomly selected locations around the lake I measured metrics related to fish habitat such as but not limited to macrophyte cover and coarse woody debris within the littoral zone. Additionally, I characterized riparian ground and vegetation cover. I then combined these measures into two composite indices to represent riparian habitat complexity (eq. 1), littoral habitat complexity (eq. 2). I then averaged the littoral and riparian complexity to create a composite score for combined littoral-riparian habitat complexity (eq. 3) modified from (Kaufmann et al. 2014a, b).

$$Riparian = \frac{W + C - I}{3} \tag{1}$$

$$Littoral = \frac{N + S + E}{3} \tag{2}$$

$$LittRip = \frac{Riparian + Littoral}{2} \tag{3}$$

In equation 1, W indicates the scaled average areal proportion of woody vegetation cover, C represents proportion of observation sites with large tree cover (diameter at breast height > 0.3 m), and I represents the average areal proportion of impervious surfaces at each lake. In equation 2, N is the sum of the areal proportion of fish habitats including boulders, woody brush, ledges, overhanging vegetation, and inundated live trees. Large, submerged snags (S) and areal cover of emergent and floating vegetation (E) were added separately to increase their influence on the overall littoral complexity metric. Finally, the two habitat complexity metrics (eq. 1 and eq. 2) were averaged to get a composite metric of overall habitat complexity (eq. 3). In all cases, any scaled metrics were based on the observed maximum value. All values are proportions and are therefore dimensionless. These indices range from zero to one with a score of one representing the maximum value observed. The presence of abundant fish habitat within the littoral zone, including emergent aquatic macrophytes and coarse woody debris, increased littoral habitat complexity result in higher littoral habitat complexity. Additionally, low hanging bushes and shrubs increased the riparian complexity while the presence of impervious surfaces decreased riparian complexity (Kaufmann et al. 2014a, b).

In addition to habitat complexity, I recorded mean summer (June – September) pelagic chlorophyll-a concentration ($\mu g L^{-1}$) and lake size (km^2) based on county monitoring records (Snohomish County Surface Water Management 2022; Water and Land Resources Division 2022). While not the central focus of this study, the size of the ecosystem can alter food web structure; for example, food chain length has been linked to both the area of an ecosystem and the systems productivity (Godinho et al. 1997; Ward and McCann 2017). Pelagic chlorophyll-a measurements for Star Lake, Shadow Lake, and North Lake were missing for 2022. Shadow Lake and North Lake have been monitored consistently for the past decade and showed little interannual variation in their pelagic chlorophyll-a concentration; therefore, I used 2021 averages. King County ceased monitoring Star Lake in 2008 because the previous 10 years indicated consistently low pelagic chlorophyll-a concentrations (C. Knutson, personal communication, April 24, 2024). Therefore, I used the 2008 measurement in the analyses and assume that it continues to be representative of pelagic chlorophyll-a concentration in Star Lake.

To evaluate diet composition of the fish and macroinvertebrates sampled, I used a combination of stomach content analysis and stable isotope analysis. First, I weighed the fish and measured total fish length, to allow for tracking of impacts of size on diet for each individual. Then each fish was dissected for dorsal muscle plugs and stomach contents. Stomach contents were preserved in ethanol and then later identified to varying taxonomic levels. For example, aquatic insects were identified to order while fish were identified to species if remains were identifiable. Some fish specimens found in stomachs were small and lacked identifying characteristics such as fins, coloration, and heads, making a positive identification impractical.

In addition to fishes, crayfish and snail individuals were also dissected for muscle tissue to run bulk stable isotope analysis (SIA). Other aquatic macroinvertebrate individuals were combined by order and homogenized to meet minimum mass requirements for SIA and then run in triplicate. Similarly, small sections of leaves from multiple individual plants were combined and run in triplicates. All stable isotope samples were dried in an oven at 60 °C and then crushed and homogenized using a mortar and pestle. Tissue samples were then packed in 8x5mm tin capsules. Sample masses for fishes, crayfishes, and snails were between 0.44 and 0.46 µg, while plant sample mass ranged between 1.485 and 1.515 µg. All samples were analyzed using an Elemental Analyzer (NA 2500; CE Instruments, Wigan, United Kingdom) interfaced with a Delta V Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts). Consumer muscle tissue was referenced to 2 glutamic acid standards and Bristol Bay Sockeye Salmon (*Oncorhynchus nerka* Walbaum, 1792). For plants a Peach Leaf Standard from the National Institute of Standards and Technology (NIST SRM 1547, USA) as a reference. Stable isotope ratios are reported in delta notation relative to Vienna Pee Dee Belemnite for C and air for N in per mil (‰; Hayes 2004; Fry 2006).

Food Web Network Modeling:

To quantify diet proportions for all predators within the food web, I combined fish diet information from three different data sources into a single Bayesian model–EcoDiet (Hernvann et al. 2022). First, literature data of presence/absence and proportions of prey in diets serves as *a priori* knowledge in the Bayesian model. The literature data create a joint prior distribution for both food web topology and for diet proportions. In the food web topology matrix, each component of the matrix is given an independent Bernoulli distribution based on the expected probability of a given trophic link existing. This in turn, is based on the literature data and the weight placed on the literature data. The prior distribution for the matrix of diet proportions is conditional on the topology matrix. The diet proportions for a given consumer are drawn from a Dirichlet prior so that they sum to one. When the probability of a link existing is 0, the corresponding parameter in the Dirichlet prior is also set to zero.

Next, the likelihood functions are generated. The SCA data are used to create a likelihood function to update the topology matrix. The probability of a given link existing is considered proportional to the frequency of prey occurrences in stomachs, where variation is dependent on sample size. Thus, smaller sample sizes are less informative than larger ones. Then, an SIA mixing model is used to quantify the percent diet composition of prey items for each predator. EcoDiet calculates the mean expected stable isotope value for each consumer based on the mixtures of the possible source values and the matrix of prior diet proportions from the literature. The expected mean values are then modeled as independent multivariate normal distributions, and the likelihood of the stable isotope values based on the data is calculated using a multivariate normal distribution for each trophic group. The combined likelihood for the stable isotope values is calculated by multiplying the multivariate normal likelihood terms across all individuals and trophic groups within the food web. The joint prior for the network of link probabilities and the network of diet proportions is then updated based on the estimated likelihoods using MCMC simulations. This produces both a network weighted by the probability of a link existing and one whose link weights are based on the median posterior diet proportions.

To find relevant literature values, I used search terms including the name of the taxa in this study, either common or scientific, and the key words “diet”, “foraging”, “food”, “prey”, “gut content”, or “stomach content” in Web of Science. For example, one search would include “yellow perch” AND “diet,” the next “Perca flavescens” AND “diet,” the next “yellow perch” AND “foraging,” and so on to find literature detailing yellow perch diet composition. Additionally, I looked at sources in FishBase (Froese and Pauly 2024) and Google Scholar to supplement these results. To be included in these analyses the study had to provide quantitative diet proportions from stomach or gut content analysis using either mass or percent importance. Each literature study was given a “pedigree” based on a modified version of the one found in Hernvann et al. (2022) (Figure A1). In short, more recent papers from ecosystems that were more similar to the lakes in this study with higher sample sizes were given more weight than others as prior information in the EcoDiet model. These literature data created a network of diet proportions that included all taxa across all the lakes. However, within each lake the taxa not found in the lake were removed from the literature network and the proportions were re-adjusted so that all prey items summed to one. Therefore, while the original literature network is the same across all lakes, the actual prior literature distributions varied slightly by lake.

The food web sampled in this study required some modifications to the data formatting to meet EcoDiet requirements. Crayfish and other aquatic macroinvertebrates did not have observed stomach content data. Therefore, for these taxa, prior diet proportions were based solely on literature data. Informative literature on the stomach contents of both signal crayfish

(*Pacifastacus leniusculus*) and red swamp crayfish (*Procambarus clarkii*) were used to estimate prior diet proportions. Prior diet information for benthic macroinvertebrates, other than crayfish, was based on functional feeding groups for each taxon so that prior diet proportions were uniformly distributed across potential prey items. For example, damselflies and dragonflies (*Odonata*) prior diet proportions were uniformly distributed across their potential prey, other benthic invertebrates in the food web. Additionally, I included all primary producers in the food web networks. However, upon inspection of the results from the EcoDiet model it became apparent that the large variety of littoral macrophytes biased the mixing model estimates. This, coupled with the absence of seston and algae, meant the available end members were insufficient for evaluating the consumption patterns of non-predatory macroinvertebrates. Removing primary producers allowed zooplankton and non-predatory benthic invertebrates to act as end members in the system. Therefore, I chose to run analyses on webs without primary producers.

EcoDiet produces posterior probability distribution for the existence of a link and a posterior distribution for the proportion of diet for each prey item in reference to a given predator. To account for this variation in estimates I used a bootstrapping framework to randomly draw estimated diet proportions from the posterior distributions. Within each iteration I calculated each network metric, described in detail below, to produce a bootstrap distribution for each network metric. These metrics were compared visually. To simplify analyses, I extracted the median value from each predator-by-taxon diet proportion from the EcoDiet model results to create weighted networks. I then removed links representing low diet proportions (median values < 0.01) from the food web network. I chose the limit of 0.01 because it fell well within the range of similar limits in previous literature and increasing the value further removed many links from the food webs (Figure A2).

Traditional network metrics view weighted links as path lengths, for example the distance from one node to another. In a food web context, however, higher weights represent greater diet proportions between two taxa. Therefore, to examine food web complexity I calculated weighted connectance based on the equation found in (Bersier et al. 2002). Additionally, I assessed the mean number of links for a given taxon (degree). Finally, I examined the distribution of median diet proportions within the web.

To evaluate species-specific responses to lakeshore development I calculated diet breadth and diet evenness for predators, and betweenness centrality for fish and macroinvertebrates located within the center of the food web. Diet breadth is a weighted measure of the diversity of prey diet proportions for a given predator (i.e., a weighted estimate of diet breadth). The higher the value, the more diverse the taxon's diet (Bersier et al. 2002). I also modified the Shannon-Weiner diversity measure as suggested in Austin (1999) to calculate evenness of diet proportions for predators. This evenness parameter was scaled by the number of taxa within the web, after low diet proportions were removed. Values close to 1 indicate all diet proportions are equal. Conversely, values close to 0 indicate the diet proportion for one prey is very high while other prey items have low proportions, indicating uneven diet distribution (Austin 1999). Finally, betweenness centrality is one way to measure relative importance of species to connecting disparate subgroups within the food web (Gsell et al. 2016). Betweenness centrality counts the number times a taxon lies on the shortest path between two other taxa (Start et al. 2020; Xing et al. 2021). I used the *tnet* package in R (Opsahl et al. 2010) to calculate weighted betweenness centrality. This calculation of betweenness centrality (hereafter centrality) rewards diet proportions with higher weights (Opsahl et al. 2010). Therefore, taxa with both high diet proportions and that are a dominant prey item for their predators' diets are ranked higher than those with many low diet proportions and that are rarely consumed by their predators.

Statistical Analyses:

I performed the following analyses on all predators in the food that were found in at least six of the studied lakes. I analyzed species-specific diet breadth, zooplankton reliance, diet evenness, and centrality of three common and potentially influential fish species in this system: yellow perch, pumpkinseed, and largemouth bass. Each species plays a different role within the food web and can impact the populations and behavior of lower trophic levels (Bernot and Turner 2001; Vander Zanden and Vadeboncoeur 2002; Schindler and Scheuerell 2002; Wydoski and Whitney 2003). Neither largemouth bass nor pumpkinseed consumed significant amounts of zooplankton in the study lakes, therefore I did not evaluate patterns in zooplankton consumption for largemouth bass and pumpkinseed. Due to their central location in the food web and importance in littoral food web dynamics (Diehl 1992) predatory macroinvertebrates were also included in the analyses. Dragonflies and damselflies predate on aquatic insects and are then consumed by fish. Thus, they have the potential to be important sources of food for upper trophic levels.

For each taxon, I fit generalized linear models to evaluate the correlation between the network metrics (diet breadth, centrality, and diet evenness), habitat complexity (riparian habitat, littoral habitat, and combined littoral and riparian habitat), and environmental variables (lake size, and mean pelagic chlorophyll-a concentration). Additionally, I fit generalized linear models for community-wide parameters–connectance, mean link strength, and mean degree. Previous work suggests that many of these network metrics depend on the number of taxa within the food web (e.g., Morozumi et al. 2022). Therefore, I included the number of taxa within the food webs in the bivariate regression analysis.

Diet breadth and mean degree are continuous variables greater than 0. Therefore, I modeled both with a simple linear regression. I used a logistic regression with a logit-link function for connectance, mean link strength, and diet evenness because all range from 0 to 1.

Connectance, mean degree, and mean link strength are whole-lake metrics and therefore are only modeled once per explanatory variable. However, diet breadth and evenness are modeled independently for each taxon. Centrality is a measure of count data; therefore, I started by using a Poisson regression with a log-link function. However, upon inspection, these model results exhibited overdispersion. Thus, I used a negative-binomial regression with a log-link function to model centrality. By definition, taxa on the edge of the food web with either no predators or no prey have a centrality value of zero; therefore, I did not analyze centrality for non-predacious aquatic macroinvertebrates nor largemouth bass. To evaluate shifts in reliance on benthic and pelagic resources, I modeled the median diet proportion of zooplankton for yellow perch. Similar to evenness, zooplankton reliance is a proportion, and I used a logistic regression with a logit-link function. Since I fit many pairwise models for each network metric and each species, I used a Bonferroni correction to reduce the chance of Type I error.

While bivariate regressions provide a basic understanding of the individual relationships among the network metrics of interest and the environmental and habitat complexity variables, many of these explanatory variables are interrelated with one another as well. Therefore, I used redundancy analysis (RDA) to evaluate the relationships among the explanatory variables as well as among all the network metrics of interest (Legendre and Legendre 2012). RDA allows for these interrelationships more effectively than the simple bivariate regressions. However, RDA assumes that the relationships between each network metric (response variable) and each explanatory variable is linear and that the explanatory variables are centered. Therefore, I transformed the network metrics using the “maximum” method. In the “maximum method” each observation is divided by the maximum value of each network metric. This ensures that every network metric is scaled from 0 to 1; thus, zero values are preserved and differences in scale for the network metrics do not bias the RDA (Legendre and Legendre 2012). I then standardized the explanatory variables so that each variable had a mean of 0 and variance of 1. Again, this ensures that results are not influenced by differences in the scale of the explanatory variables.

RDA is also sensitive to collinearity among explanatory variables. Therefore, before fitting the models I calculated the Variance Inflation Factor (VIF) to determine which variables had little ability to uniquely predict the network metrics. The habitat complexity variables, littoral complexity and riparian complexity were strongly correlated with the combined habitat complexity variable. All other variables had low VIF values. Therefore, I fit an RDA which included one of the habitat complexity metrics as well as the dock density (km^{-2}), pelagic chlorophyll-a concentration (Chl-a μgL^{-1}), and lake area (km^2). I then compared the resulting adjusted R^2 values to determine which model had the best fit. All subsequent analyses were conducted with the best RDA model for each species and for the community.

After selecting the best of the candidate models, I used permutation tests to evaluate whether the explanatory matrix was a significant predictor of the network metrics. First, I used a PERMANOVA on the response and explanatory matrices directly to evaluate whether the RDA model performed better than the null model, which assumes the response matrix and explanatory matrix are unrelated (Legendre and Legendre 2012). Secondly, I used a PERMANOVA on the explanatory variables to evaluate if any significantly explained variation in the response variables.

I did this for yellow perch, pumpkinseed and the community-wide network metrics, but largemouth bass were only captured in sufficient quantities to analyze in six of the twelve study lakes. Similarly, dragonflies (Odonata Anisoptera) and damselflies (Odonata Zygoptera) were only captured in eight and seven of the twelve lakes respectively. Red swamp crayfish (*Procambarus clarkii*) were only captured in four out of the twelve lakes, so they were not included in the following analyses. Therefore, for these species, there were too many explanatory and response variables to analyze using an RDA. I am unaware of a formal framework to evaluate which variables are most influential, and evaluating all possible combinations was infeasible. Therefore, to reduce the number of variables while maintaining the ability to account for relationships among the explanatory variables I used a Principal Component Analysis (PCA). I identified the correlation between each of the response variables with both the first and second principal component axes. Additionally, I used a broken-stick method to evaluate whether each principal component axis contributed significantly to explaining variation within the data (Legendre and Legendre 2012). This method stems from the concept that the variance within the data can be compared to a stick of unit length. This stick can be broken at random locations along its length for each parameter included in the model. If the fraction of variance explained by the i^{th} eigenvalue is greater than the expected length of the i^{th} longest "piece of the unit stick," then the eigenvalue explains more of the variance than would be expected by random processes (i.e., contributes significantly to explaining variation within the data).

Results

Lake Wilderness had the highest littoral complexity (Table 1), with one shore of the lake being covered in coarse woody debris and natural forest. Pine Lake and Lake Shoecraft had the lowest littoral habitat complexity; both lakes have public access points, many houses, and receive heavy use during the summer. The density of docks was moderately and negatively correlated with riparian complexity, the littoral-riparian complexity metric, and mean summer pelagic chlorophyll-a concentrations, but was less correlated with littoral habitat complexity (Figure 2). Pelagic chlorophyll-a concentration was not correlated with any of the habitat metrics, while area of the lake and docks km^{-1} of lakeshore were slightly positively correlated.

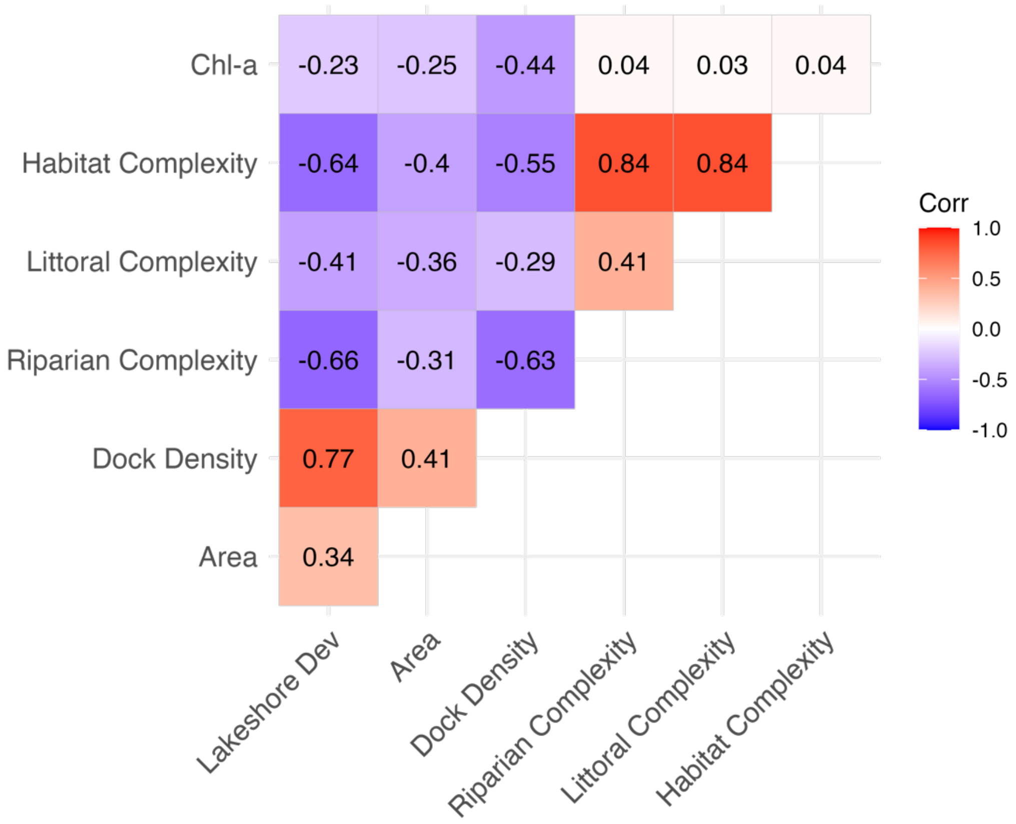

Figure 2: Correlation between variables of interest. The other environmental variables are Lake area (km^2), dock density (km^{-1}), and mean summer pelagic chlorophyll-a concentration (Chl-a μgL^{-1}).

Community Structure:

The EcoDiet food web models estimated diet proportions for all species within the food webs. Fishes had higher $\delta^{15}N$ values than aquatic macroinvertebrates indicating they occupied higher trophic levels (Figure 3). Additionally, in most lakes, zooplankton had lower $\delta^{13}C$ than benthic macroinvertebrates. Aquatic macroinvertebrates covered the span of $\delta^{13}C$ values for consumers in most of the study lakes. However, in Lake Shoecraft it appears that a $\delta^{13}C$ enriched food source is missing for the fish in the lake.

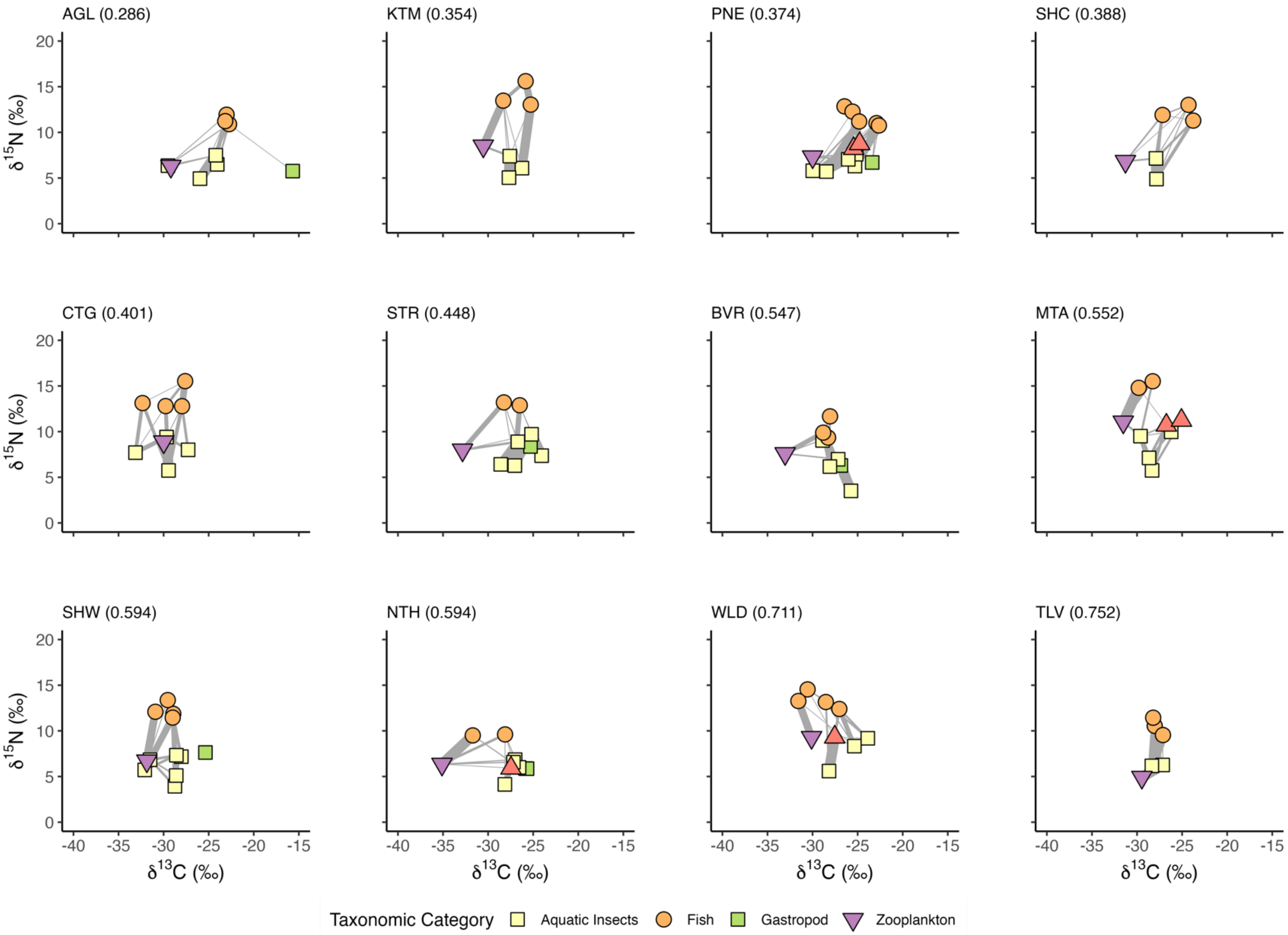

Figure 3: Whole-lake food webs estimated using EcoDiet plotted in stable isotope space. The webs are ordered by combined riparian-littoral habitat complexity, lowest in the upper left corner to highest in the lower right corner. Location of the points corresponds with each taxon's mean stable isotopic values. Shapes and colors of the points indicate major taxonomic groupings for each taxon, while the weight of the lines indicates the mean proportion of diet for each prey item to a given predator. See Table 1 for lake name abbreviations.

Connectance, mean link strength, and mean degree were best explained by an RDA model with the littoral habitat complexity metric (Table 2; Figure 4), which explained 29.2% of the variation in the data. The first axis was described by a combination of littoral habitat complexity (RDA loading = 0.886), lake area (RDA loading = -0.667), and dock density (RDA loading = -0.607). The second axis was driven primarily by pelagic chlorophyll-a concentration (RDA loading = 0.582) and dock density (0.406). However, none of the explanatory variables contributed significantly to explaining the variation in the fitted response matrix.

The response variable for mean link strength was negatively associated with the dock density (Figure 4). Connectance was weakly associated with low littoral complexity and pelagic chlorophyll-a concentration and high dock density and lake area. Mean degree was weakly associated with low pelagic chlorophyll-a concentration and larger lakes. However, the RDA model did not significantly outperform the null model in explaining variation in the fitted response matrix (F = 0.721, p = 0.691). Lake Shoecraft's fitted value was most strongly associated with low pelagic chlorophyll-a concentration and relatively low littoral complexity. Angle Lake's, Beaver Lake's, Wilderness Lake's, and Cottage Lake's fitted values were associated with high pelagic chlorophyll-a and high dock density. Fitted values for Lake Ketchum and Lake Number Twelve were most strongly associated with low dock density and high littoral complexity. Other lakes, such as Star Lake, Angle Lake, and Pine Lake had fitted values most strongly associated with higher dock density and lake area, and low littoral complexity. The fitted value for Martha Lake, however, had intermediate values among all variables.

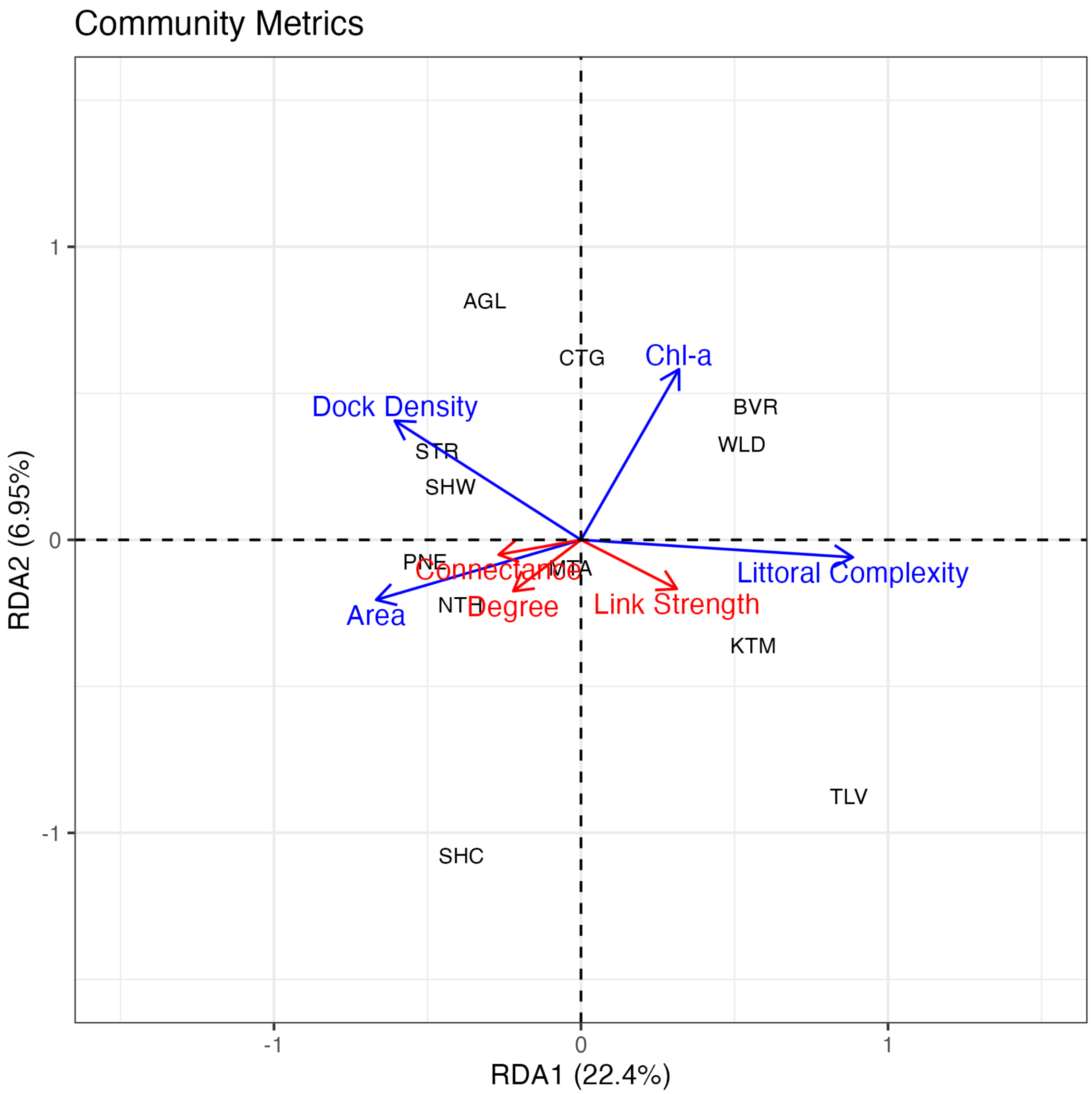

Figure 4: RDA results for community metrics from the best fitting model. Blue lines represent explanatory variable where the length of the line indicates the relative contribution of that variable to explaining variation in the fitted response matrix while the direction of each arrow indicates a positive association with the corresponding explanatory variable. Red arrows represent the weighted response variables for the species-specific network metrics. Length from origin of the biplot indicates the strength of the association with the explanatory variables within the ordination space while angle indicates the directionality of the relationship. Finally, black text indicates the projected lake values for each lake within the study.

Table 2: R^2 and adjusted R^2 for each RDA model of community network metrics, yellow perch species-specific metrics, and pumpkinseed species-specific metrics for the different models including each of the habitat complexity covariates.

Habitat Complexity Variable	Community		Yellow Perch		Pumpkinseed	
	R^2	Adjusted R^2	R^2	Adjusted R^2	R^2	Adjusted R^2
Combined Littoral-Riparian	0.259	-0.165	0.551	0.192	0.543	0.282
Littoral	0.291	-0.113	0.691	0.443	0.521	0.246
Riparian	0.209	-0.243	0.410	-0.062	0.549	0.291

When evaluating the relationships between the community wide network metrics and environmental variables individually, mean degree varied the most across lakes. Mean degree was positively correlated with the number of nodes and lake area, and negatively correlated with littoral habitat complexity and pelagic chlorophyll-a concentration (Figure 5); however, these results were not significant (Table A9). Additionally, connectance was positively correlated with lake area, but this correlation was not significant (Figure 6; Table A9). Mean link strength was relatively consistent across the environmental variables but did exhibit a slight positive correlation with the three habitat complexity measures and a negative correlation with the number of taxa (Figure 7). Again, these relationships were nonsignificant (Table A9).

Examining the distribution of both degree and mean link strength across lakes did not reveal any further patterns. Lakes such as Wilderness (WLD) and Beaver (BVR) have relatively narrow degree distributions, with many species having a medium number of connections (Figure A4). Conversely, North Lake (NTH) and Pine Lake (PNE) have wide distributions. There is no consistent pattern, however, as littoral complexity increases. Many lakes had a several species with very few links and then an almost uniform distribution of stronger links (proportion > 0.25); for example, Lake Number Twelve (Figure A3). Other distributions, especially Shadow Lake (SHW) and Pine Lake (PNE), were less variable and mostly weak links. Shadow Lake (SHW) and Pine Lake (PNE) have the two largest food webs and Lake Number Twelve (TLV) has the smallest. This pattern is consistent with the observed negative correlation between mean link strength and the number of taxa within the food web.

When accounting for variation in the diet proportions estimated by EcoDiet, connectance exhibited a large amount of uncertainty (Figure 8). Lakes with smaller food webs, such as Lake Shoecraft and Lake Number Twelve exhibited greater variation in connectance than lakes with larger food webs such as Pine Lake (Figure 8). Furthermore, there is significant overlap in the connectance distributions and median connectance is relatively similar across all lakes.

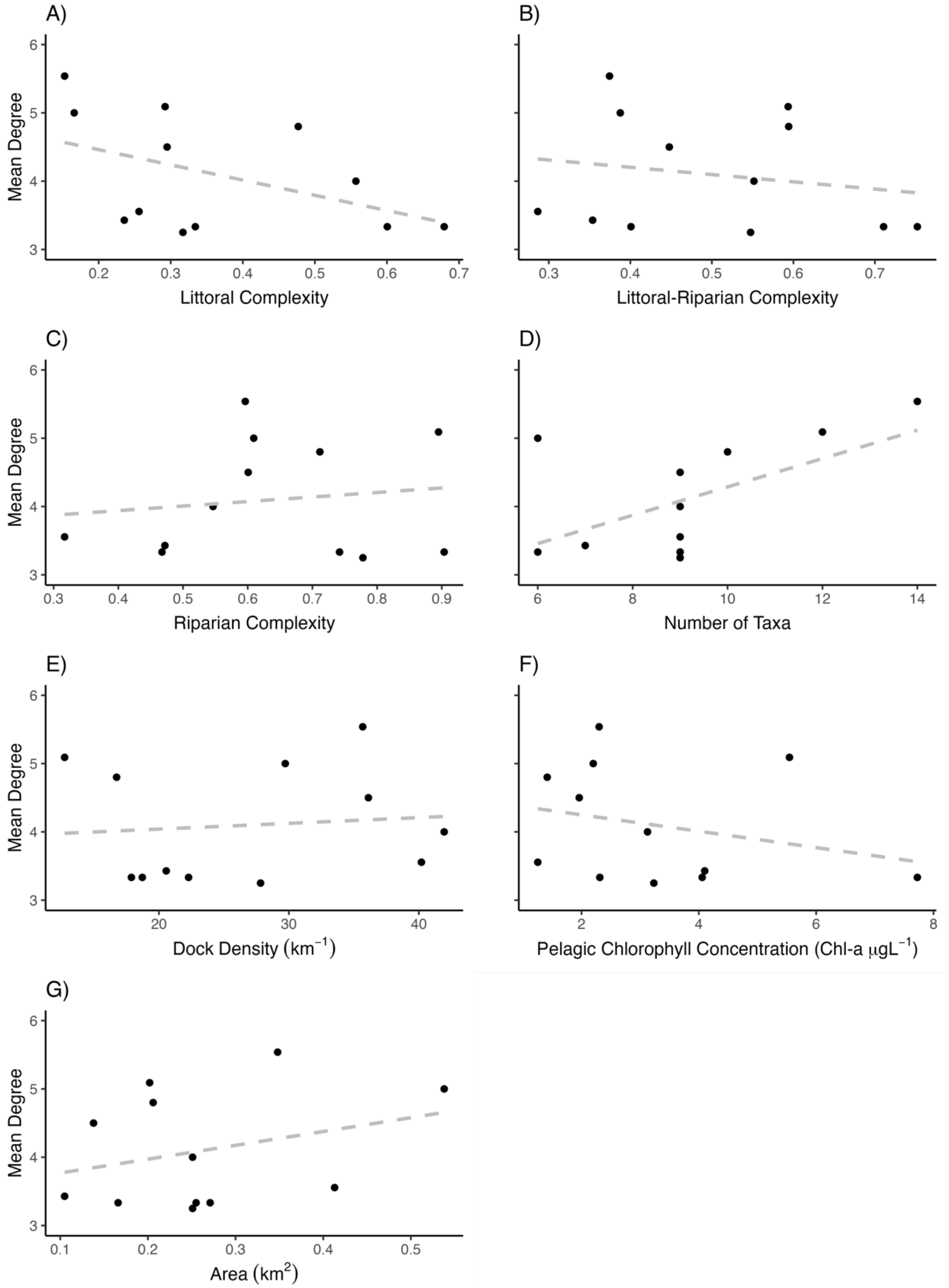

Figure 5: Bivariate regressions for mean degree within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density, F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area. The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

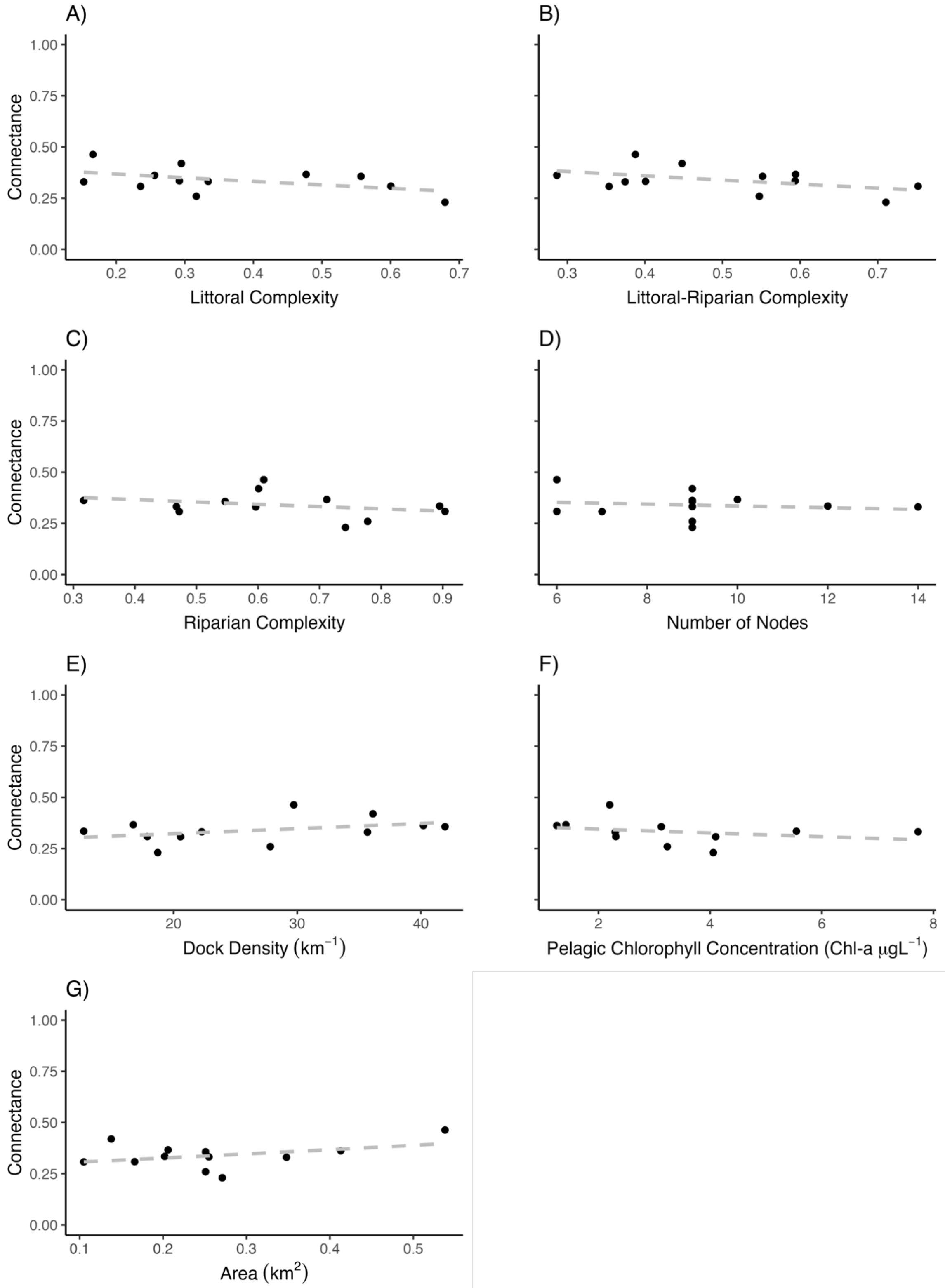

Figure 6: Bivariate regressions for weighted connectance within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density, F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area. The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

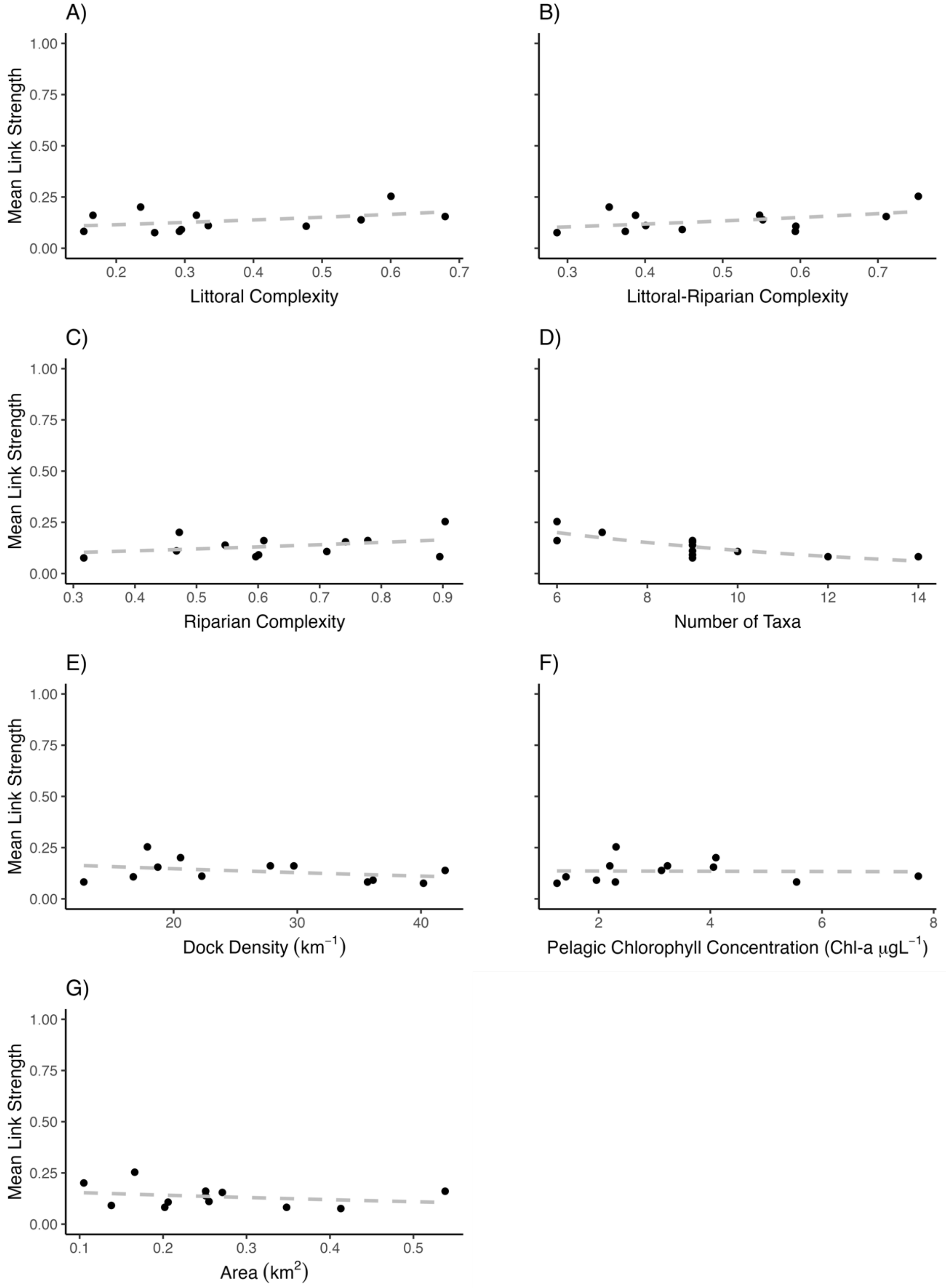

Figure 7: Bivariate regressions for mean link strength within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density, F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area. The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

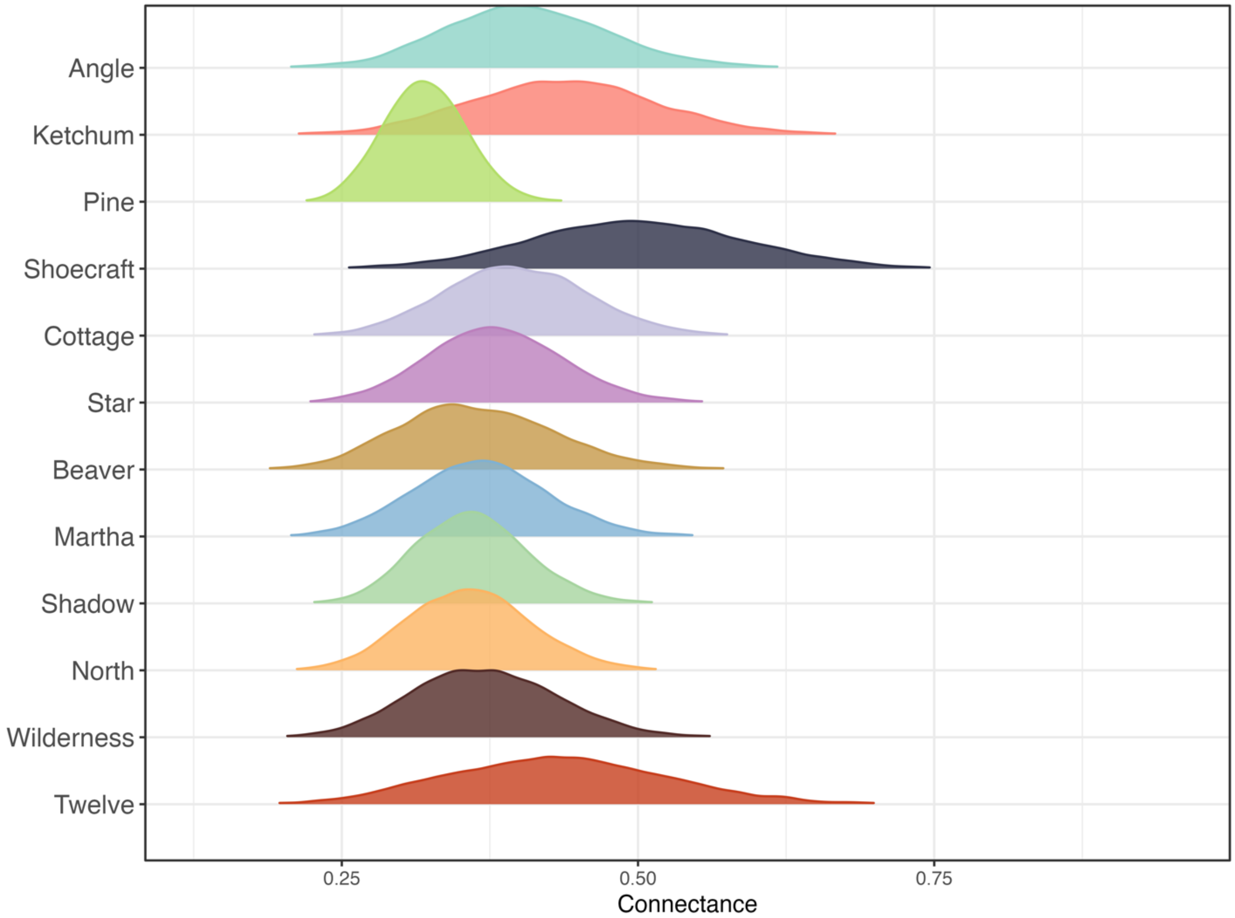

Figure 8: Connectance bootstrap distribution for each lake. Lakes are ordered by combined habitat complexity metric so that the most developed lake is at the top and the least is at the bottom.

Species-Specific Network Metrics:

The Lakes with yellow perch were spread relatively evenly throughout the explanatory variable space (Figure 9). The fitted values of two lakes (Shadow Lake and Lake Ketchum) were most strongly associated with high pelagic chlorophyll-a concentration and low dock density. Lake Martha’s, North Lake’s, and Wilderness Lake’s fitted values were most strongly associated with high littoral complexity. Additionally, there was a group of three lakes (Pine, Cottage, and Angle) whose fitted values were positively correlated with both lake area and dock density. The fitted values for the remaining two lakes, Lake Shoecraft and Beaver Lake, were negatively associated with littoral complexity.

Visual examination of the RDA reveals some associations among network metrics and explanatory variables (Figure 9), but few of these associations were significant. The model that had the highest adjusted R^2 value (0.444) for yellow perch included littoral complexity as the habitat variable (Figure 9; Table 2), and explained 69.1% of the variation in the response matrix. Additionally, the model performed significantly better at explaining the variation in the response matrix than a null model ($F = 2.79$, $p = 0.038$). The primary canonical axis explained 51.08% of the constrained variation. The loadings for the axis demonstrated that littoral complexity was the primary explanatory variable contributing to the first canonical axis (RDA loading = 0.863) followed by lake area (RDA loading = -0.463). Both explanatory variables contributed significantly to explaining variation in the response matrix (littoral complexity, $F = 4.994$, $p = 0.019$; lake area, $F = 3.337$, $p = 0.049$). Variation along the secondary canonical axis primarily driven by dock density (RDA loading = 0.863), lake area (RDA loading = 0.752), and pelagic chlorophyll-a concentration (RDA loading = -0.414). When considering all explanatory and response variables using RDA, zooplanktivory was strongly associated with littoral habitat complexity. Additionally, diet breadth and diet evenness were negatively correlated with littoral complexity, though to a lesser extent. Finally, centrality was positively correlated with pelagic chlorophyll-a concentration and low dock density (Figure 9).

Examining relationships between individual explanatory variables also revealed that yellow perch diet breadth was significantly and negatively correlated with littoral complexity (Figure 10A; $p = 0.002$). However, diet breadth was not significantly correlated with any of the other environmental variables after performing a Bonferoni correction for multiple comparisons (Figure 10; Table A6). Diet evenness exhibited similar associations to diet breadth (Figure 10), suggesting that diet evenness was negatively associated with littoral complexity but not strongly associated with any of the other environmental variables. However, the correlation between diet evenness and littoral complexity was insignificant (Figure 11A; Table A7). The other environmental variables were not significantly correlated with diet evenness when compared individually (Figure 11B - G; Table A7).

Yellow perch zooplanktivory was positively associated with littoral complexity (Figure 9). However, the individual correlation between zooplanktivory and littoral complexity was insignificant (Table A10). Yellow perch zooplanktivory was also positively correlated with riparian complexity and combined-riparian habitat, but these correlations were insignificant (Figure 12B and C; Table A10). Yellow perch zooplanktivory varied at low levels of pelagic chlorophyll-a concentration, but they had minimal reliance on zooplankton at higher levels of chlorophyll-a concentrations (Figure 12F). Meanwhile, perch reliance on zooplankton showed little correlation with dock density (Figure 12E).

Yellow perch centrality was positively associated with high pelagic chlorophyll-a concentration, but weakly associated with all other environmental variables (Figure 9). Additionally, there was a positive correlation between yellow perch centrality and pelagic chlorophyll-a concentration in all lakes except for Cottage Lake (Figure 13E). Cottage Lake had the highest pelagic chlorophyll-a concentration of the lakes I sampled, but yellow perch centrality was 0. While the correlation was not significant (Table A8), this was likely influenced by Cottage Lake as this observation had a high hat-value and Cook’s distance and removing Cottage Lake significantly decreased the p-value (p = 0.008). None of the other environmental variables were significantly correlated with centrality (Table A8).

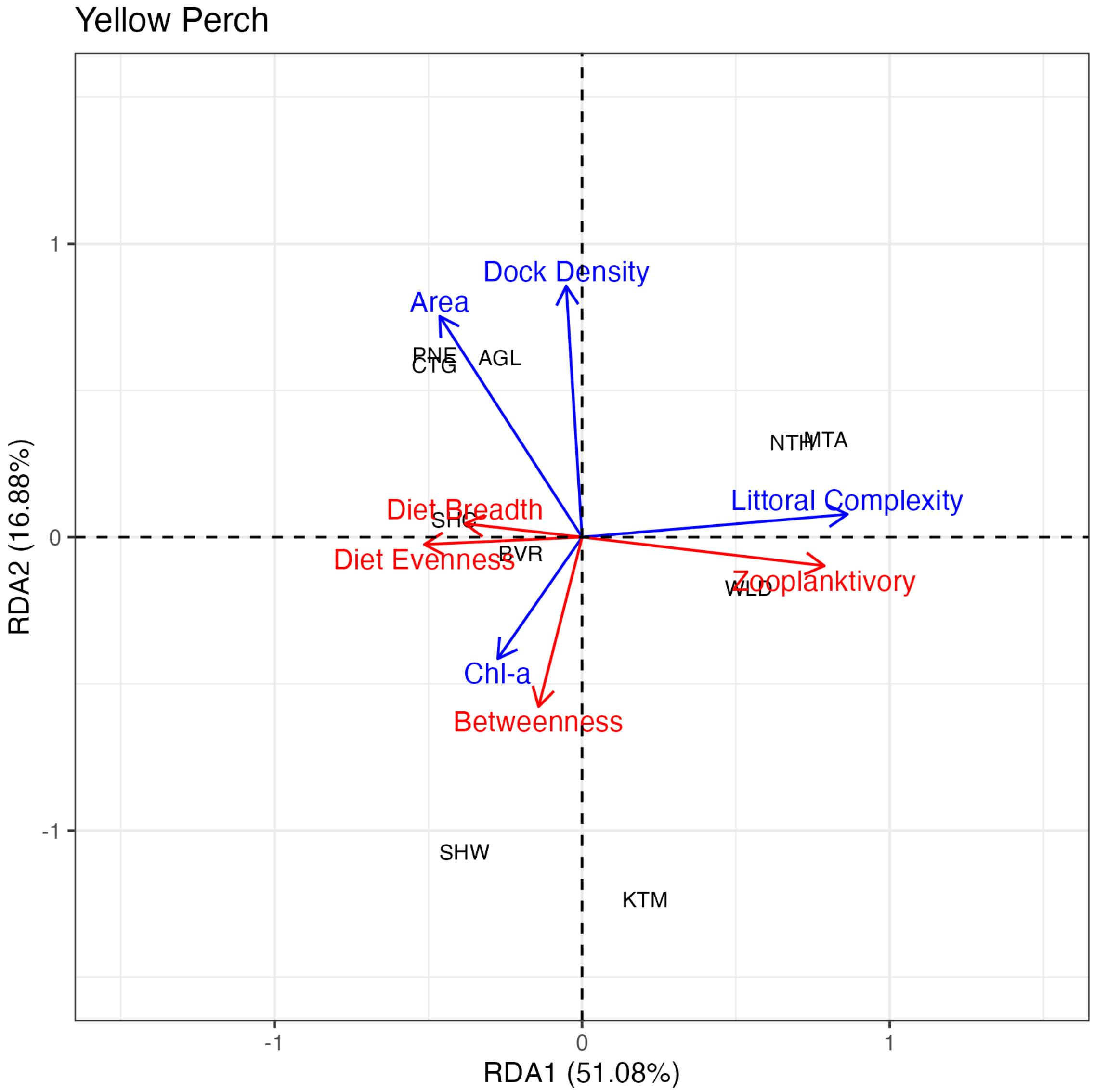

Figure 9: RDA results for yellow perch from the best fitting model. Blue lines represent explanatory variable where the length of the line indicates the relative contribution of that variable to explaining variation in the fitted response matrix while the direction of each arrow indicates a positive association with the corresponding explanatory variable. Red arrows represent the weighted response variables for the species-specific network metrics. Length from origin of the biplot indicates the strength of the association with the explanatory variables within the ordination space while angle indicates the directionality of the relationship. Finally, black text indicates the projected lake values for lakes containing yellow perch within the study.

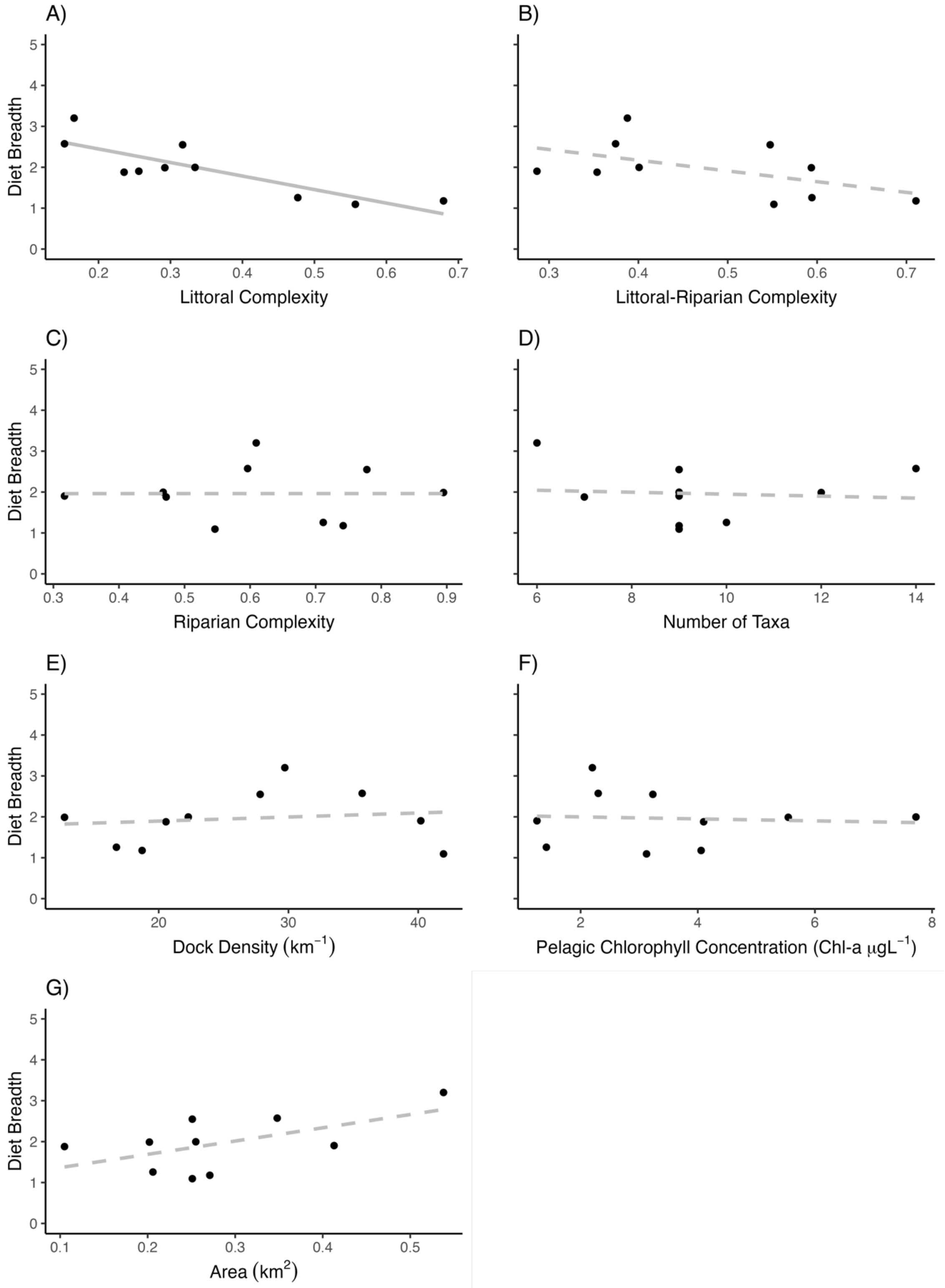

Figure 10: Bivariate regressions for yellow perch diet breadth within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (µgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

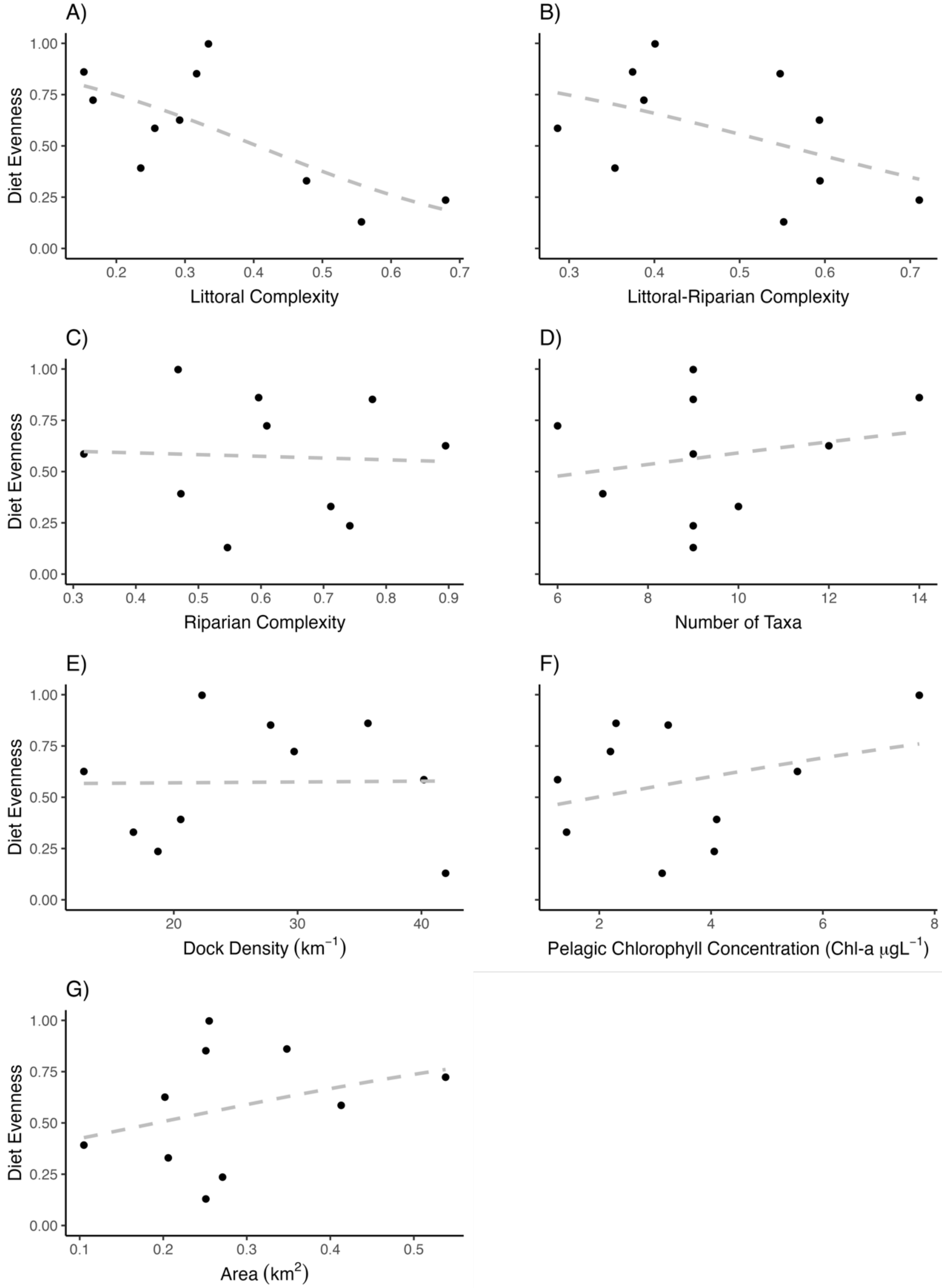

Figure 11: Bivariate regressions for yellow perch diet evenness within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

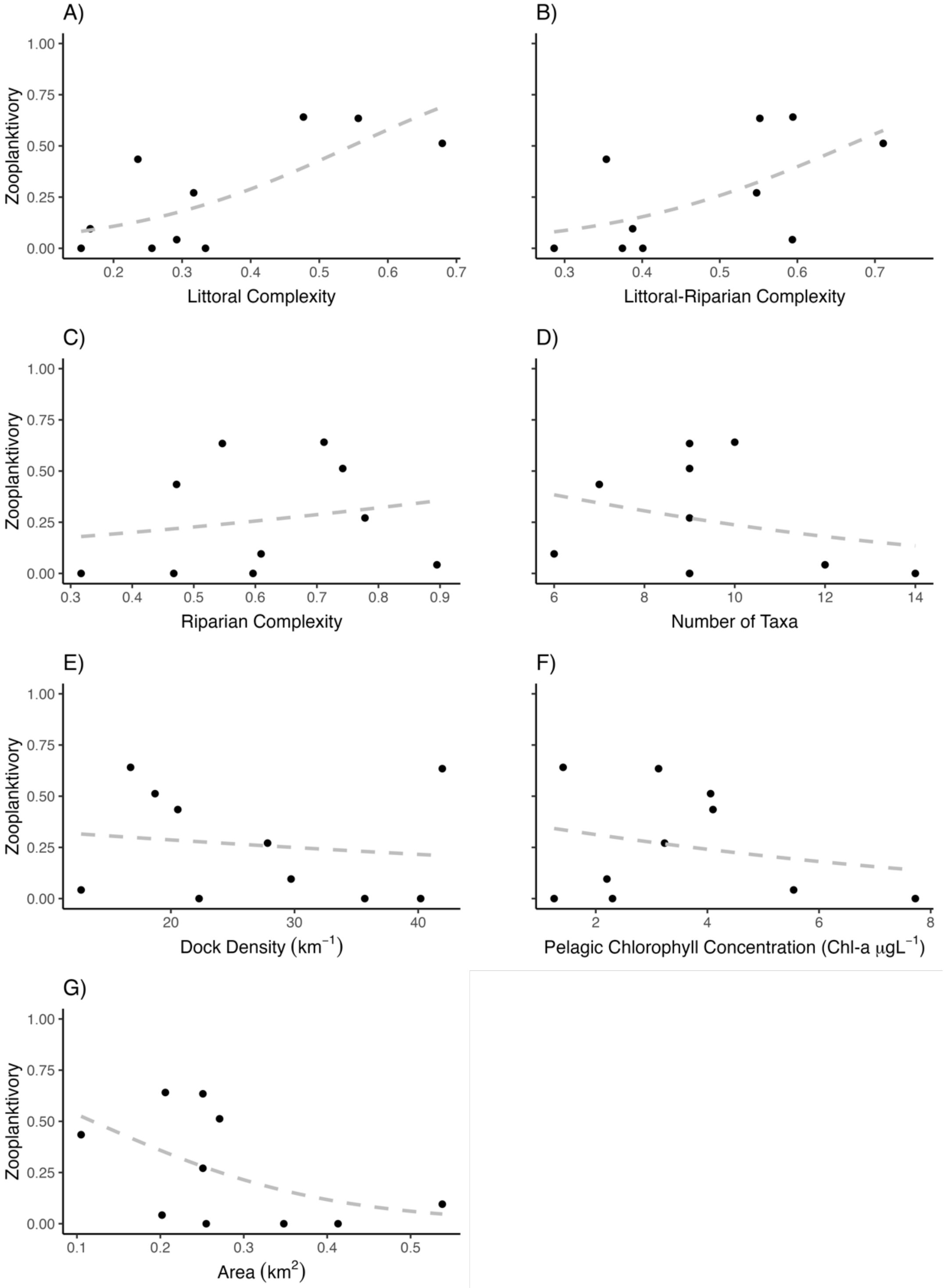

Figure 12: Estimated median diet proportion of zooplankton in yellow perch diets compared to: A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

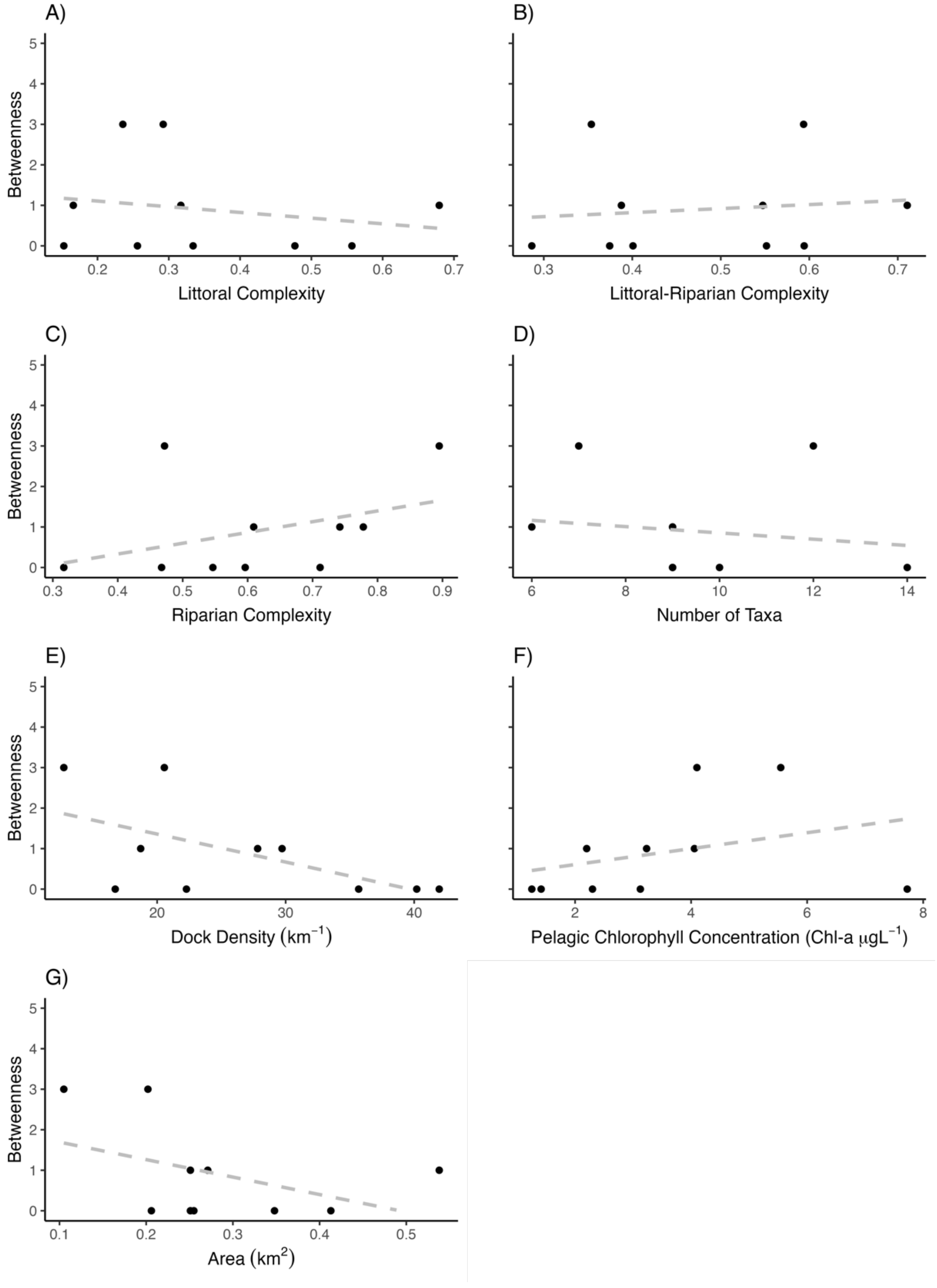

Figure 13: Bivariate negative binomial regressions for yellow perch betweenness centrality within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships after conducting a Bonferroni correction. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

The fitted values for the lakes with pumpkinseed differed slightly because the best fitting model included riparian habitat complexity rather than littoral habitat complexity (Table 2; Figure 14). Fitted values for Lake Ketchum and Lake Number Twelve were strongly and positively correlated with riparian complexity, and negatively correlated with lake area. North Lake's, Pine Lake's, and Star Lake's fitted values were positively correlated with riparian complexity and negatively correlated with pelagic chlorophyll-a concentration. Additionally, fitted values for Angle Lake, Lake Wilderness, Shadow Lake, and Martha Lake were all positively correlated with dock density and lake area, but had varying levels of riparian habitat complexity and pelagic chlorophyll-a concentration. Cottage Lake's fitted value was positively correlated with pelagic chlorophyll-a concentration and lake area, and negatively correlated with riparian complexity and dock density. Finally, fitted values for Beaver Lake and Lake Shoecraft were associated with moderate pelagic chlorophyll-a concentrations and low levels of riparian complexity.

The RDA model of best fit for Pumpkinseed explained 54.9% of the variance in the response matrix (Figure 14). However, the model did not perform better than the null model ($F = 2.131$, $p = 0.066$). The primary canonical axis was strongly associated with pelagic chlorophyll-a concentration (RDA loading = -0.610), lake area (RDA loading = -0.556), and riparian habitat complexity (RDA loading = 0.486). While a combination of dock density (RDA loading = 0.657), lake area (RDA loading = 0.632), and pelagic chlorophyll-a concentration (RDA loading = -0.429) contributed to explaining variation along the secondary canonical axis. None of the explanatory variables, however, contributed significantly to explaining the variation in the response matrix. Pumpkinseed diet breadth was positively correlated with lake area and negatively correlated with riparian complexity, though only weakly (Figure 14). Diet evenness was more strongly correlated with lake area and negatively correlated with riparian complexity. Similar to yellow perch, pumpkinseed centrality was positively correlated with pelagic chlorophyll-a concentration and was negatively correlated with riparian habitat complexity (Figure 14).

Comparisons between individual explanatory variables and pumpkinseed network metrics were similar to those observed in the RDA. Pumpkinseed diet breadth and diet evenness were positively associated, though weakly, with lake area and dock density (Figure 15E&F; Figure 16E & F). None of the individual correlations, however, were significant (Table A6). Additionally, pumpkinseed diet breadth exhibited very weak and insignificant correlations with all three habitat complexity metrics and pelagic chlorophyll-a concentration (Figure 15A, B, C, & E; Table A6). Diet evenness was also weakly but positively correlated with the number of taxa within the food web. However, there was little correlation between diet evenness and habitat complexity or pelagic chlorophyll-a concentration (Figure 16A, B, C, & E; Table A7).

Pumpkinseed centrality was strongly and positively associated with pelagic chlorophyll-a concentrations (Figure 17). The individual relationship, however, was not significant after correcting for multiple comparisons ($p = 0.021$; Table A8). This correlation may be driven by Cottage Lake which has both high production and high pumpkinseed centrality, resulting in a high Cook's distance. Furthermore, removing Cottage Lake increased the p-value significantly ($p = 0.826$). However, there is no obvious ecological reason to remove Cottage Lake from these analyses. Pumpkinseed centrality exhibited a weak positive association with lake area as well, though this correlation was insignificant (Figure 17E; Table A8). The other environmental variables showed little correlation with pumpkinseed centrality (Figure 17) and none of the relationships were significant (Figure 17A – E & G; Table A8).

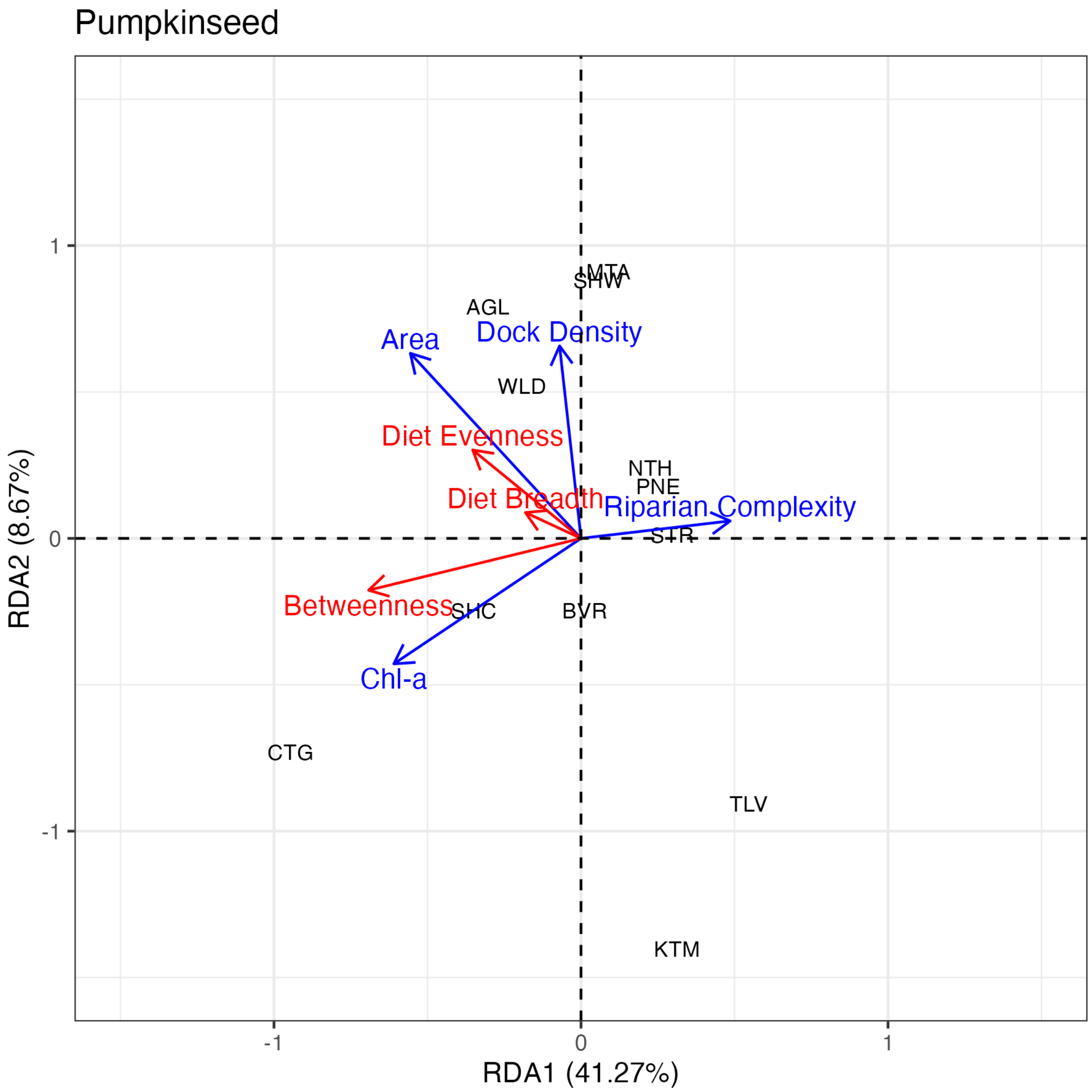

Figure 14: RDA results for pumpkinseed from the best fitting model. Blue lines represent explanatory variable where the length of the line indicates the relative contribution of that variable to explaining variation in the fitted response matrix while the direction of each arrow indicates a positive association with the corresponding explanatory variable. Red arrows represent the weighted response variables for the species-specific network metrics. Length from origin of the biplot indicates the strength of the association with the explanatory variables within the ordination space while angle indicates the directionality of the relationship. Finally, black text indicate the projected lake values for lakes containing pumpkinseed in the explanatory variable space.

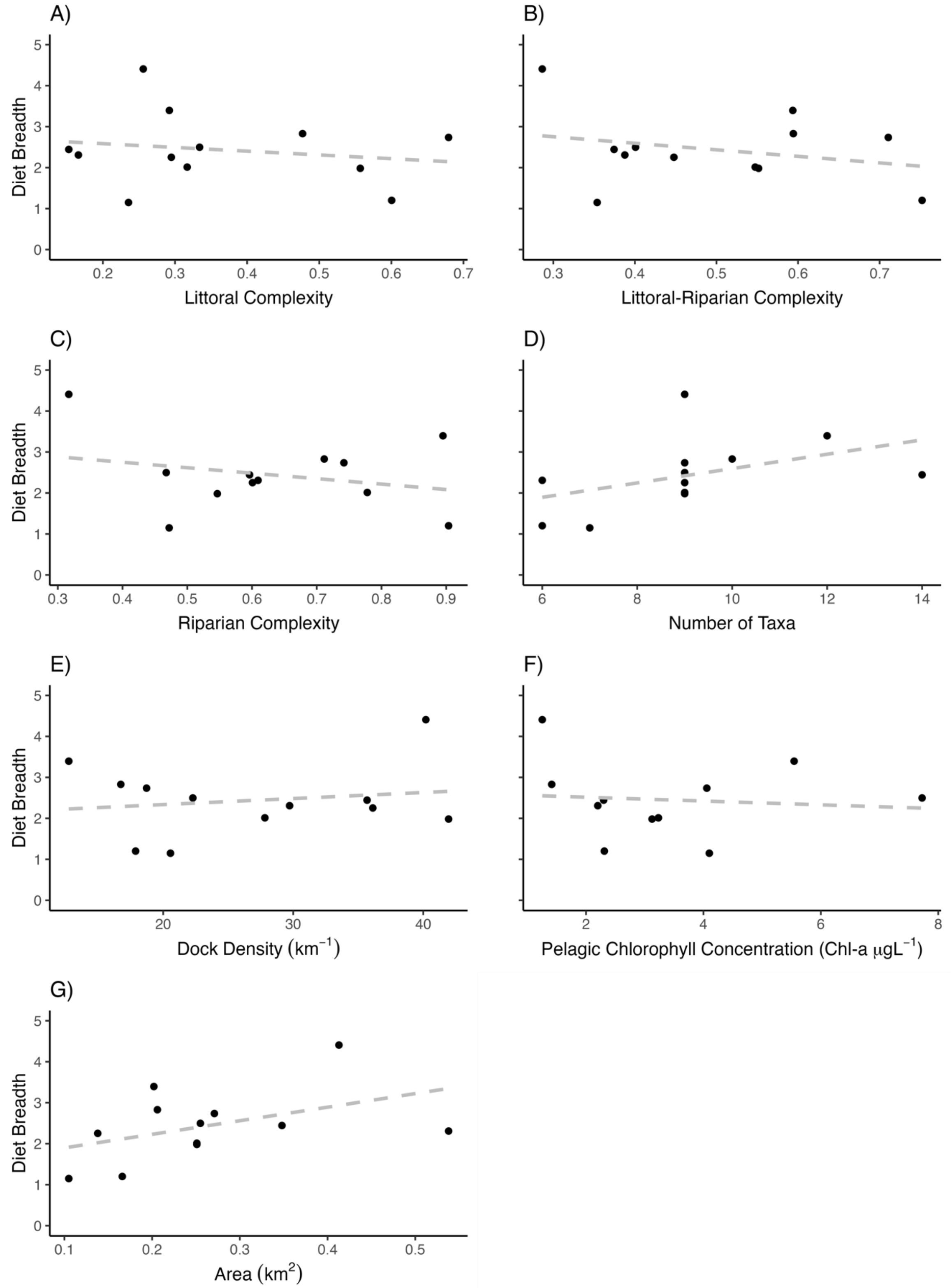

Figure 15: Bivariate regressions for pumpkinseed diet breadth within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships after conducting a Bonferroni correction. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

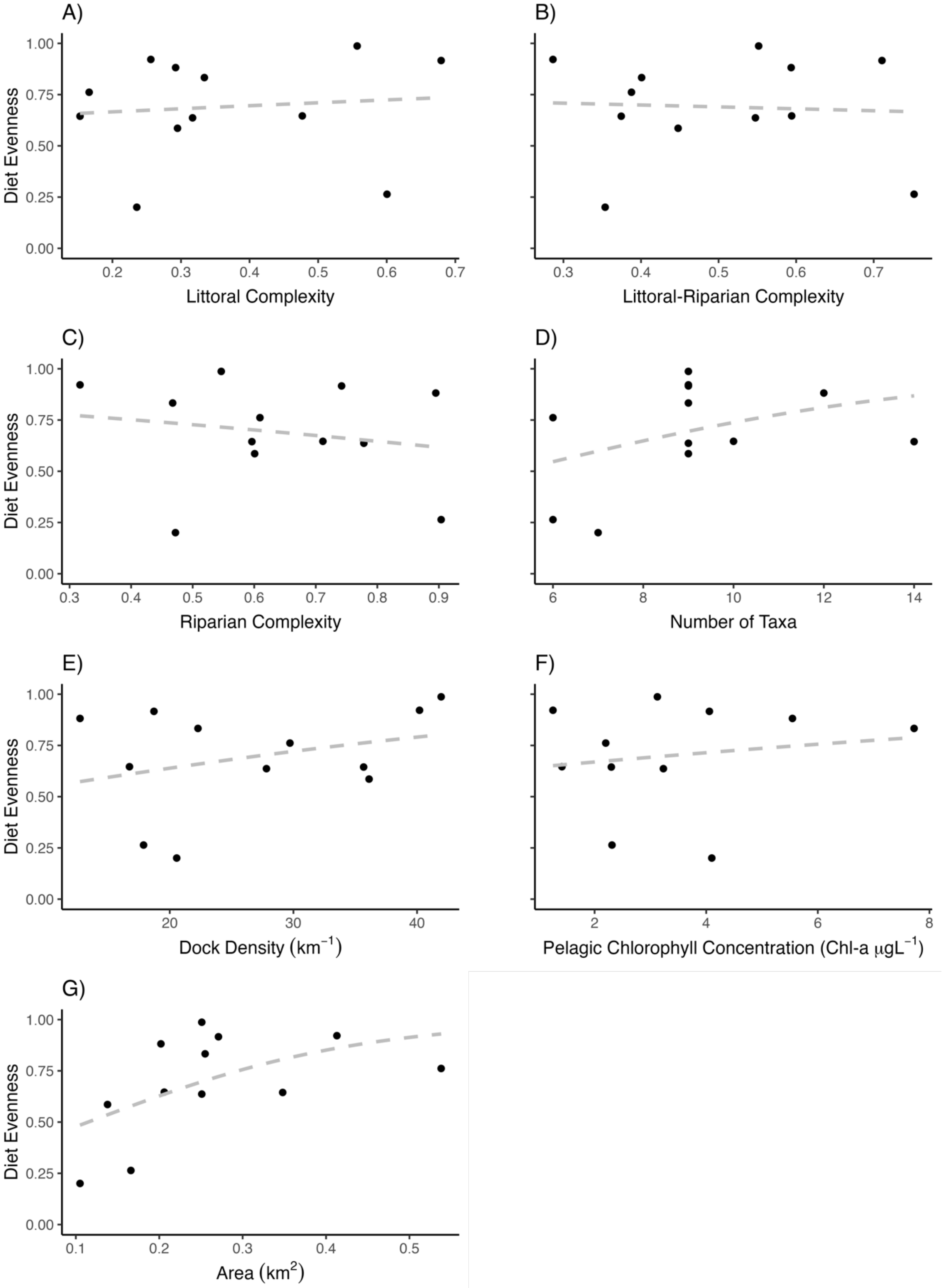

Figure 16: Bivariate logistic regression models for pumpkinseed diet evenness within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships after conducting a Bonferroni correction. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

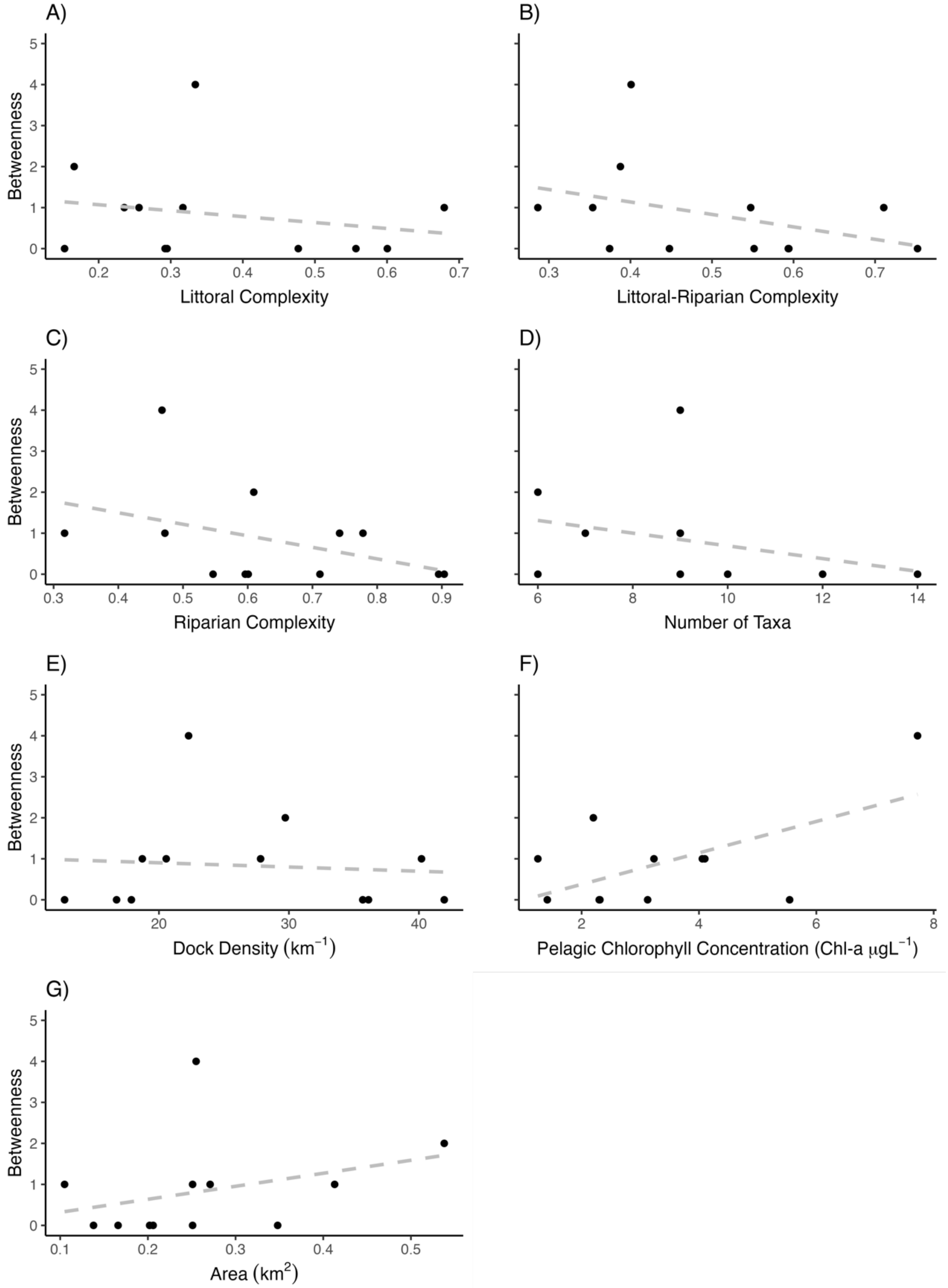

Figure 17: Bivariate negative binomial regression models for pumpkinseed betweenness centrality within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships after conducting a Bonferroni correction. The habitat complexity metrics (A – C) potentially range from 0 – 1, but only the measured complexity values are shown in the figure.

Largemouth bass were much more difficult to capture than yellow perch and pumpkinseed, so there were only six lakes with enough largemouth bass to analyze. Therefore, there were not enough observations to perform the RDA as for the other species. Instead, I used PCA on the explanatory variables to evaluate the correlation among each network metric for largemouth bass and each principal component axis. Visual examination of the ordination biplot illustrated that the habitat complexity measures and dock density were negatively correlated with one another along the first principal component axis, though this relationship is imperfect. Combined habitat complexity explained the most variation in the explanatory variables along the first component axis, followed by riparian complexity and dock density. Lakes with high PC1 values (to the right of the graph) were associated with more complex habitats and fewer docks, i.e. are less developed. I will subsequently refer to this axis as the lakeshore development axis. The secondary axis was primarily driven by pelagic chlorophyll-a concentration. The lakeshore development axis explained 53.5% of the variation within lakes and significantly contributed to explaining variation in the explanatory variables when compared to expected contribution from a broken stick model (Figure 18). The secondary axis, however, did not explain more variation in the data than would be expected by a broken stick model (Figure A5).

Examining largemouth bass response to the two principal component axes revealed that largemouth bass diet breadth was positively correlated with the first component axis, but not the second (Figure 19 A and B). Despite the strong correlation between largemouth bass diet breadth and the first component axis, the individual comparisons revealed only weak positive correlations between diet breadth and the three habitat complexity metrics and the number of taxa within the food web (Figure 20A, B, C). Meanwhile, dock density and pelagic chlorophyll-a concentration were weakly and negatively correlated with largemouth bass diet breadth (Figure 20E & F). None of the individual comparisons between largemouth bass diet breadth and the environmental variables were statistically significant (Table A6). These results suggest that while individual variables are only weakly correlated with largemouth bass diet breadth, the combination of increased littoral and riparian habitat complexity and decreasing dock density and lake area are correlated with higher diet breadth.

Largemouth bass diet evenness was consistently high across lakes and was not strongly correlated with the environmental variables. Diet evenness was only weakly correlated with both the first component axis and the secondary component axis (Figure 19C & D). Furthermore, diet evenness was weakly correlated with all habitat variables individually (Figure 21) and none were significant (Table A7). As a top predator in the system, largemouth bass only had a centrality greater than zero in one lake. This is to be expected as it would be rare for these piscivores to lie on the shortest path between two other taxa. Therefore, I did not evaluate patterns in largemouth bass centrality.

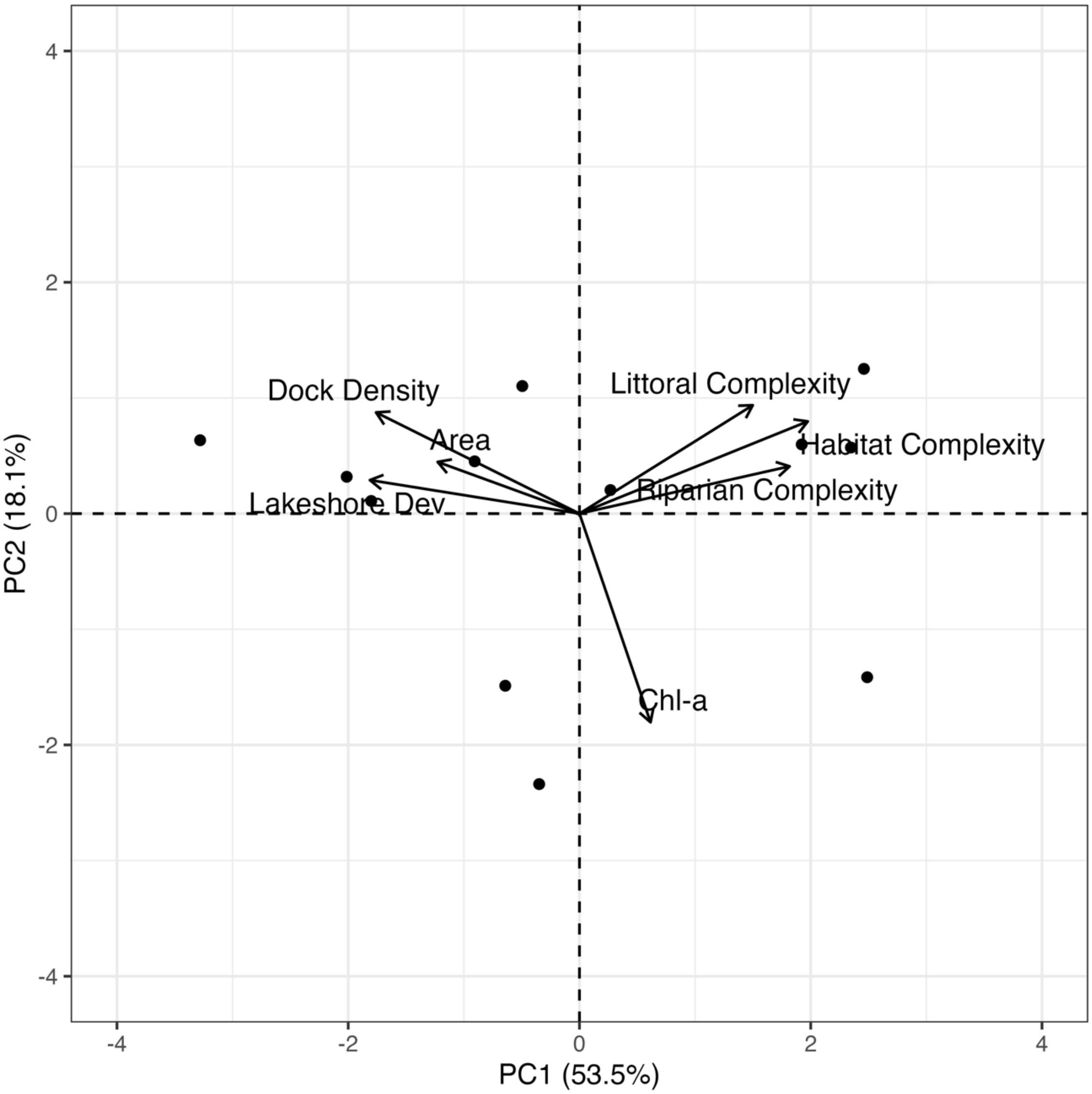

Figure 18: Ordination biplot plot with arrow magnitude indicating relative contribution to the variation in the data for each independent variable. The directionality of the arrow demonstrates an increase in the given variable. Chlorophyll-a concentration is measured in (Chl-a μgL^{-1}), Habitat complexity represents combined littoral and riparian habitat complexity (dimensionless), Area is lake area in km^2, and Dock Density is the number of docks km^{-1}. Points indicate to lakes in this system in relation to the explanatory variables.

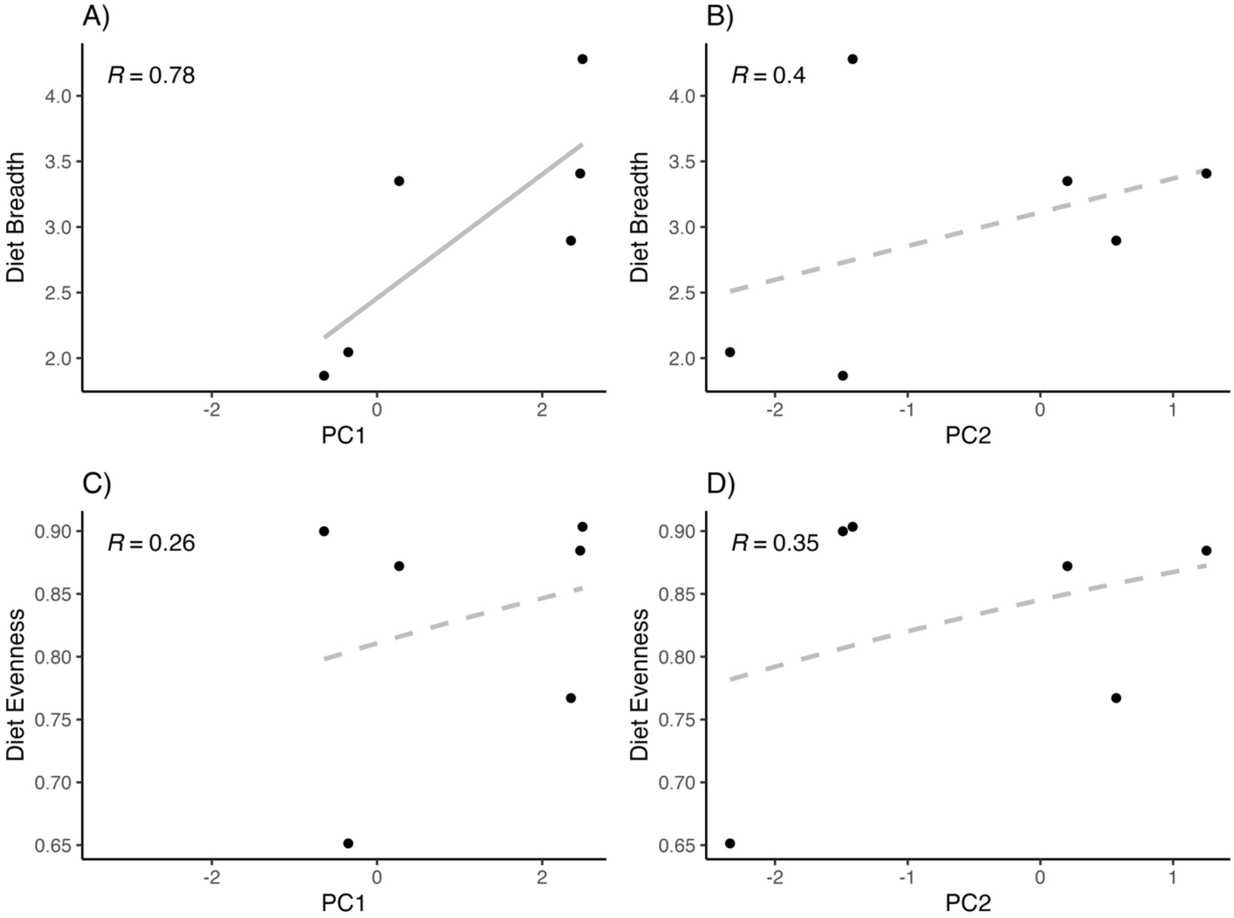

Figure 19: Comparison of largemouth bass network metrics and the first two axes from the PCA. R indicates Pearson's correlation coefficients. The solid line indicates relatively strong correlations (R > 0.5) while dashed lines indicate weak or moderate correlations (R < 0.5). The top row compares diet breadth to component 1 (A) and component 2 (B). The bottom row compares diet evenness to component 1 (C) and component 2 (D).

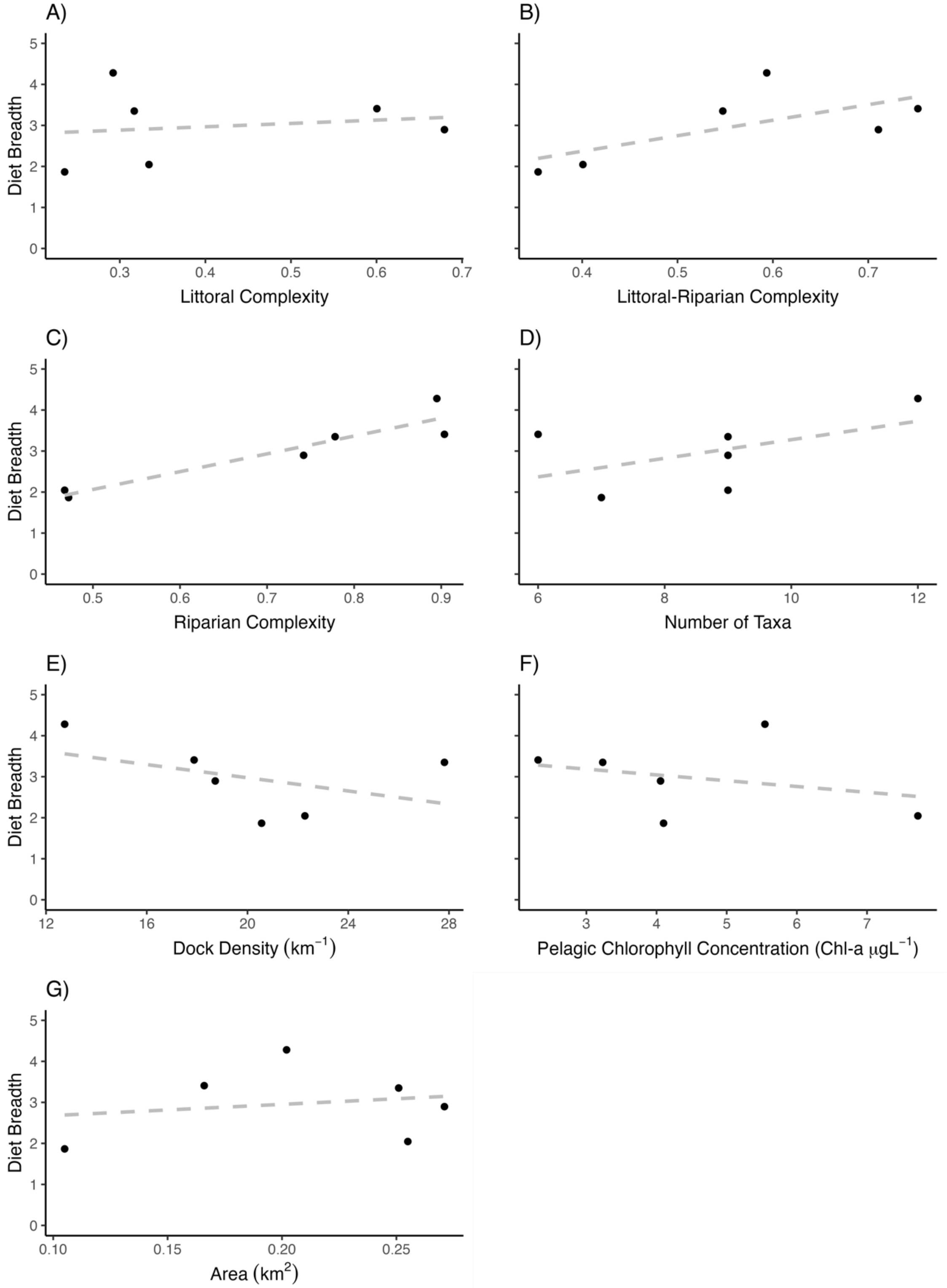

Figure 20: Bivariate linear regressions for largemouth bass diet breadth within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

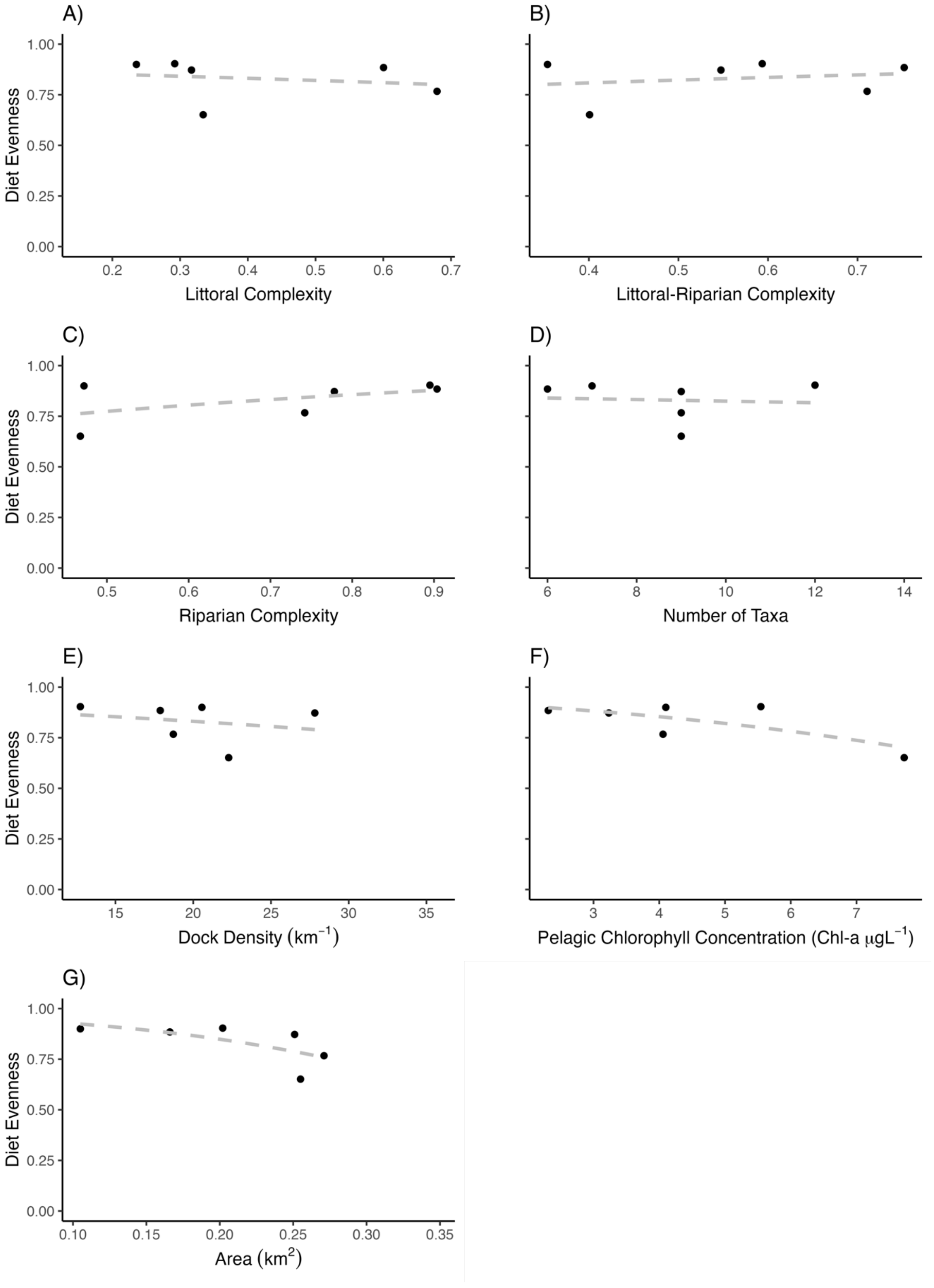

Figure 21: Bivariate logistic regressions for largemouth bass diet evenness within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

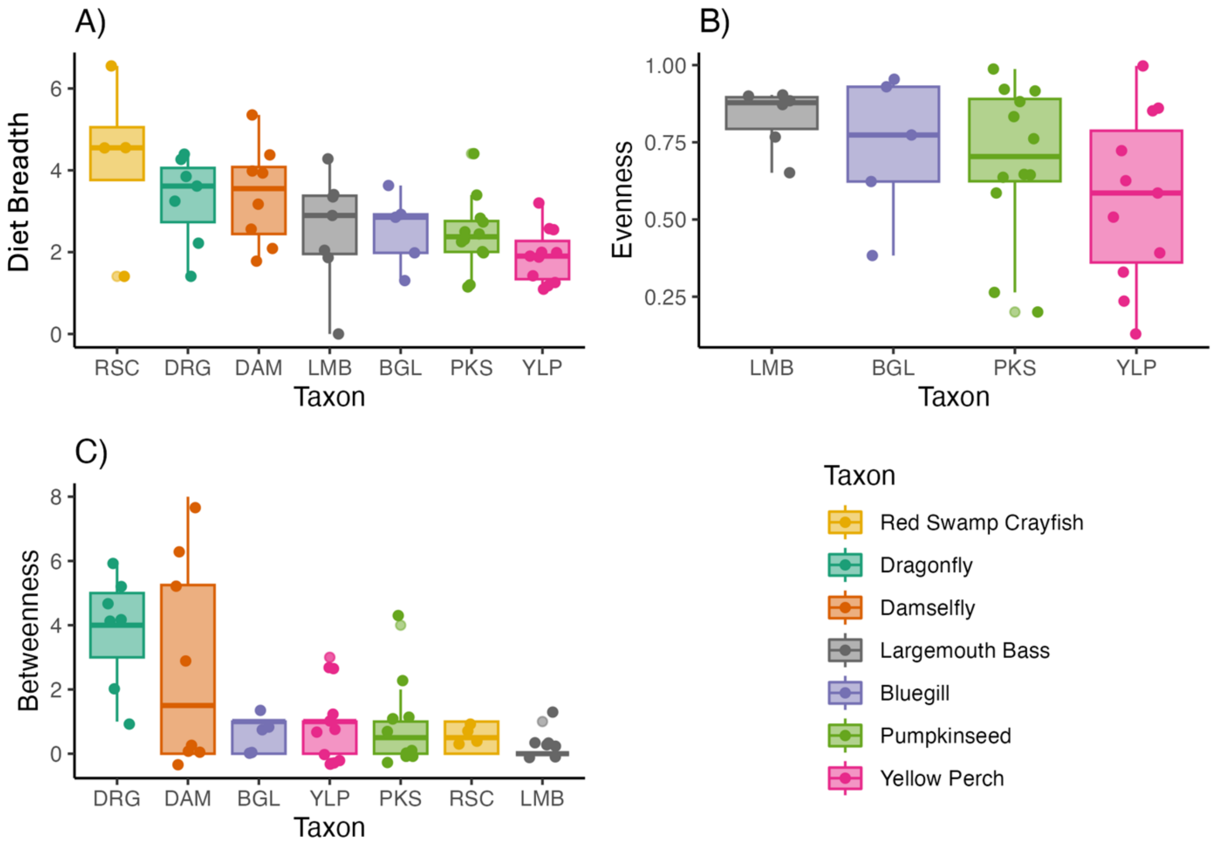

Figure 22: Boxplots for network metrics of common taxa. Points indicate observed data with added jitter to avoid overlap of similar values. Color indicates taxon. A) Diet breadth for each predatory taxon. B) Diet evenness of the four common fish species. C) Species-specific betweenness centrality. See table 2 for species abbreviations.

Predacious macroinvertebrate diets were only weakly correlated with the environmental variables measured in this study. Damselflies and dragonflies both exhibited wider diet breadth than the fish in the study lakes (Figure 22A). Additionally, both the damselflies and dragonflies had higher centrality values than the fish in these systems, while red swamp crayfish had centrality values similar to fish (Figure 22C). Damselfly diet breadth was strongly and negatively correlated with principal component 2, but not principal component 1 (Figure 23A & B). Diet evenness was positively correlated with principal component 1 and negatively correlated with principal component 2, though, only moderately (Figure 23C & D). Centrality was not strongly correlated with either principal component (Figure 23E & F). Dragonfly diet breadth and diet evenness were only weakly and positively correlated with both principal components (Figure 24A – D). Centrality, however, was weakly and negatively correlated with both principal component 1 and principal component 2 (Figure 24E & F). Additionally, neither damselfly nor dragonfly diet breadth was significantly correlated with any of the individual explanatory variables (Figure 25, Figure 26, Table A6). Furthermore, there were no significant associations between diet evenness and the individual explanatory variables (Figure 27, Figure 28, Table A7), nor between centrality and the individual explanatory variables (Figure 29, Figure 30, Table A8).

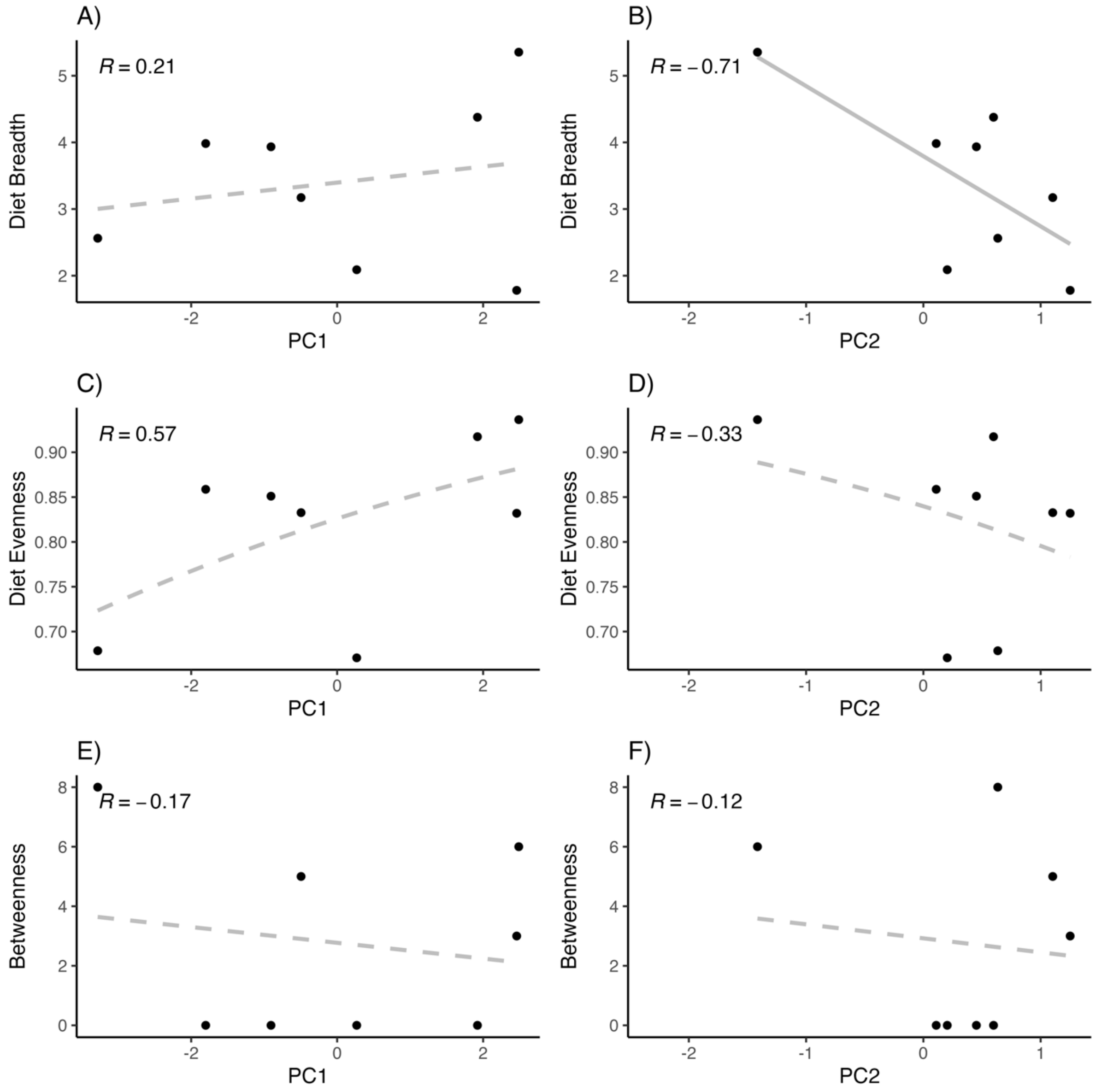

Figure 23: Comparison of damselfly network metrics and the first two axes from the PCA. R indicates Pearson's correlation coefficients. Solid lines indicate relatively strong correlations (R > 0.5) while dashed lines indicate weak or moderate correlations (|R| < 0.5). The top row compares diet breadth to component 1 (A) and component 2 (B). The middle row compares diet evenness to component 1 (C) and component 2 (D). The bottom row compares betweenness centrality to component 1 (E) and component 2 (F).

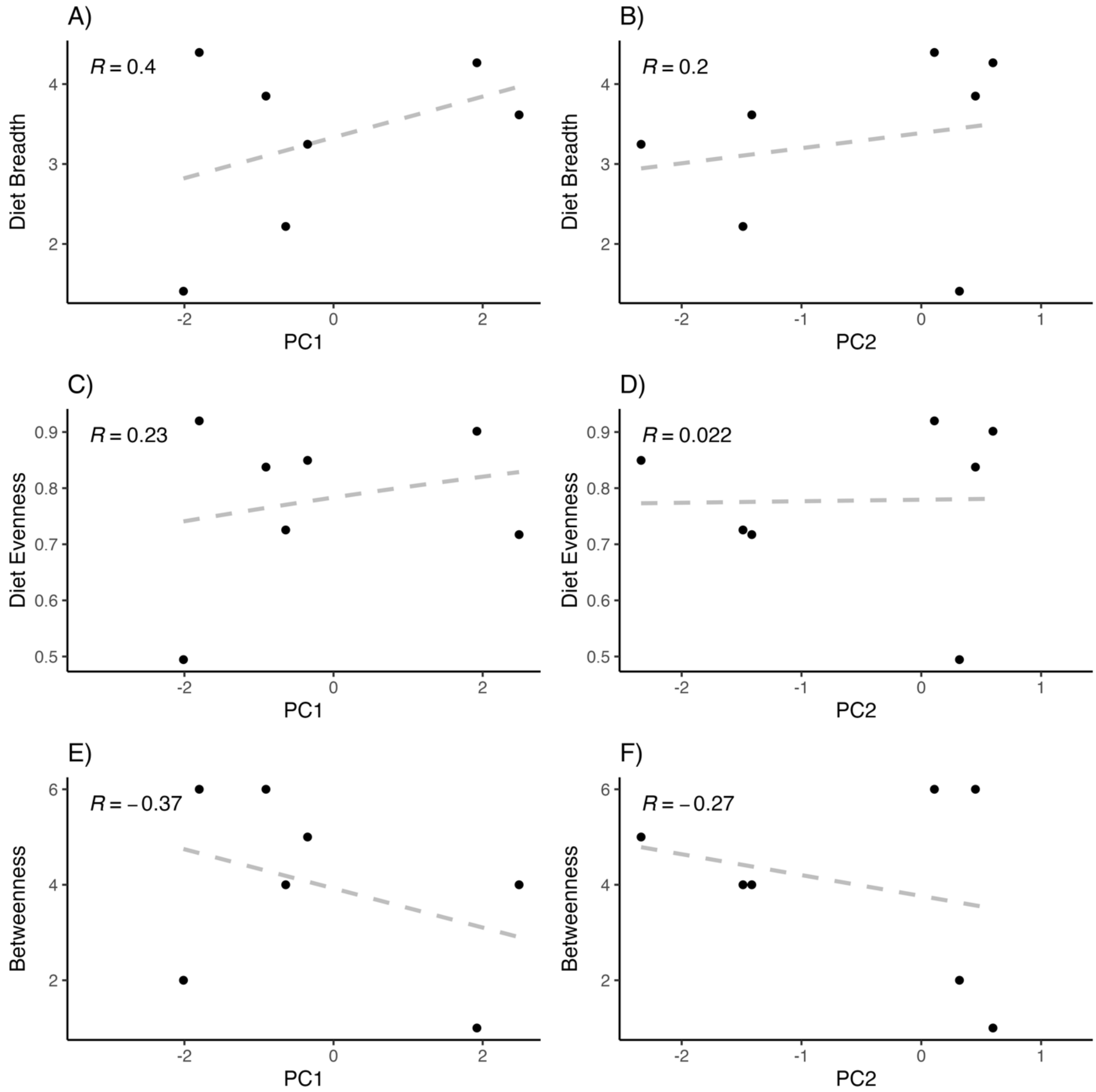

Figure 24: Comparison of dragonfly network metrics and the first two axes from the PCA. R indicates Pearson's correlation coefficients. Solid lines indicate relatively strong correlations (R > 0.5) while dashed lines indicate weak or moderate correlations (R < 0.5). The top row compares diet breadth to component 1 (A) and component 2 (B). The middle row compares diet evenness to component 1 (C) and component 2 (D). The bottom row compares betweenness centrality to component 1 (E) and component 2 (F).

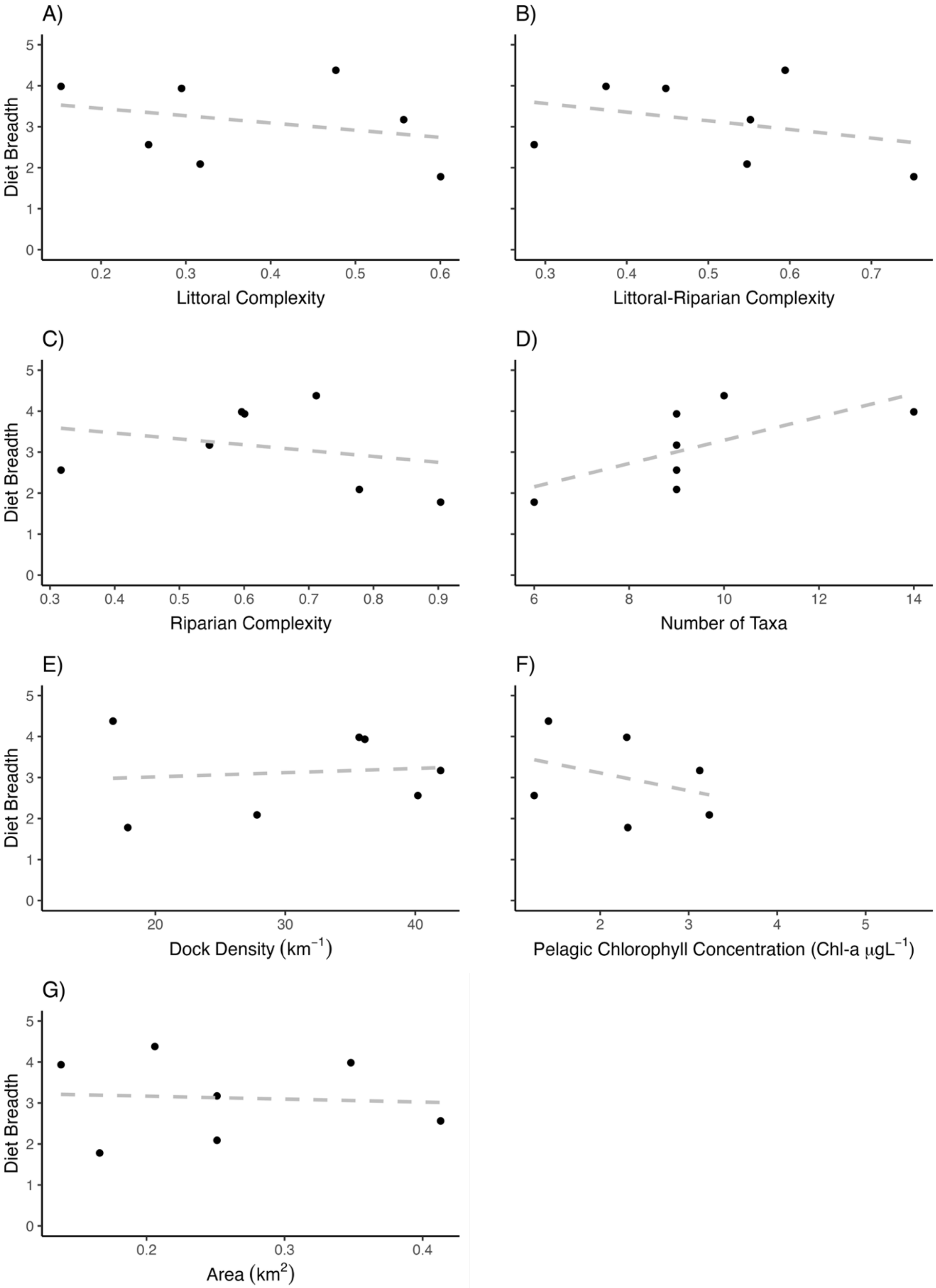

Figure 25: Bivariate linear regressions for damselfly diet breadth within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

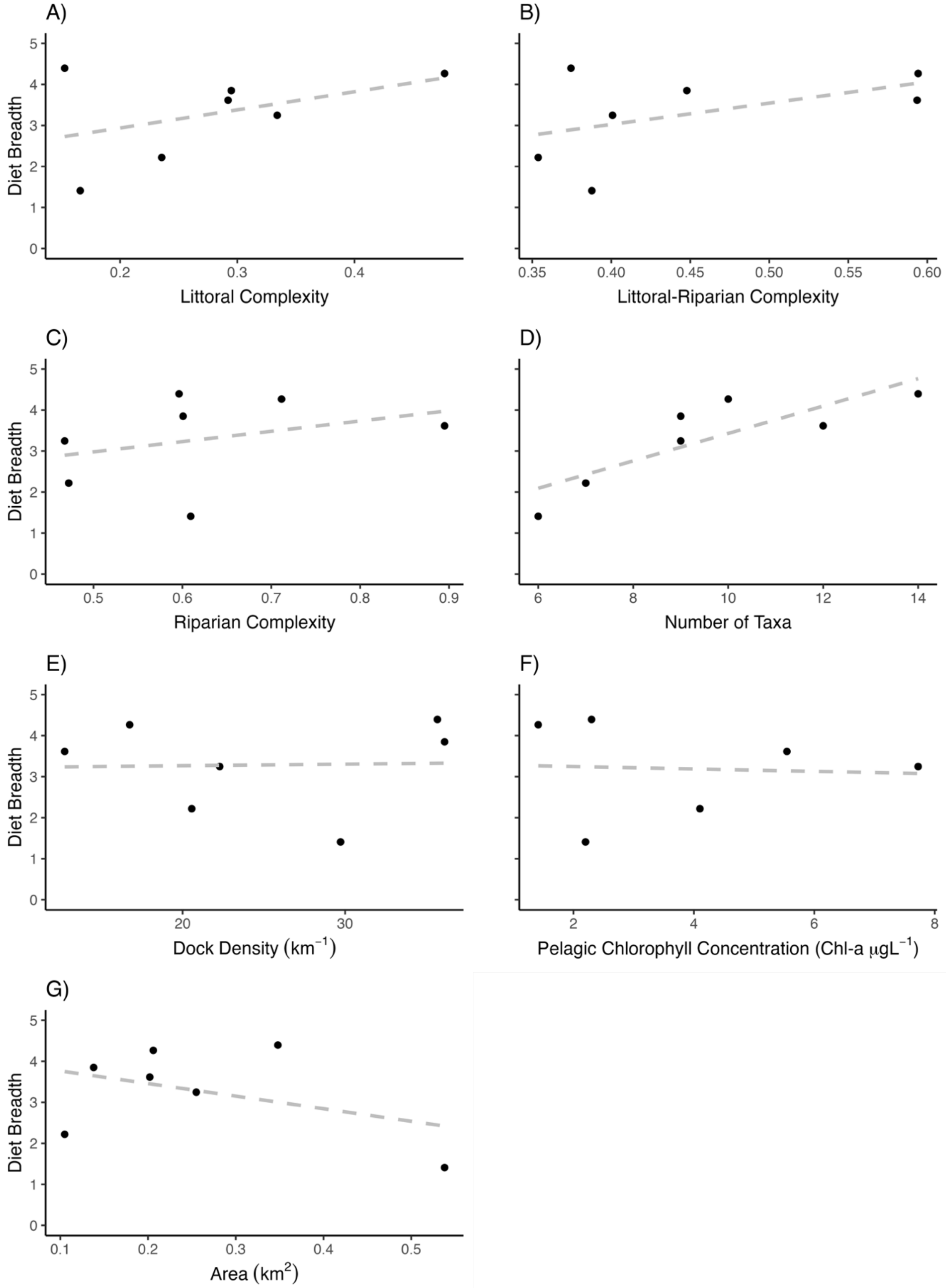

Figure 26: Bivariate linear regressions for dragonfly diet breadth within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

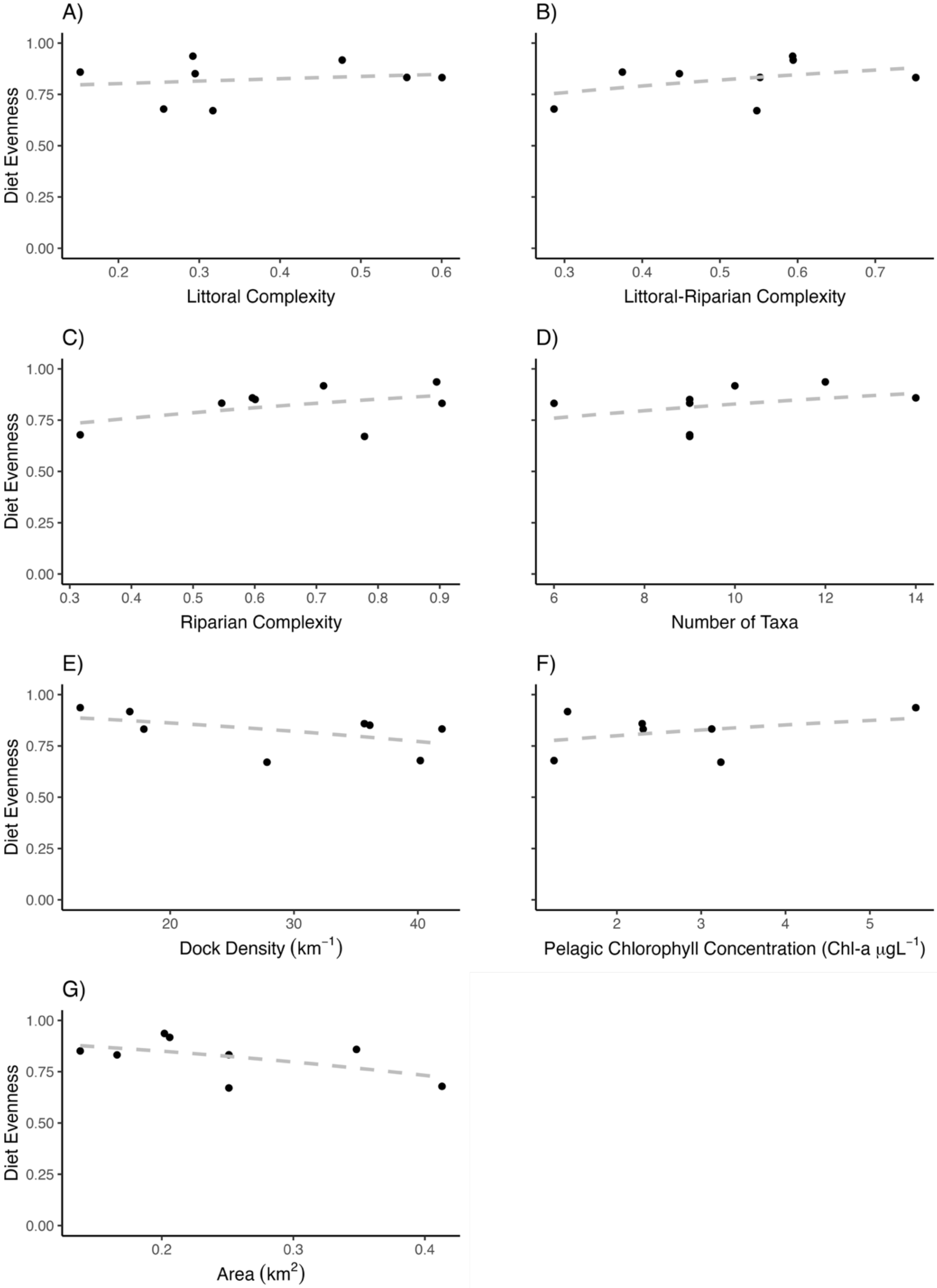

Figure 27: Bivariate logistic regressions for damselfly diet evenness within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

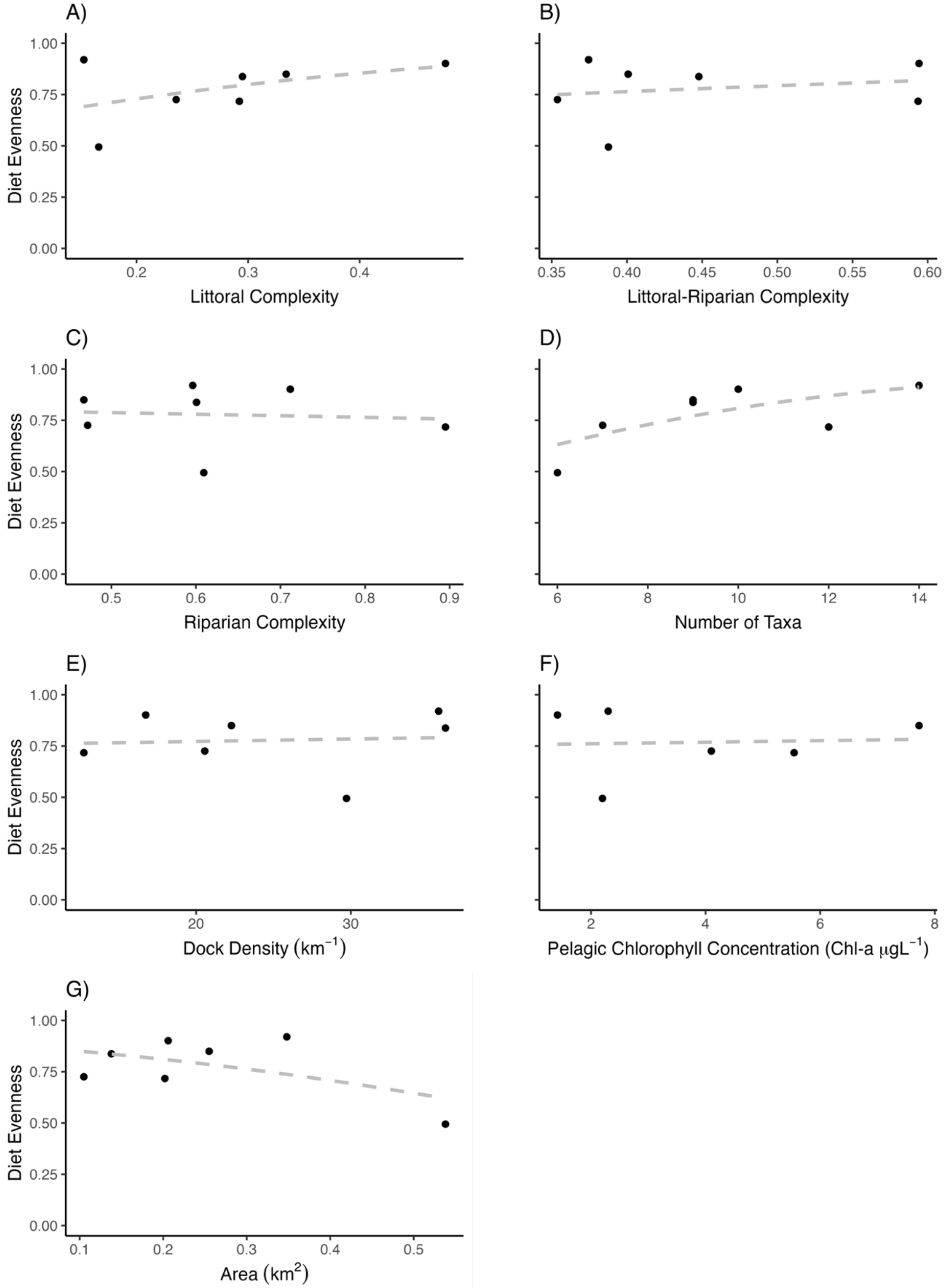

Figure 28: Bivariate logistic regressions for dragonfly diet evenness within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

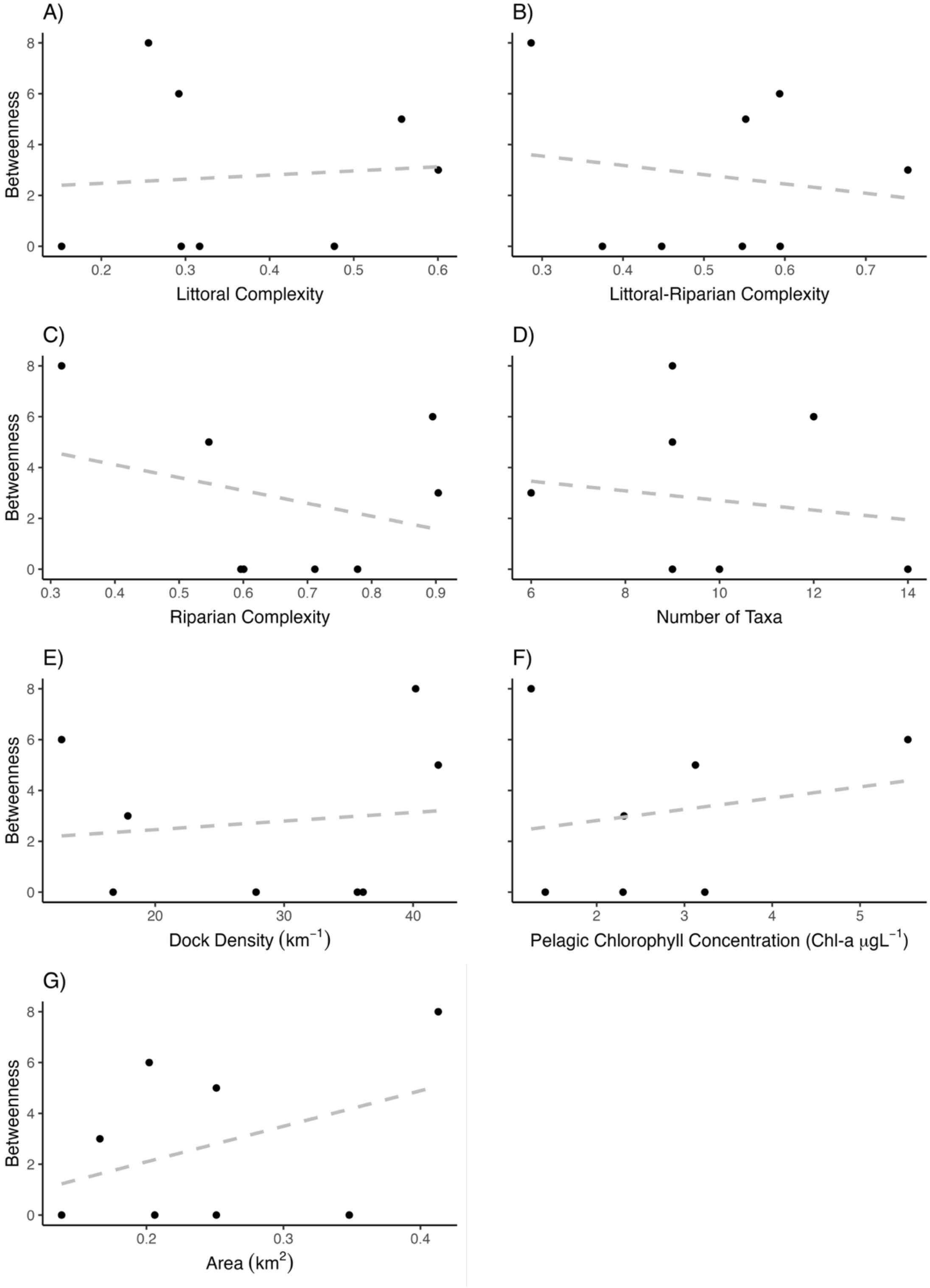

Figure 29: Bivariate logistic regressions for damselfly betweenness centrality within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^2). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

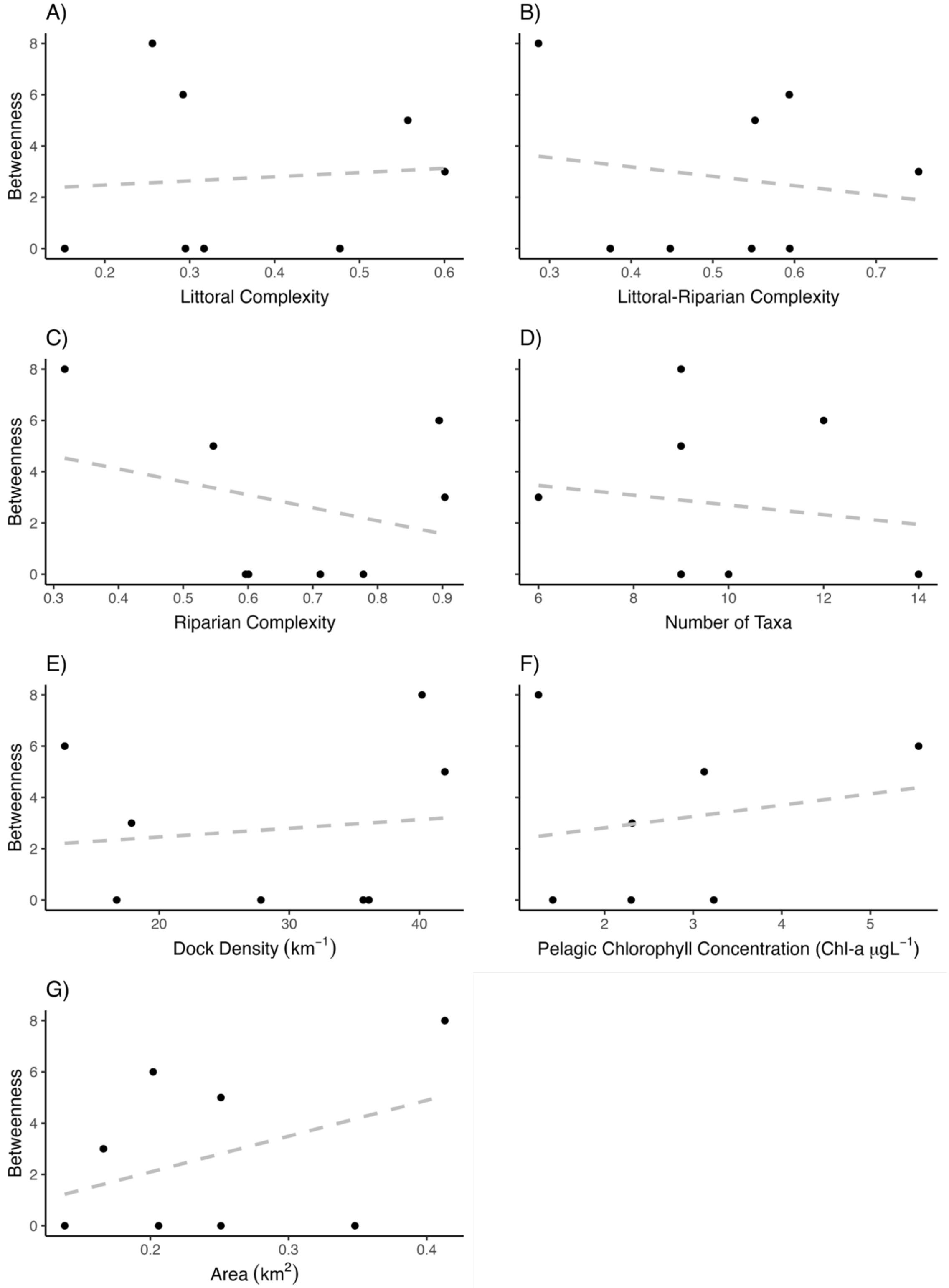

Figure 30: Bivariate negative binomial regressions for dragonfly betweenness centrality within each lake compared to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (μgL^{-1}), and G) lake area (km^{2}). The grey lines denote model estimates with line-type indicating significance of the slope coefficient. Dashed lines denote nonsignificant relationships while solid lines denote significant relationships after conducting a Bonferroni correction.

Similar to the community network metrics, the high variation in the EcoDiet estimates of diet proportion led to large variation in the network metrics for all fishes. There are no consistent patterns in diet breadth for any of the species as habitat complexity declines and lakeshore development increases (Figure 31A, Figure 32A, Figure 33A). Diet evenness distributions are especially left skewed with long trailing tails, indicating a relatively high occurrence of uneven diets (Figure 31B, Figure 32B, Figure 33B). In fact, the diet evenness distributions span most of the possible values, even though the majority of the mass is condensed at higher evenness values. Centrality values also varied considerably within species (Figure 31C, Figure 32C, Figure 33C). The many peaks are indicative of the peaks at discrete values, since centrality is a discrete count variable. Largemouth bass centrality was more concentrated around 0 than the other species, but the variation indicates that in some food web iterations other taxa consumed largemouth bass.

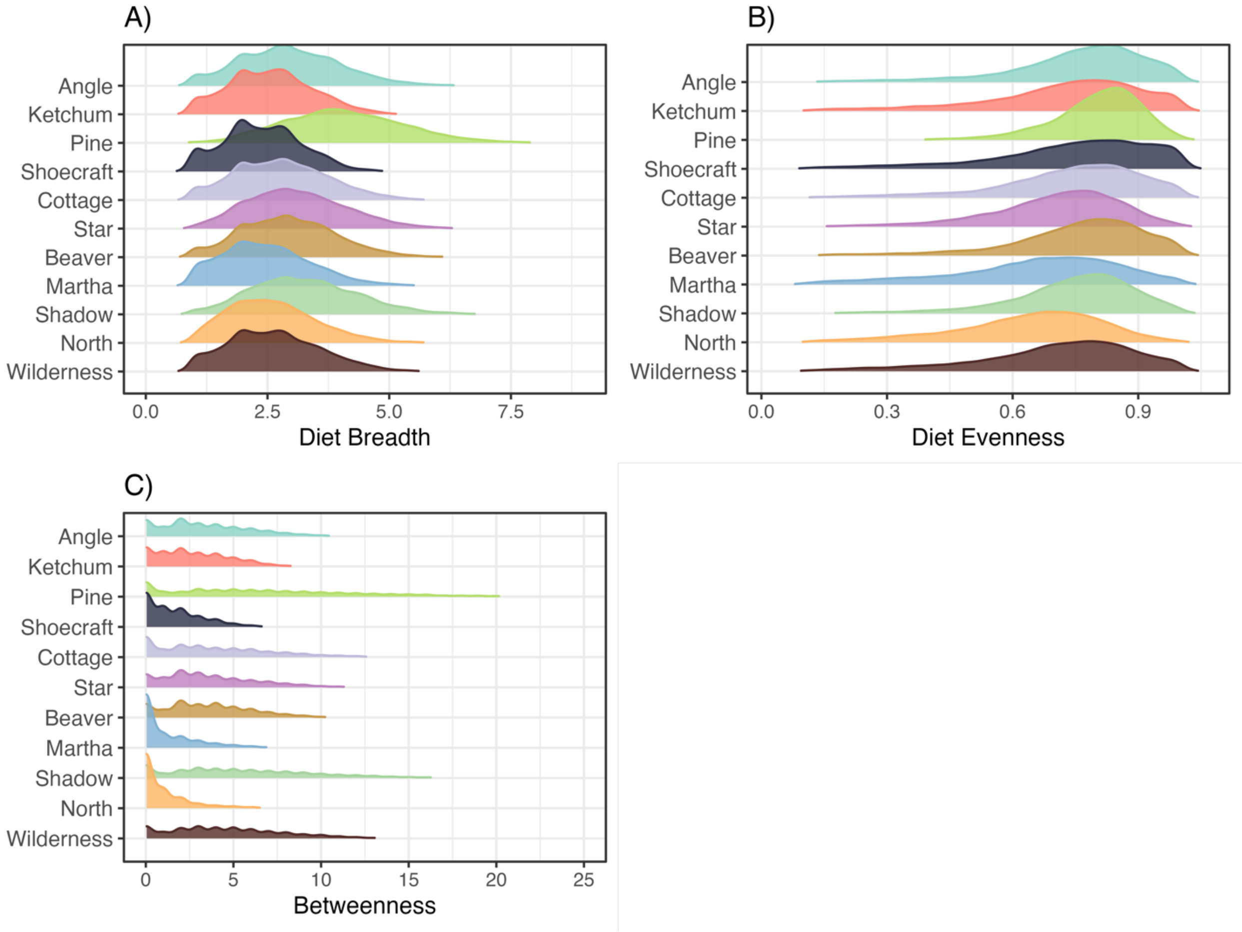

Figure 31: Yellow perch bootstrapped distributions for network metrics by lake on the y-axis. Lakes are ordered by combined habitat complexity metric so that the most developed lake is at the top and the least is at the bottom. A) Bootstrapped distributions for diet breadth of yellow perch at each lake. B) Bootstrapped distributions for diet evenness of yellow perch at each lake. C) Bootstrapped distributions for betweenness centrality of yellow perch at each lake.

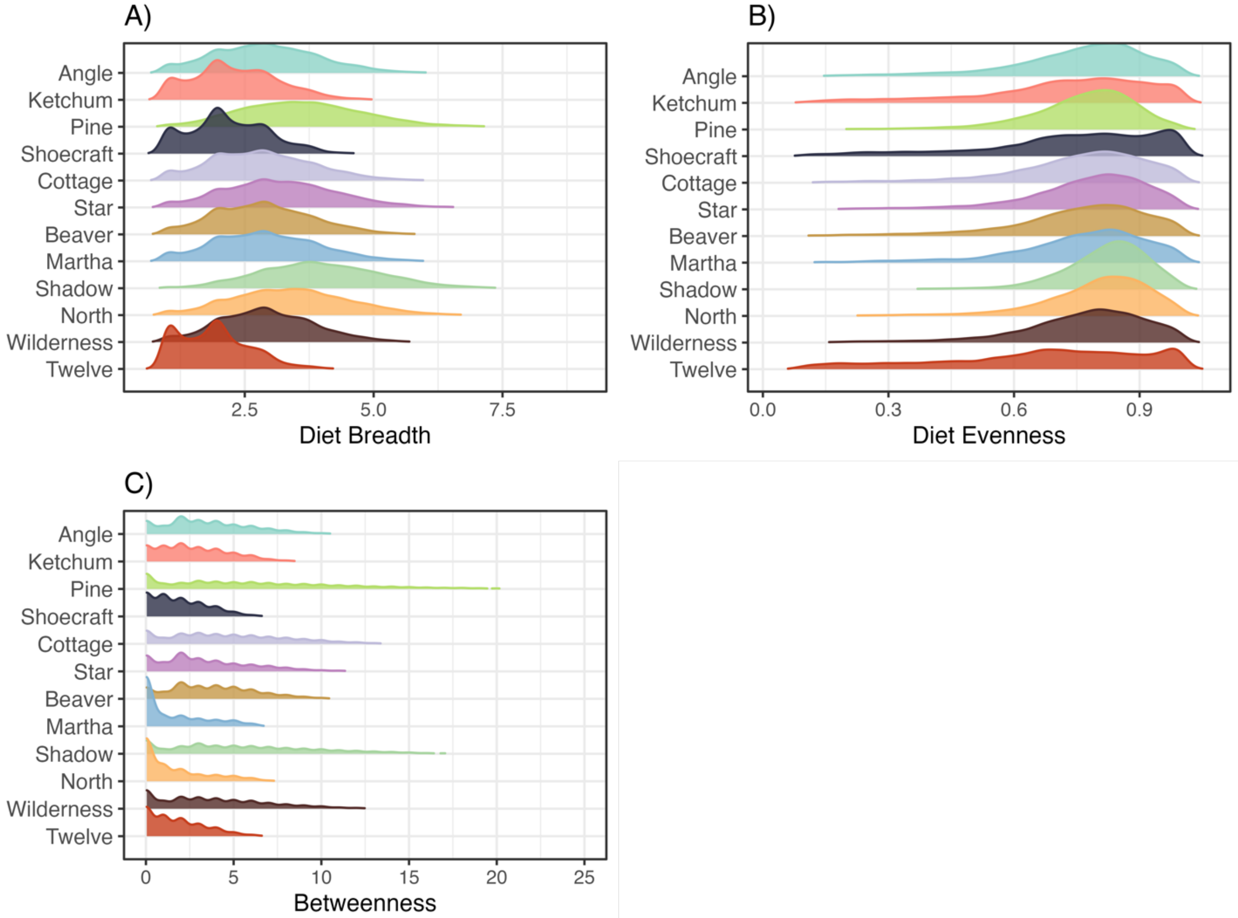

Figure 32: Pumpkinseed bootstrapped distributions for network metrics by lake on the y-axis. Lakes are ordered by combined habitat complexity metric so that the most developed lake is at the top and the least is at the bottom. A) Bootstrapped distributions for diet breadth of pumpkinseed at each lake. B) Bootstrapped distributions for diet evenness of pumpkinseed at each lake. C) Bootstrapped distributions for betweenness centrality of pumpkinseed at each lake.

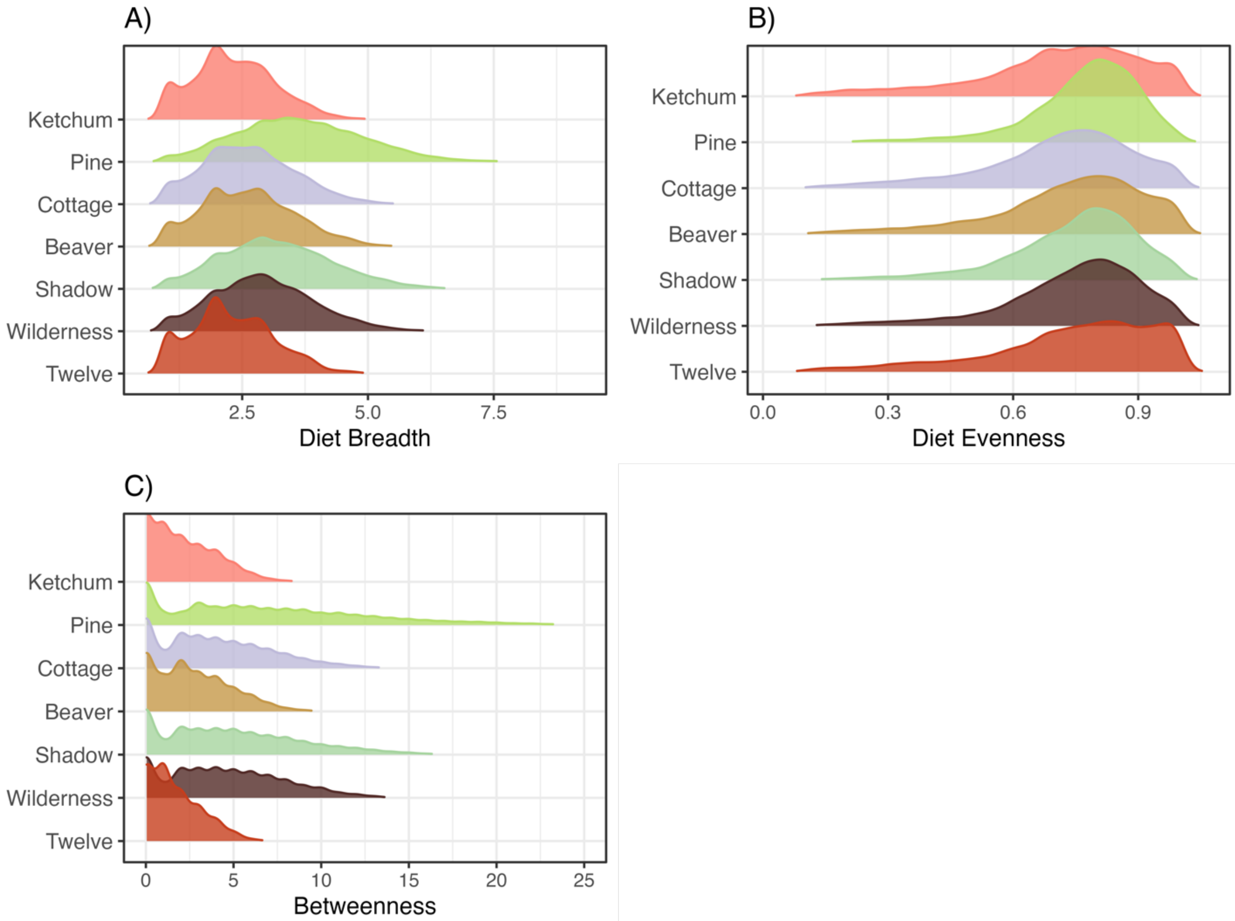

Figure 33: Largemouth bass bootstrapped distributions for network metrics by lake on the y-axis. Lakes are ordered by combined habitat complexity metric so that the most developed lake is at the top and the least is at the bottom. A) Bootstrapped distributions for diet breadth of largemouth bass at each lake. B) Bootstrapped distributions for diet evenness of largemouth bass at each lake. C) Bootstrapped distributions for betweenness centrality of largemouth bass at each lake.

Discussion:

In this study, I aimed to evaluate how lakeshore residential development affects food web network structure using both community-wide and species-specific network metrics. Results indicate that connectance is only weakly correlated with lake area and habitat complexity. This weak correlation may be due to contrasting responses among fish species in their diet breadth. Overall connectance within the food webs showed minimal changes in response to variation in habitat complexity. However, pelagic chlorophyll-a concentration was associated with an increased centrality of yellow perch and pumpkinseed within the food webs. This suggests that as primary production increases, both species become more important in connecting basal resources to higher trophic levels. Nevertheless, the overall model fit was relatively poor, and variation in the estimates of diet proportions resulted in imprecise network metrics. Therefore, the strength of these relationships should be interpreted with caution.

Overall food web structure, measured as connectance, mean degree, and mean link strength, exhibited minimal change in response to lakeshore residential development. Consistent with expectations based on optimal foraging theory, connectance and mean degree were and positively associated with dock density and lake area, though weakly. In contrast, mean link strength was weakly and negatively correlated with dock density, as well as weakly and positively correlated with littoral habitat complexity. These findings align with work done by Sullivan and Manning (2019), who examined food web structure in rivers across an urban to rural landscape gradient and found no consistent patterns between land use type and linkage density, connectance, or compartmentalization. Previous work comparing food web structure in lakes from around the world have also found that connectance was not well explained by environmental variables (Sánchez-Carrillo et al. 2018). In contrast, Brauns et al. (2011) demonstrated that at developed sites within three North German lowland lakes had a lower diversity of benthic macroinvertebrates and fewer connections among them. However, they did not evaluate how the changes to macroinvertebrate communities impacted higher trophic levels in the lakes nor measure the proportion of potential connections (connectance). Additionally, Hansen et al. (2017) discovered variations in food web topology between sandy and cobble habitats within the same lake, despite the presence of similar macrpohytes, aquatic macroinvertebrates, and fish species. Thus, it is possible that within-lake differences in food web structure at finer, site-specific scales are more pronounced than lake-wide differences. When aggregating food web structure to a larger scale, such finer-scale variations may be obscurred, especially if they contrast with one another.

An alternative explanation for the limited response in connectance is that the lakes included in this study did not span a broad enough disturbance gradient. The lakes ranged in percent lakeshore residential development from 25% to 95%, indicating the absence of completely natural lakes. Moreover, the majority of the lakes had lakeshore residential development levels between 60% and 95%. Francis and Schindler (2009) demonstrated that lakeshore residential development as low as 15% caused a severe decline in terrestrial inputs to fish diets, with little change after this initial decline. A similar threshold effect might alter food web network structure at lower levels of lakeshore residential development than those considered in this study.

Yellow perch diet breadth was negatively correlated with littoral habitat complexity. Furthermore, perch diet evenness decreased and reliance on zooplankton increased as littoral complexity improved. This aligns with the hypothesis that yellow perch's consumption of zooplankton is positively correlated with littoral habitat complexity. However, the increased reliance on zooplankton may be related to size rather than habitat complexity. Numerous studies have demonstrated that yellow perch, along with other species, exhibit ontogenetic diet shifts as their size increases (e.g., Keast 1985; Wu and Culver 1992; Mittelbach and Persson 1998; Fullhart et al. 2002; Graeb et al. 2006). Juvenile yellow perch (total length < 50mm) consume mostly zooplankton, switch to benthic invertebrates at intermediate sizes (total length 50 – 130 mm), and begin to consume fish, along with benthic macroinvertebrates, once they exceed a total length of 130 mm (Keast 1985; Fullhart et al. 2002). Laboratory experiments have demonstrated that changes in foraging efficiency and energy gain from zooplankton and benthic invertebrates for yellow perch of different sizes contribute to these observed diet shifts. Zooplankton provide sufficient energy for small yellow perch, but as they grow, benthic invertebrates offer higher energy returns due to increased foraging efficiency (Graeb et al. 2006). Thus, yellow perch decrease their consumption of zooplankton in accordance with expectations based on optimal foraging theory, i.e., larger fish consume proportionally less zooplankton (Graeb et al. 2006). The yellow perch I collected ranged in size from 130 – 172 mm total length and are therefore expected to consume a combination of prey fishes and benthic macroinvertebrates. However, I found a small, but significant, negative correlation ($R = -0.265$, $p = 0.004$) between yellow perch size and littoral complexity. Thus, I can’t rule out that size contributes to the pattern of zooplanktivory and consequently diet breadth and evenness observed in these lakes.

Largemouth bass exhibited a decrease in diet breadth associated with lower habitat complexity, opposite to the response observed in yellow perch. Largemouth bass diet breadth increased as habitat complexity increased and dock density decreased, indicating a negative correlation between lakeshore residential development and diet breadth. This finding aligns with previous work demonstrating that largemouth bass consume fewer fish and have decreased diet breadth in habitats with less aquatic vegetation (Anderson 1984; Tsunoda and Mitsuo 2018). Furthermore, experiments by Sass et al. (2006) to remove CWH from one basin in Little Rock Lake and by Ahrenstorff et al. (2009) to add CWH to half of Camp Lake in Wisconsin, revealed that largemouth bass increased diet breadth in lake basins with more CWH. Ahrenstorff et al. (2009) demonstrated that in environments with high habitat complexity due to CWH and abundant prey, largemouth bass reduced time spent actively swimming but consumed a wider variety of less energetically beneficial prey because their energetic demands were lower. Thus, largemouth bass altered their foraging strategy in accordance with optimal foraging theory (Ahrenstorff et al. 2009). My results align with this past work, suggesting that changes in largemouth bass foraging strategy may drive the observed positive correlation between largemouth bass diet breadth and habitat complexity.

Pumpkinseed diet breadth and evenness were weakly and positively correlated with lake area but not strongly correlated with habitat complexity. Furthermore, variation in pumpkinseed diet breadth, diet evenness, and centrality was poorly explained by the combination of dock density, lake area, habitat complexity and pelagic chlorophyll-a concentration. Several past studies have also reported minimal changes in pumpkinseed diet breadth or evenness in response to lake-wide disturbances such as lakeshore development (Godinho et al. 1997; Declerck et al. 2002; Tetzlaff et al. 2011; Luek et al. 2013). While Godinho et al. (1997) demonstrated pumpkinseed did not alter their diet in response to aquatic vegetation, their results suggest that the presence of predators (such as largemouth bass) and the size of the individual were the main drivers behind diet variation. Pumpkinseed relative abundance and stomach fullness have been found to be positively correlated with aquatic macrophyte cover (Laughlin and Werner 1980; French 1988). Thus, it is possible that rather than shifting foraging habits, they are simply consuming more or less of the same prey items as lakeshore development increases and aquatic macrophyte cover decreases. However, Twardochleb and Olden (2016a) revealed that Chinese mystery snails in developed lakes provided an alternative food source for pumpkinseed in place of native snails that are sensitive to lakeshore residential development, mitigating some of the negative effects of lost native prey options. Many of the lakes in this study contain Chinese mystery snails, thus pumpkinseed may be able to maintain consistent diet patterns across the development gradient.

While pumpkinseed diet breadth and evenness showed weak correlations with environmental variables, pumpkinseed centrality and yellow perch centrality were both positively associated with pelagic chlorophyll-a concentration. Largemouth bass presence, however, may also influence the increase in centrality for pumpkinseed and yellow perch, as they are both common prey of largemouth bass (Wydoski and Whitney 2003; Golub et al. 2005). All lakes where yellow perch had non-zero centrality contained largemouth bass, except for Cottage Lake. This is logical, since in these model food webs there are no other predators consuming yellow perch, positioning them near the top of the food web. Consequently, without other species to consume yellow perch, the yellow perch cannot lie on the shortest path between two species, resulting in a centrality of zero. Additionally, in Cottage Lake, pumpkinseed had a high centrality. In Cottage Lake pumpkinseed consumed many taxa and were heavily relied upon by largemouth bass, making their position in the food web more central than yellow perch in this lake. The lakes in this study which contained largemouth bass, had higher pelagic chlorophyll-a concentrations than the lakes without, and the five lakes with the highest pelagic chlorophyll-a concentrations all contained largemouth bass. Therefore, it is difficult to completely disentangle the ecological mechanisms driving the increases in centrality. However, it is more probable that the presence of largemouth bass drives this pattern as yellow perch and pumpkinseed are both commonly consumed by bass, and many studies have demonstrated largemouth bass exert top-down pressure on food web structure (Carpenter et al. 1985; Carpenter 1987; Paukert et al. 2003; Fetzer et al. 2016). Regardless, for the lakes in this study those with high primary production that contain largemouth bass, yellow perch and pumpkinseed become more central within the food web and are important prey for largemouth bass in these lakes.

Yellow perch and pumpkinseed modify their diet patterns and behavior in the presence of largemouth bass (Golub et al. 2005; Ferrari et al. 2010). Pumpkinseed respond by spending more time in aquatic macrophytes consuming benthic invertebrates and gastropods when largemouth bass are present (Mittelbach 1984). Yellow perch, in the presence of predators, increase shoaling cohesion, move toward the sediment, and use shelter more frequently (Mirza et al. 2003). Additionally, Lippert et al. (2007) demonstrated that yellow perch increased their consumption of benthic invertebrates and reduced consumption of zooplankton in lakes with predators such as walleye (*Sander vitreus*), northern pike (*Esox Lucius*), and smallmouth bass (*Micropterus dolemieu*). Yellow perch diet breadth and evenness were slightly greater in lakes with largemouth bass while pumpkinseed diet breadth and evenness decreased slightly, but there was substantial overlap in diet breadth across lakes for both species (Figure A7). Therefore, while it is likely largemouth bass impact yellow perch and pumpkinseed behavior, I do not have evidence to suggest that this is driving the patterns or lack there-of in diet breadth or diet evenness.

Damselflies exhibited a negative correlation between diet breadth and the second principal component axis but not between diet breadth and chlorophyll-a concentration individually. Additionally, damselflies' diet evenness and centrality were not strongly correlated with the measured environmental variables. Meanwhile, dragonfly diet breadth, diet evenness, and centrality were not strongly associated with any of the measured environmental variables. Damselflies in Shadow Lake displayed the highest diet breadth across the observed lakes, and removing Shadow Lake reduced the strength of the correlation between diet breadth and the second principal component axis. Shadow Lake, in addition to having a relatively high chlorophyll-a concentration, also has a high diversity of aquatic macroinvertebrates and high habitat complexity. Yet, none of the individual comparisons between chlorophyll-a, number of taxa, and the habitat complexity metrics were significant. Therefore, it is possible that only the combination of high chlorophyll-a concentration, diversity of aquatic macroinvertebrates, and habitat complexity is positively correlated with diet breadth of damselflies. To my knowledge, studies examining the correlation between damselfly diet breadth and primary production are lacking. However, Thompson (1978) measured diet of Odonata (Zygoptera *Ischnura elegans*) from April to October 1975 in Pocklington Canal, York, England and found that their diets reflected the abundance of prey items. Additionally, an experiment by Lombardo (1997) testing predation success by Odonata (*Enallagma sp.*) revealed no difference between predation success in complex macrophyte habitats and noncomplex macrophyte habitats. This supports the assertion that it is the combination of elevated primary production, complex habitat structure, and diversity of prey items that is associated with increased diet breadth in damselflies.

Terrestrial prey items can play an important role in lake food webs (Milardi et al. 2016), even though they were not included in this study. For example, Sass et al. (2006) revealed that largemouth bass consumed greater proportions of terrestrial prey when CWH was removed; however, they did not consider changes in terrestrial habitat in addition to the loss of CWH. The lakes in this study changed not only in littoral habitat complexity but also riparian habitat complexity. Research by Francis and Schindler (2009) in many of the same lakes indicated that overall contribution of terrestrial prey to rainbow trout (*Oncorhynchus mykiss*) diets decreased significantly even when only 15% of the lakeshore had residential development. Beyond this threshold, the contribution of terrestrial prey remained low and relatively constant. The lakes included in this study range from 25% to 95% developed, well above the threshold identified by Francis and Schindler (2009), meaning that terrestrial prey contribution to these lakes is already quite low. Therefore, it is unlikely that terrestrial subsidies would change significantly across the development gradient in the study.

The environmental variables that we measured—including littoral, riparian, and overall habitat complexity as well as pelagic chlorophyll-a concentration—have all been associated with lakeshore residential development (Moore et al. 2003; Sass et al. 2006, 2012; Carpenter et al. 2011). However, these relationships are not necessarily linear (e.g., Francis and Schindler 2009). For instance, primary production can peak in peri-urban environments where homeowners use septic systems rather than city sewer systems (Moore et al. 2003), but this pattern was not observed in the lakes in this study. There was, however, a strong negative correlation between the percentage of lakeshore with residential development and both riparian habitat complexity and littoral complexity, as well as a strong positive correlation with dock density. Thus, while the habitat metrics and other environmental variables are not perfectly correlated with lakeshore residential development, they address the underlying drivers of community responses.

Another assumption of this study is that each fish species exhibited consistent selectivity patterns across lakes driven by habitat complexity, but this is not always the case. For instance, Dieter et al. (2022) demonstrated seasonal shifts in bloater (*Coregonus hoyi*) selectivity changed seasonally, while rainbow smelt (*Osmerus mordax*) selectivity remained consistent in Lake Huron. An experiment by Weber et al. (2010) evaluated the selectivity of yellow perch in simple and complex habitats. They found that yellow perch preferentially selected alewives (*Alosa pseudoharengus*) in both habitat types, as alewives were the most energetically beneficial prey items. However, when alewives were removed, yellow perch's selection of the northern crayfish (*Oronectes virilis*) and round gobies (*Neogobius melanostomus*) differed between simple and complex habitats. Furthermore, diets of yellow perch in Lake Michigan mirrored patterns observed in the mesocosms. These results suggest that yellow perch preferentially select energetically beneficial prey, and these patterns are relatively consistent across large spatial scales. Additionally, Anderson (1984) demonstrated that largemouth bass selectivity changes in structured habitats, leading to increased diet breadth, although this study did not examine whether these patterns remained consistent across other populations. I did not quantitatively sample macroinvertebrates in the study lakes; therefore, I cannot evaluate changes in selectivity across lakes. It is possible that differences in selectivity across populations is driving changes in diet breadth and evenness rather than littoral habitat complexity.

My literature review found that largemouth bass diets contained high proportions of fish, and consequently the prior data weighted fish species more heavily than macroinvertebrate prey. The largemouth bass I collected ranged in size from 79 mm to 475 mm in total length, with all but two individuals exceeding 100mm in total length. Largemouth bass undergo an ontogenetic diet shift from invertebrates to fish at around 40 – 50 mm standard length, approximately 73 mm total length (Binohlan et al. 2011). Therefore, I expected most of the largemouth bass I captured to consume proportionally more fish than macroinvertebrates. However, during stomach content identification, it was often challenging to positively identify fish remains due to sample degradation. Consequently, these samples could not contribute to the EcoDiet model. As a result, with high prior diet proportions for high fishes and low evidence for fish in the samples, the model could not adjust to increase macroinvertebrate diet proportions. I evaluated the impact of creating networks without informative literature priors; however, this approach resulted in all diet items being evenly weighted, leading to homogenized diet proportions across the estimated food webs. This was especially undesirable as diet evenness was one of the parameters I assessed. Since stomach content data used in EcoDiet do not require quantification of diet items but only frequency of occurrence, future work would benefit from using DNA metabarcoding methods to reduce uncertainties in stomach content identification.

While EcoDiet has several advantages over other Bayesian mixing models, it is still limited in its ability to discriminate among mixtures with many variables (Hernvann et al. 2022). Estimating too many parameters can lead to diffuse posterior diet proportions (Phillips et al. 2014). In this study, I used the median posterior diet proportion from EcoDiet, which does not account for the variation within the posterior distributions. Employing a boostrapping method to calculate network metrics across the estimated distribution of diet proportions resulted in imprecise network metrics. Mixing models are also sensitive to missing sources (Phillips et al. 2014). I excluded primary producers due to the absence of seston and algae, combined with the number of littoral and terrestrial primary producers biased model results towards littoral habitats. Although this bias was reduced after removing primary producers, fish from Lake Shoecraft fish were enriched in $\delta^{13}C$ compared to the aquatic macroinvertebrates that I collected. Excluding Lake Shoecraft from the community RDA diminished the influence of pelagic chlorophyll-a concentration on the secondary axis, as Lake Shoecraft had one of the lowest pelagic chlorophyll-a concentrations. However, associations among the community metrics and the environmental variables were not changed significantly (Figure A6). Network analyses hold potential for drawing insightful conclusions about community-wide responses to disturbances. Future researchers should carefully consider sampling requirements before utilizing the EcoDiet modeling framework.

Conclusions:

Species-specific responses were complex and potentially influenced by species' traits, interspecific interactions, and the surrounding environment. Consequently, there was only a weak association between community network metrics and lakeshore residential development. Yellow perch exhibited a negative correlation with littoral complexity, likely due to an increased reliance on zooplankton in habitats with complex littoral zones. However, yellow perch also decreased in size as littoral complexity increased, suggesting that the increased zooplanktivory may be related to size rather than habitat complexity. In contrast to yellow perch, largemouth bass diet breadth increased as littoral and riparian complexity increased. Field studies have indicated that largemouth bass in complex habitats tend to adopt a sit-and-wait foraging strategy, which is less energetically demanding than actively searching for food. This strategy allows largemouth bass to consume a wider variety of prey items including those that are less energetically profitable, to maintain energetic equilibrium (Ahrenstorff et al. 2009). Conversely, pumpkinseed diet varied minimally in response to the measured environmental variables.

Additionally, network connectance and mean degree were weakly and positively correlated with dock density around the lakeshore and lake area. In contrast, mean link strength within the food web was weakly and negatively correlated with dock density. Connectance integrates the diet breadth and evenness of all the taxa within the food web. Therefore, the contrasting responses in largemouth bass and yellow perch diet may offset each other, resulting in minimal change in network connectance.

A lack of change in connectance does not necessarily imply that there were no changes within the food web. Connectance measures the presence and weight of links rather than the arrangement of these links within the food web. Yet, there was evidence for different link arrangements among these lakes. The centrality of yellow perch and pumpkinseed both demonstrated positive correlations with pelagic chlorophyll-a concentration and the presence of largemouth bass. Thus, while the overall connectance of the food web varied little among lakes, yellow perch and pumpkinseed became more important in connecting basal resources to upper trophic levels in lakes characterized by high primary production and the presence of largemouth bass.

These results suggest that environmental variables associated with lakeshore residential development impact species-specific responses, thereby modifying consumptive interactions and the structure of the food web. However, the contrasting responses in diet breadth among different species offset each other, resulting in similar connectance in food webs across the studied lakes' food webs. Connectance and weak links can contribute to stabilizing food webs (McCann et al. 1998; Rooney and McCann 2012). The weak correlation between connectance and lakeshore residential development suggests that food web network stability may not significantly change within the disturbance levels observed in this study. These findings underscore the resilience of food web structure as lakes transition from moderate to high lakeshore residential development. Future research should investigate whether more pronounced changes in food web structure occur at lower levels of lakeshore development. Understanding these thresholds is crucial for ensuring a healthy food web and effectively managing aquatic ecosystems.

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Appendix:

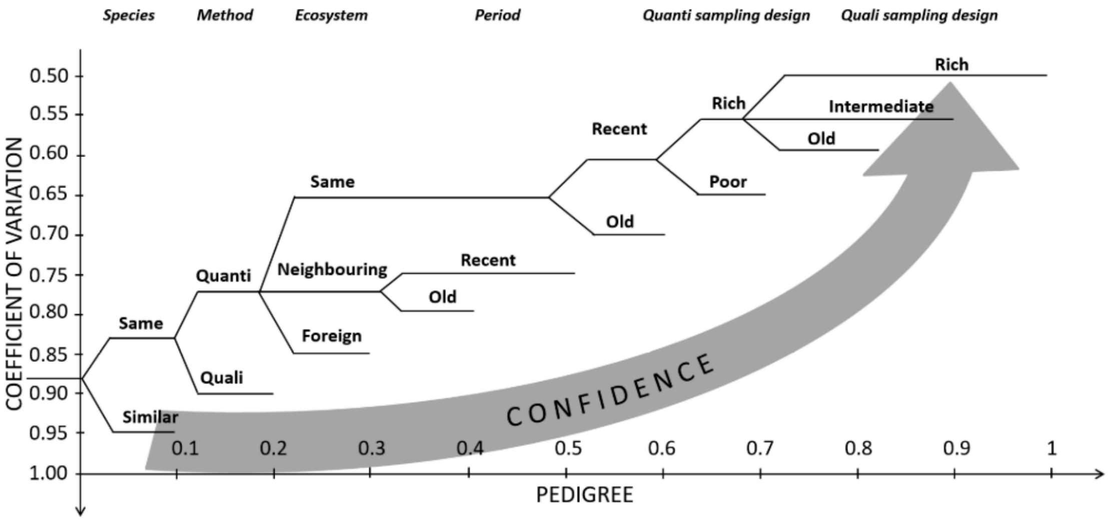

Figure A1: Literature decision tree from Hernvann et al. (2022) modified for lakes in the Puget Sound lowlands. Definitions for decision making can be found in Table A1.

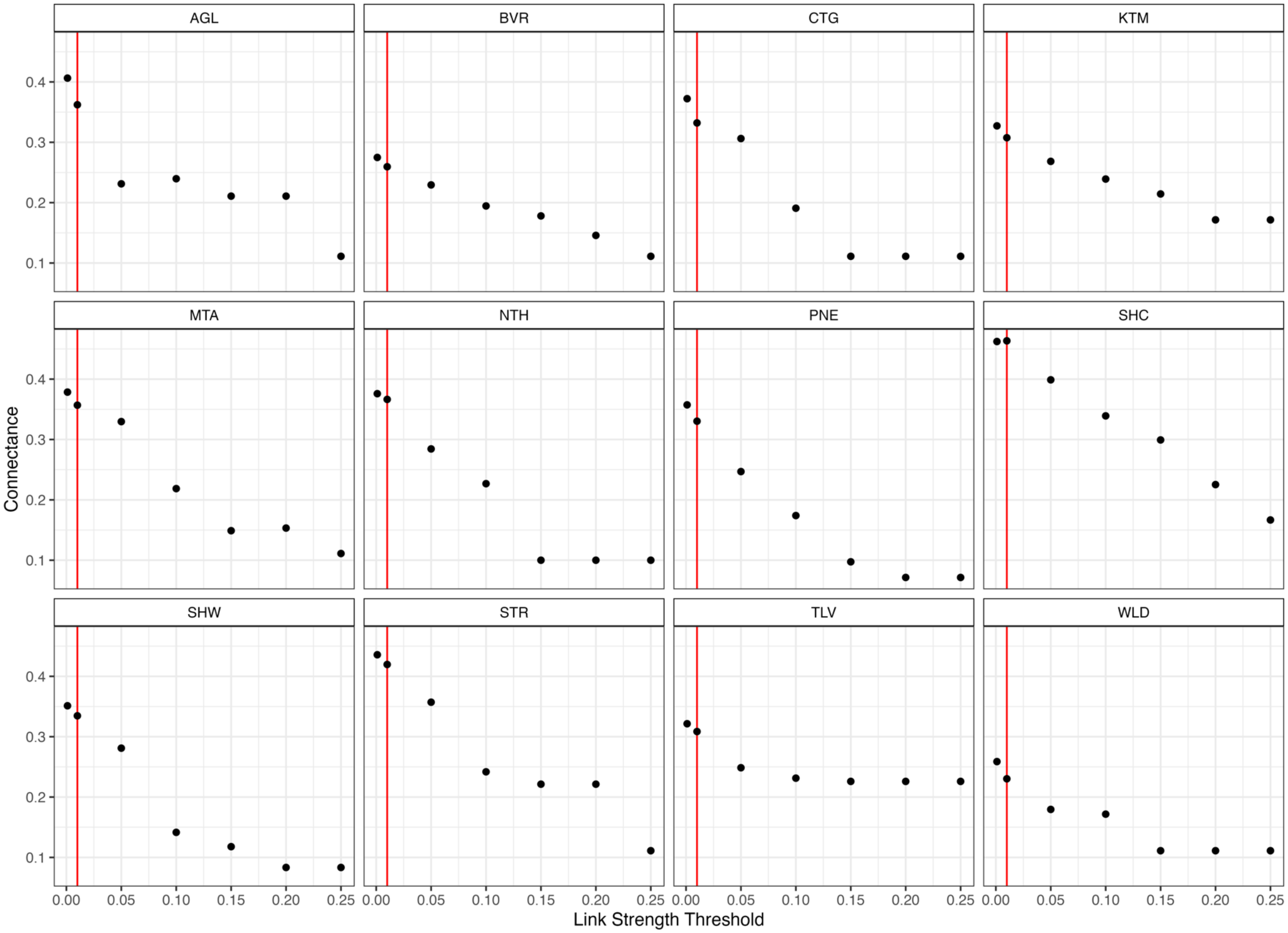

Figure A2: Connectance values for food webs at different values for removal of weak links.

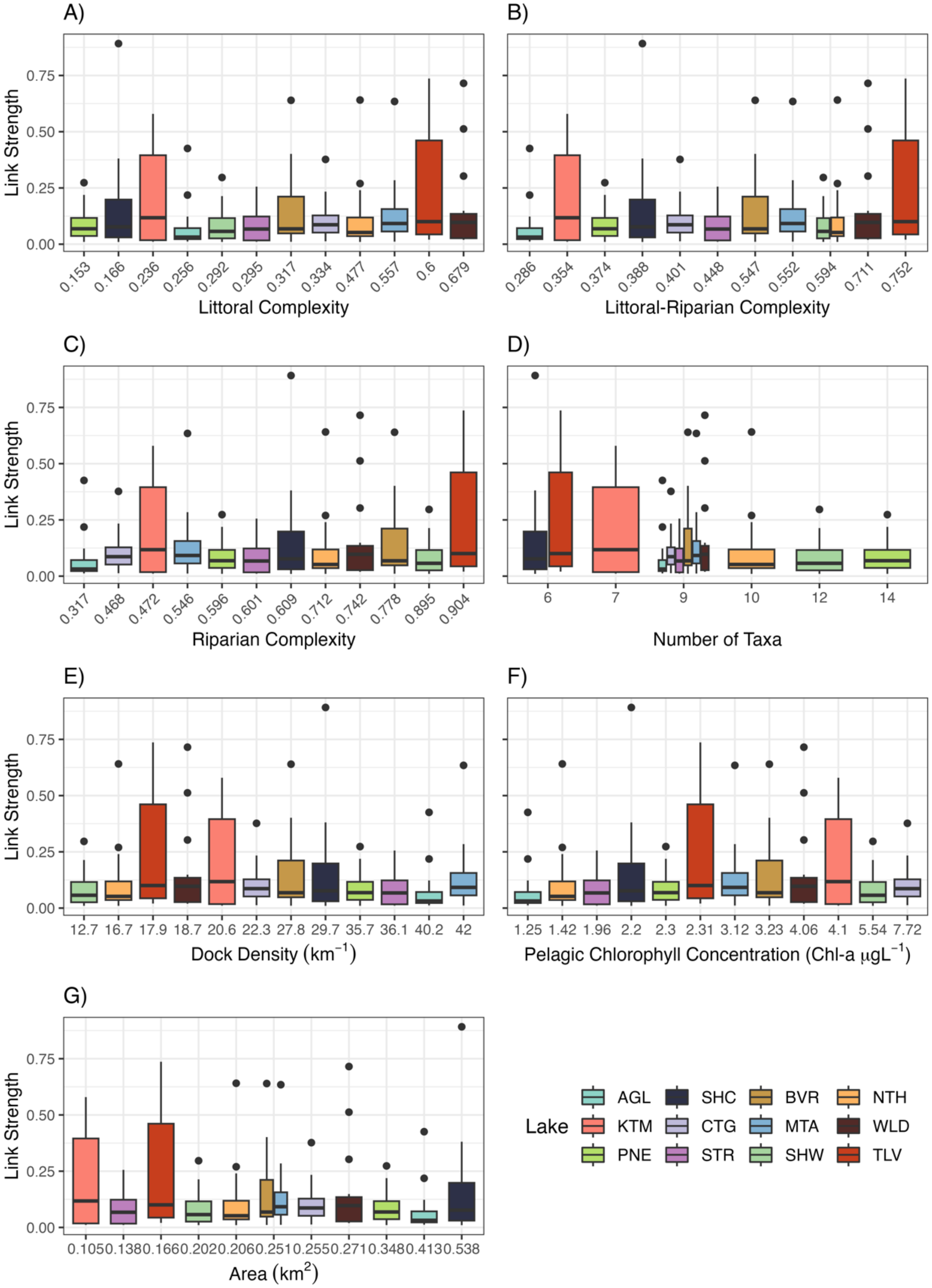

Figure A3: Distribution of linkage strengths within each lake ordered according to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (µgL^{-1}), and G) lake area (km^2).

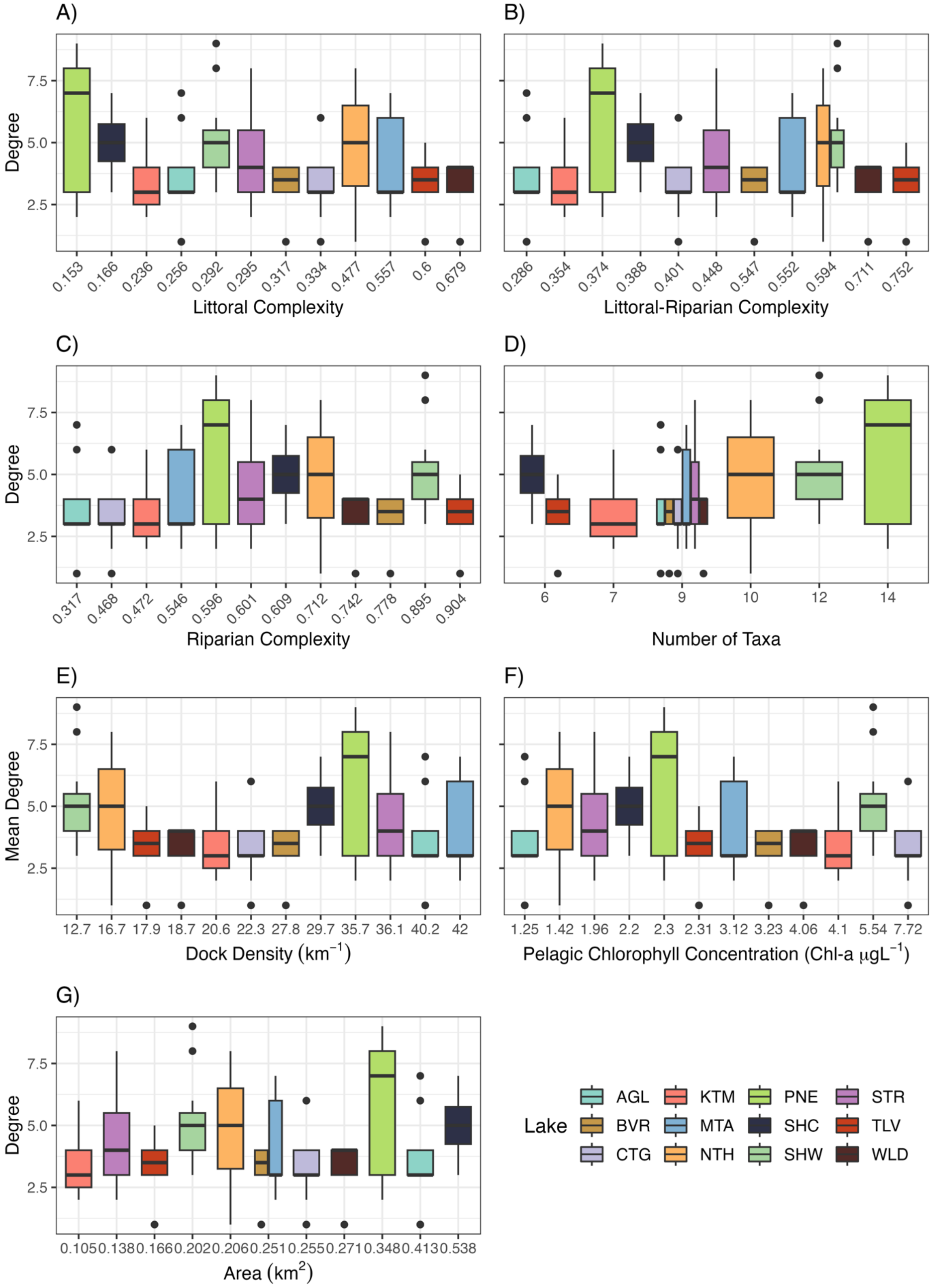

Figure A4: Distribution of degree within each lake ordered according to A) littoral complexity, B) combined littoral-riparian complexity, C) riparian complexity, D) number of taxa within the food web, E) dock density (km^{-1}), F) pelagic chlorophyll-a concentration (µgL^{-1}), and G) lake area (km^{2}).

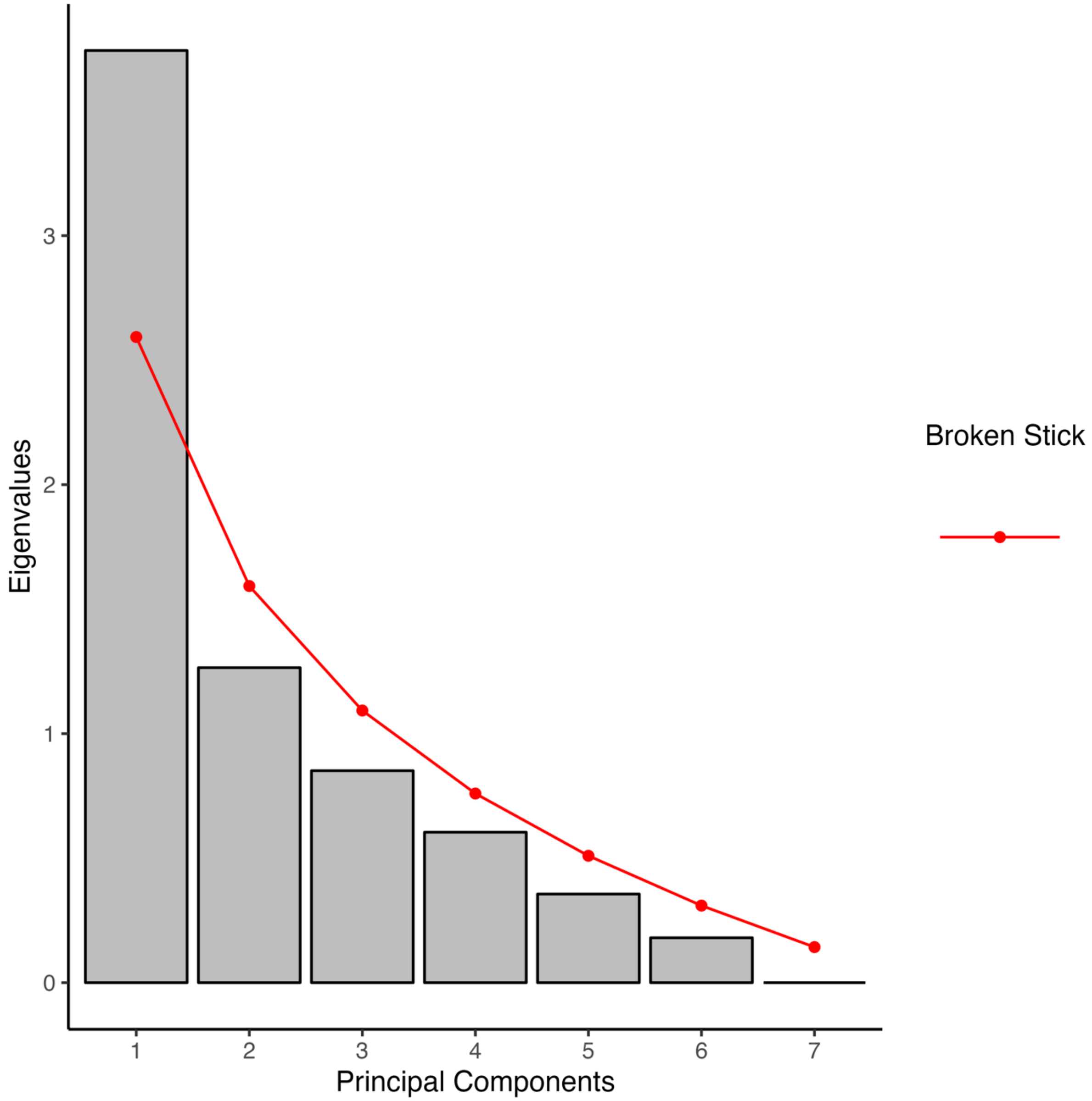

Figure A5: Broken stick comparison for principal component analysis of environmental variables.

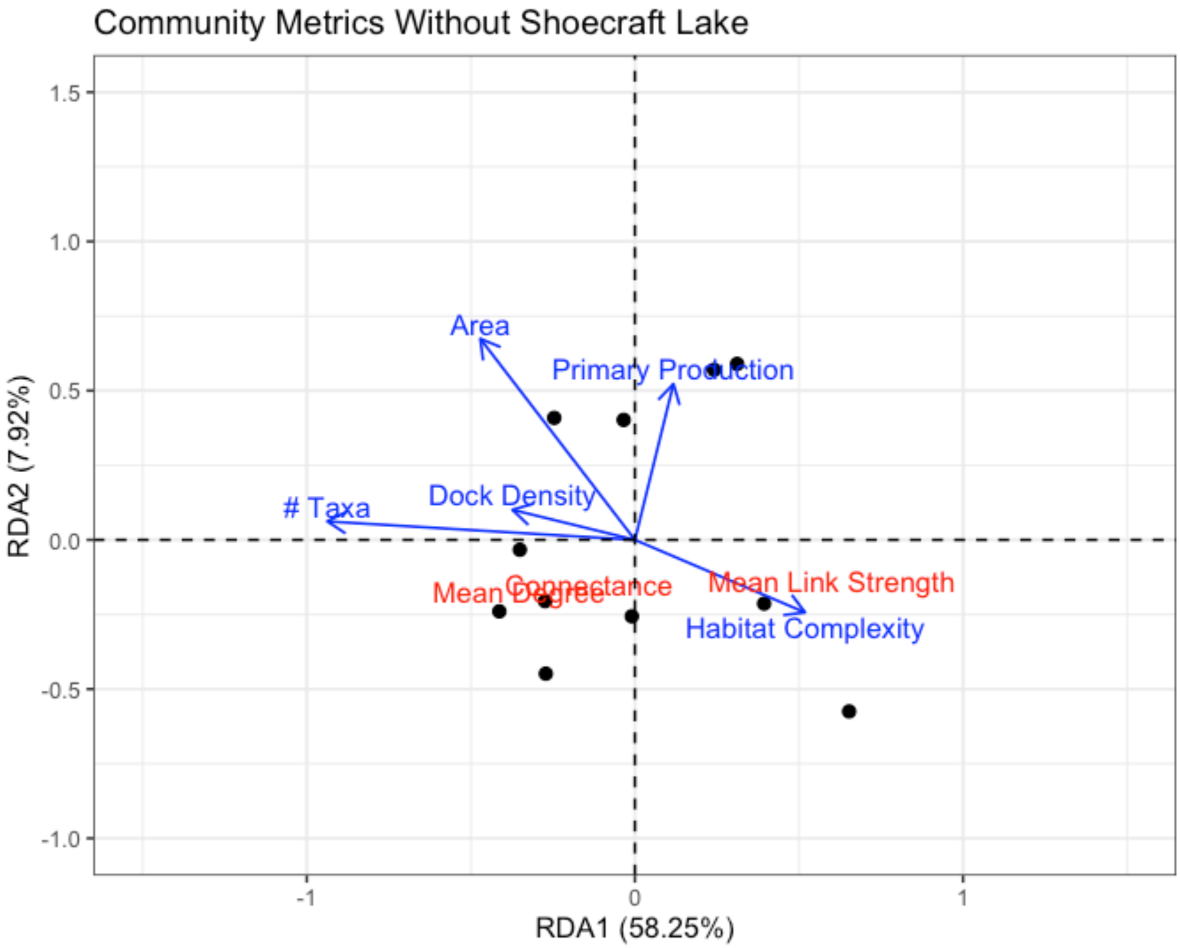

Figure A6: Updated RDA based on removing Shoecraft Lake. Blue lines represent explanatory variable where the length of the line indicates the relative contribution of that variable to explaining variation in the fitted response matrix while the direction of each arrow indicates a positive association with the corresponding explanatory variable. Red words represent the weighted response variables for the species-specific network metrics. Finally, black dots indicate the projected lake values for lakes containing pumpkinseed in the explanatory variable space.

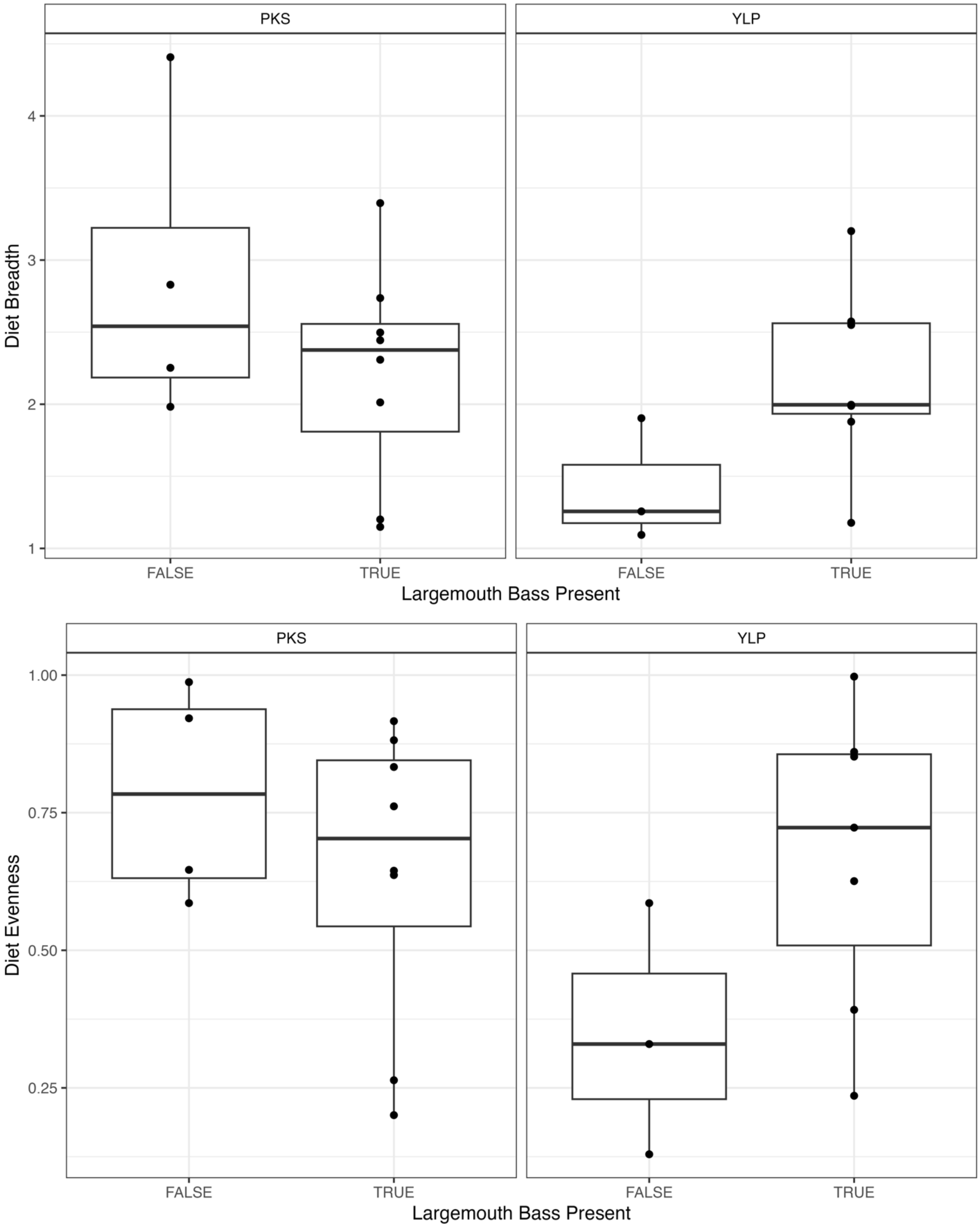

Figure A7: Comparison of diet breadth and diet evenness in yellow perch and pumpkinseed in lakes with and without largemouth bass. Points indicate observed values, while boxplot indicates median and the interquartile range.

Table A1: The descriptions of each branch of the decision tree (Figure A1) based on this study system and used to assign a literature pedigree to each study.

Species	Whether the species discussed in the paper are the "same" or "similar" to the species of interest. For Aquatic insects I will use the order rather than the species.
Method	Whether the study described uses qualitative (quali) or quantitative (quanti) methods to estimate the percent of diet in the stomachs for the species of interest.
Ecosystem	Whether the ecosystem in the study is the "same" ecosystem, "neighbouring" this system, or in a different country/ecosystem (foreign). Any lakes that are either in the PNW (Idaho, Washington, Oregon, BC) or the upper midwest (Michigan, Wisconsin, Minnesota, Southeastern Canada/southern Ontario) are the same. Northern Canada and other parts of the US are considered neighboring. Anywhere else is considered foreign. Rivers that are in the PNW are "neighboring" while rivers elsewhere are foreign.
Period	If the paper is from more than 10 years ago it is "old" if the paper is from10 years ago or more recent it is "recent"
N_Samples	The number of samples evaluated for the focus species.
Quanti_Samp_Des	This stands for quantitative sampling design. If the paper has a data rich design (> 50 samples per species) the paper is "rich" otherwise it is data "poor".
Quali_Samp_Des	The quality of the sampling design. If the paper is new and using new methods the paper qualifies as "rich". If the sampling design is relatively new and somewhat thorough the paper is "intermediate". If the paper uses an old sampling design then the paper is "old”.

Table A2: Abbreviations used in the diet and literature data tables with select common names and scientific names.

Abbreviation	Common Name	Scientific
AMF		*Amphipoda*
ARC		*Arachnida*
BBH	brown bullhead	*Ameiurus nebulosus*
BGL	bluegill	*Lepomis macrochirus*
BLC	black crappie	*Poxomis nigromaculatus*
BVL		*Bivalvia*
CHI		*Chironomidae*
CMS	Chinese mystery snail	*Cipangopaludina chinensis*
COL		*Coleoptera*
DAM	damselfly	*Zygoptera*
DPT		*Diptera*
DRG	dragonfly	*Epiprocta*
EFM	mayfly	*Ephemeroptera*
GPD	snail	*Gastropoda*
GSF	green sunfish	*Lepomis cyanellus*
HMI		*Hemiptera*
HMO		*Hymenoptera*
HYD		*Hydrachnidia*
HYG		*Hygrophila*
ISO		*Isopoda*
LMB	largemouth bass	*Micropterus salmoides*
MGA		*Megaloptera*
OLI		*Oligocheata*
PKS	pumpkinseed	*Lepomis gibbosus*
PLC		*Plecoptera*
RSC	red swamp crayfish	*Procambarus clarkii*
SC	Signal Crayfish	*Pacifastacus leniusculus*
SMB	smallmouth bass	*Micropterus dolomieu*
TBA		*Turbellaria*
TRB		*Trombidiformes*
TRI	caddisfly	*Trichoptera*
YLP	yellow perch	*Perca flavescens*
ZOO	zooplankton	*Cladocera, Copepoda, Rotifera*

Table A3: Mean diet proportions for each species based on the literature data for EcoDiet model. Each lake has different literature prior values due to the differences in prey items present in each lake. Empty cells indicate that these taxa were not included in the given lake. Taxa at the bottom of the food web are given diet proportions equal to zero and literature pedigree equal to one. They are distinguished from observations of predators that do not consume a given prey item by the lack of decimal point.

Lake	Diet Item	AMF	BGL	BLC	CMS	DAM	DPT	DRG	GSF	ISO	LMB	OLI	PKS	RKB	RSC	SC	SMB	TRI	YLP	ZOO
AGL	AMF	0			0	0.25	0			0			0.17	0.11					0.11	0
	CMS	0			0	0.00	0			0			0.21	0.00					0.08	0
	DAM	0			0	0.00	0			0			0.17	0.11					0.11	0
	DPT	0			0	0.25	0			0			0.17	0.11					0.11	0
	ISO	0			0	0.25	0			0			0.17	0.11					0.11	0
	PKS	0			0	0.00	0			0			0.00	0.17					0.07	0
	RKB	0			0	0.00	0			0			0.00	0.00					0.07	0
	YLP	0			0	0.00	0			0			0.00	0.17					0.00	0
	ZOO	0			0	0.25	0			0			0.10	0.20					0.34	0
	pedigree	**1**			**1**	**0.60**	**1**			**1**			**0.53**	**0.33**					**0.63**	**1**
BVR	CMS				0	0.00	0			0	0.00	0	0.21						0.08	0
	DAM				0	0.00	0			0	0.06	0	0.17						0.11	0
	DPT				0	0.33	0			0	0.06	0	0.17						0.11	0
	ISO				0	0.33	0			0	0.06	0	0.17						0.11	0
	LMB				0	0.00	0			0	0.00	0	0.00						0.07	0
	OLI				0	0.00	0			0	0.06	0	0.17						0.11	0
	PKS				0	0.00	0			0	0.37	0	0.00						0.07	0
	YLP				0	0.00	0			0	0.37	0	0.00						0.00	0
	ZOO				0	0.33	0			0	0.01	0	0.10						0.34	0
	pedigree				**1**	**0.60**	**1**			**1**	**0.45**	**1**	**0.53**						**0.63**	**1**
CTG	AMF	0	0.19				0	0.25		0	0.06		0.23						0.12	0
	BGL	0	0.00				0	0.00		0	0.25		0.00						0.05	0
	DPT	0	0.19				0	0.25		0	0.06		0.23						0.12	0
	DRG	0	0.19				0	0.00		0	0.06		0.23						0.12	0
	ISO	0	0.19				0	0.25		0	0.06		0.23						0.12	0
	LMB	0	0.06				0	0.00		0	0.00		0.00						0.05	0
	PKS	0	0.06				0	0.00		0	0.25		0.00						0.05	0
	YLP	0	0.06				0	0.00		0	0.25		0.00						0.00	0
	ZOO	0	0.06				0	0.25		0	0.01		0.10						0.36	0
	pedigree	**1**	**0.40**				**1**	**0.60**		**1**	**0.45**		**0.53**						**0.63**	**1**
KTM	DPT						0	0.33		0	0.08		0.30						0.16	0
	DRG						0	0.00		0	0.08		0.30						0.16	0
	ISO						0	0.33		0	0.08		0.30						0.16	0
	LMB						0	0.00		0	0.00		0.00						0.08	0
	PKS						0	0.00		0	0.37		0.00						0.08	0
	YLP						0	0.00		0	0.37		0.00						0.00	0
	ZOO						0	0.33		0	0.01		0.10						0.36	0
	pedigree						**1**	**0.60**		**1**	**0.45**		**0.53**						**0.63**	**1**
MTA	AMF	0				0.25	0			0	0.05		0.21		0.19	0.20			0.11	0

Lake	Diet Item	AMF	BGL	BLC	CMS	DAM	DPT	DRG	GSF	ISO	LMB	OLI	PKS	RKB	RSC	SC	SMB	TRI	YLP	ZOO
	DAM	0				0.00	0			0	0.05		0.21		0.19	0.20			0.11	0
	DPT	0				0.25	0			0	0.05		0.21		0.19	0.20			0.11	0
	ISO	0				0.25	0			0	0.05		0.21		0.19	0.20			0.11	0
	LMB	0				0.00	0			0	0.00		0.00		0.00	0.00			0.07	0
	PKS	0				0.00	0			0	0.28		0.00		0.00	0.00			0.07	0
	RSC	0				0.00	0			0	0.11		0.03		0.00	0.13			0.05	0
	SC	0				0.00	0			0	0.11		0.03		0.20	0.00			0.05	0
	YLP	0				0.00	0			0	0.28		0.00		0.00	0.00			0.00	0
	ZOO	0				0.25	0			0	0.01		0.10		0.04	0.05			0.33	0
	pedigree	**1**				**0.60**	**1**			**1**	**0.45**		**0.53**		**0.30**	**0.30**			**0.63**	**1**
NTH	AMF	0			0	0.20	0	0.20			0.04		0.14		0.17			0	0.08	0
	CMS	0			0	0.00	0	0.00			0.00		0.19		0.11			0	0.06	0
	DAM	0			0	0.00	0	0.20			0.04		0.14		0.17			0	0.08	0
	DPT	0			0	0.20	0	0.20			0.04		0.14		0.17			0	0.08	0
	DRG	0			0	0.20	0	0.00			0.04		0.14		0.17			0	0.08	0
	LMB	0			0	0.00	0	0.00			0.00		0.00		0.00			0	0.06	0
	PKS	0			0	0.00	0	0.00			0.28		0.00		0.00			0	0.06	0
	RSC	0			0	0.00	0	0.00			0.22		0.03		0.00			0	0.09	0
	TRI	0			0	0.20	0	0.20			0.04		0.14		0.17			0	0.08	0
	YLP	0			0	0.00	0	0.00			0.28		0.00		0.00			0	0.00	0
	ZOO	0			0	0.20	0	0.20			0.01		0.10		0.05			0	0.32	0
	pedigree	**1**			**1**	**0.60**	**1**	**0.60**			**0.45**		**0.53**		**0.30**			**1**	**0.63**	**1**
PNE	AMF	0	0.08		0	0.20	0	0.20		0	0.04		0.14		0.14	0.16	0.06		0.08	0
	BGL	0	0.00		0	0.00	0	0.00		0	0.14		0.00		0.00	0.00	0.06		0.03	0
	CMS	0	0.34		0	0.00	0	0.00		0	0.00		0.19		0.09	0.01	0.00		0.06	0
	DAM	0	0.08		0	0.00	0	0.20		0	0.04		0.14		0.14	0.16	0.06		0.08	0
	DPT	0	0.08		0	0.20	0	0.20		0	0.04		0.14		0.14	0.16	0.06		0.08	0
	DRG	0	0.08		0	0.20	0	0.00		0	0.04		0.14		0.14	0.16	0.06		0.08	0
	ISO	0	0.08		0	0.20	0	0.20		0	0.04		0.14		0.14	0.16	0.06		0.08	0
	LMB	0	0.04		0	0.00	0	0.00		0	0.00		0.00		0.00	0.00	0.06		0.03	0
	PKS	0	0.04		0	0.00	0	0.00		0	0.14		0.00		0.00	0.00	0.06		0.03	0
	RSC	0	0.00		0	0.00	0	0.00		0	0.11		0.01		0.00	0.13	0.23		0.05	0
	SC	0	0.00		0	0.00	0	0.00		0	0.11		0.01		0.19	0.00	0.23		0.05	0
	SMB	0	0.04		0	0.00	0	0.00		0	0.14		0.00		0.00	0.00	0.00		0.03	0
	YLP	0	0.04		0	0.00	0	0.00		0	0.14		0.00		0.00	0.00	0.06		0.00	0
	ZOO	0	0.05		0	0.20	0	0.20		0	0.01		0.10		0.04	0.05	0.00		0.32	0
	pedigree	**1**	**0.40**		**1**	**0.60**	**1**	**0.60**		**1**	**0.45**		**0.53**		**0.30**	**0.30**	**0.40**		**0.63**	**1**
SHC	DPT						0	0.50					0.45				0.23		0.25	0
	DRG						0	0.00					0.45				0.23		0.25	0
	PKS						0	0.00					0.00				0.27		0.08	0
	SMB						0	0.00					0.00				0.00		0.08	0
	YLP						0	0.00					0.00				0.27		0.00	0
	ZOO						0	0.50					0.10				0.00		0.36	0
	pedigree						**1**	**0.60**					**0.53**				**0.40**		**0.63**	**1**
SHW	AMF	0	0.07	0.12	0	0.17	0	0.17		0	0.04		0.12					0	0.07	0
	BGL	0	0.00	0.06	0	0.00	0	0.00		0	0.19		0.00					0	0.04	0

Lake	Diet Item	AMF	BGL	BLC	CMS	DAM	DPT	DRG	GSF	ISO	LMB	OLI	PKS	RKB	RSC	SC	SMB	TRI	YLP	ZOO
	BLC	0	0.04	0.00	0	0.00	0	0.00		0	0.19		0.00					0	0.04	0
	CMS	0	0.34	0.00	0	0.00	0	0.00		0	0.00		0.21					0	0.08	0
	DAM	0	0.07	0.12	0	0.00	0	0.17		0	0.04		0.12					0	0.07	0
	DPT	0	0.07	0.12	0	0.17	0	0.17		0	0.04		0.12					0	0.07	0
	DRG	0	0.07	0.12	0	0.17	0	0.00		0	0.04		0.12					0	0.07	0
	ISO	0	0.07	0.12	0	0.17	0	0.17		0	0.04		0.12					0	0.07	0
	LMB	0	0.04	0.06	0	0.00	0	0.00		0	0.00		0.00					0	0.04	0
	PKS	0	0.04	0.06	0	0.00	0	0.00		0	0.19		0.00					0	0.04	0
	TRI	0	0.07	0.12	0	0.17	0	0.17		0	0.04		0.12					0	0.07	0
	YLP	0	0.04	0.06	0	0.00	0	0.00		0	0.19		0.00					0	0.00	0
	ZOO	0	0.05	0.02	0	0.17	0	0.17		0	0.01		0.10					0	0.34	0
	pedigree	**1**	**0.40**	**0.43**	**1**	**0.60**	**1**	**0.60**		**1**	**0.45**		**0.53**					**1**	**0.63**	**1**
STR	AMF	0			0	0.20	0	0.20		0	0.05		0.14	0.09					0.09	0
	CMS	0			0	0.00	0	0.00		0	0.00		0.21	0.00					0.08	0
	DAM	0			0	0.00	0	0.20		0	0.05		0.14	0.09					0.09	0
	DPT	0			0	0.20	0	0.20		0	0.05		0.14	0.09					0.09	0
	DRG	0			0	0.20	0	0.00		0	0.05		0.14	0.09					0.09	0
	ISO	0			0	0.20	0	0.20		0	0.05		0.14	0.09					0.09	0
	LMB	0			0	0.00	0	0.00		0	0.00		0.00	0.11					0.05	0
	PKS	0			0	0.00	0	0.00		0	0.25		0.00	0.11					0.05	0
	RKB	0			0	0.00	0	0.00		0	0.25		0.00	0.00					0.05	0
	YLP	0			0	0.00	0	0.00		0	0.25		0.00	0.11					0.00	0
	ZOO	0			0	0.20	0	0.20		0	0.01		0.10	0.20					0.34	0
	pedigree	**1**			**1**	**0.60**	**1**	**0.60**		**1**	**0.45**		**0.53**	**0.33**					**0.63**	**1**
TLV	BGL		0.00			0.00	0				0.37		0.00							0
	DAM		0.38			0.00	0				0.12		0.45							0
	DPT		0.38			0.50	0				0.12		0.45							0
	LMB		0.10			0.00	0				0.00		0.00							0
	PKS		0.10			0.00	0				0.37		0.00							0
	ZOO		0.06			0.50	0				0.01		0.10							0
	pedigree		**0.40**			**0.60**	**1**				**0.45**		**0.53**							**1**
WLD	AMF	0	0.24				0		0.11		0.07		0.28		0.32			0	0.14	0
	BGL	0	0.00				0		0.07		0.14		0.00		0.00			0	0.03	0
	DPT	0	0.24				0		0.11		0.07		0.28		0.32			0	0.14	0
	GSF	0	0.05				0		0.00		0.14		0.00		0.00			0	0.03	0
	LMB	0	0.05				0		0.07		0.00		0.00		0.00			0	0.03	0
	PKS	0	0.05				0		0.07		0.14		0.00		0.00			0	0.03	0
	RSC	0	0.03				0		0.00		0.22		0.06		0.00			0	0.10	0
	TRI	0	0.24				0		0.11		0.07		0.28		0.32			0	0.14	0
	YLP	0	0.05				0		0.07		0.14		0.00		0.00			0	0.00	0
	ZOO	0	0.05				0		0.41		0.01		0.10		0.05			0	0.33	0
	pedigree	**1**	**0.40**				**1**		**0.35**		**0.45**		**0.53**		**0.30**			**1**	**0.63**	**1**

Table A4: Stomach content data as frequency of occurrence of observations for each lake. Only fish stomach contents were identified. Abbreviations can be found in Table 2.

Lake	Diet Item	LMB	PKS	RBT	RKB	YLP	BBH	BGL	SMB	BLC	GSF
AGL	AMF		1								
	BVL		3		1						
	DAM				2	1					
	DPT		4	1	5	1					
	DRG				1						
	Unk. Fish[1]				2	3					
	HMI				1						
	HYG		1			1					
	HMO		1	1							
	ISO		3			1					
	LMB				1						
	PLC				1						
	TRI		5	1	4						
	YLP					1					
	full		**8**	**2**	**8**	**5**					
BVR	AMF	1		3		3					
	BGL						1				
	COL	1									
	DAM			1							
	DPT	3	5	3		7	1				
	DRG		1			2					
	Unk. Fish[1]	1									
	HYG		2								
	ISO	1	3			5					
	LMB			1							
	ODO					1					
	PLC	1									
	GPD					6					
	TRI	2	1	1		2					
	Unknown[2]					1					
	ZOO	1	1			4					
	full	**5**	**5**	**4**		**11**	**1**				
CTG	AMF		1								
	BVL		5			1					
	DAM			1							
	DPT	1	4	4		8		4			
	DRG					1					
	Unk. Fish[1]	2		1		1		1			
	HYG							1			
	ISO		1								
	LMB	2									
	SMB	1									
	GPD		4					3			
	TRI		1								
	full	**5**	**6**	**5**		**10**		**7**			
KTM	AMF					7	1				
	ARC					1					
	DPT		3	4		1	1				
	Unk. Fish[1]	2		1			1				
	HMI			1							
	HYG		1								
	Insecta[3]	1									
	GPD		1								
	TRB			1							
	Unknown[2]						1				
	ZOO			2							
	full	**2**	**3**	**5**		**9**	**2**				
MTA	AMF			2		3					
	BVL		1								
	COL		1								

Lake	Diet Item	LMB	PKS	RBT	RKB	YLP	BBH	BGL	SMB	BLC	GSF
	DAM		1								
	DPT		1	11		3					
	HMO		1								
	ISO		1								
	TRI			7		2					
	Unknown[2]		1								
	OLI					1					
	ZOO		1			4					
	full		**3**	**12**		**8**					
NTH	AMF					2					
	COL					1					
	DAM			1							
	DPT			2		7					
	Unk. Fish[1]	1				1					
	HMO			1							
	ISO					1					
	GPD					2					
	TRI			1		3					
	Unknown[2]		1			2					
	ZOO		1	4		5					
	full	**1**	**2**	**5**		**10**					
PNE	AMF		7			7		7	1		
	BGL						1				
	BVL		2	1		4		1			
	Crayfish[4]								1		
	DPT		7	1		6		7	1		
	DRG								1		
	Fish								1		
	HYG			1							
	ISO		6	1		11		8			
	LMB	2									
	ODO	1	1								
	GPD		5	1		4		7			
	TRI		4			1		5			
	Unknown[2]	1									
	full	**4**	**9**	**1**		**11**	**1**	**12**	**4**		
SHC	AMF			1		6	7				
	BVL		1	1			5		1		
	Crayfish[4]						1		1		
	DAM						1				
	DPT		2	1		2	7		1		
	DRG					1					
	Ukn. Fish[1]		2			4			3		
	ISO		1			4	8		1		
	MGA						1				
	PLC						1				
	GPD		1	2		1	5				
	TRI		3	2		1	3		1		
	Unknown[2]										
	OLI			1							
	ZOO		1								
	full		**6**	**3**		**10**	**8**		**5**		
SHW	AMF		2	1		1		6			
	BVL					1	1				
	DAM	2	1					2		2	
	DPT	2	4	6		7	1	11		4	
	DRG					2					
	Fish	1									
	HMI							1			
	ISO		3			2		7			
	MGA		1			3					
	PLC							1			
	GPD					1					

Lake	Diet Item	LMB	PKS	RBT	RKB	YLP	BBH	BGL	SMB	BLC	GSF
	TRI		1					10			
	TRB									1	
	Unknown^2					1		2			
	ZOO	1		2		1					
	full	**5**	**4**	**7**		**8**	**1**	**12**		**4**	
STR	AMF		1	2							
	DPT			5		2					
	DRG				1						
	EFM				1						
	Unk. Fish^1	1			1						
	HYG			1							
	ISO		3		2						
	GPD				2						
	TRI		2	1	2						
	ZOO				1	1					
	full	**1**	**4**	**7**	**6**	**2**					
TLV	AMF		2								
	DAM							1			
	DPT		4					5			
	DRG	2						2			
	Fish	1									
	HMI							1			
	HYD							1			
	ISO							1			
	GPD		1								
	TRI		2								
	Unknown^2		1								
	full	**4**	**5**					**8**			
WLD	AMF	2	4	1		1		6			
	BVL		3								1
	Crayfish^4										1
	DPT	1	6	6		1		7			
	DRG					1					
	Unk. Fish^1	11		7		2		1			2
	ISO	1	6			3		7			
	LMB	1		1							
	MGA		2								
	ODO					1					
	PLC		1								
	GPD	1	2					1			1
	TRI	1	7			3	1	4			9
	TBA	2									
	OLI			1							
	ZOO					2					
	full	**11**	**8**	**11**		**7**	**1**	**10**			**9**

1. Unidentifiable fish
2. Unidentifiable diet item, for example a piece of amorphous flesh
3. Terrestrial insect
4. Crayfish were either red swamp crayfish (Procambarus clarkia) or signal crayfish (*Pacifastacus leniusculus*)

Table A5: Literature sources used to inform the literature prior data and the corresponding ranking values from the decision tree (Figure A1).

PaperID	Taxa	First Author (Last, First)	Pub_Year	Species	Method	Ecosystem	Period	N_Samples	Quanti Samp Des	Quali Samp Des	Pedigree
22	BBH	Collier, Kevin	2018	same	quanti	foreign	new	35			0.3
23	BBH	Rechulicz, Jacek	2021	same	quanti	foreign	new	>100			0.3
10	BGL	Andraso, Gregory	2005	same	quanti	neighboring	old	36			0.4
2	BGL	Flemer, David	1966	same	quanti	neighboring	old	273			0.4
11	BGL	Gerry, SP	2013	same	quanti	neighboring	recent	19			0.5
12	BGL	Olson, NW	2003	same	quanti	neighboring	old	72			0.4
1	BGL	Taguchi, T	2014	same	quanti	foreign	NA	125			0.3
36	BLC	Fieiner, Zachary	2018	same	quanti	neighboring	new	18			0.5
34	BLC	Keast, Allen	1968	same	quanti	neighboring	old	25			0.4
14	BLC	Liao, H	2002	same	quanti	neighboring	old	>100			0.4
35	BLC	Tuten, Travis	2008	same	quanti	neighboring	old	300			0.4
21	GSF	Biggins, Richard	1968	same	quanti	neighboring	old	195			0.4
20	GSF	Lemly, Dennis	1985	same	quanti	foreign	NA	250			0.3
4	LMB	Braun, Camrin	2011	same	quanti	neighboring	old	37			0.4
3	LMB	Glade, Kamden	2023	same	quanti	same	recent	620	rich	rich	1
8	LMB	Gondinho, Francisco	1997	same	quanti	foreign	NA	62			0.3
6	LMB	Hodgson, James	2005	same	quanti	same	old	3873			0.6
5	LMB	Jo, Hyunbin	2014	same	quanti	foreign	NA	27			0.3
14	LMB	Liao, H	2002	same	quanti	neighboring	old	>100			0.4
1	LMB	Taguchi, T	2014	same	quanti	foreign	NA	145			0.3
7	LMB	Tsunoda, Hiroshi	2018	same	quanti	foreign	NA	884			0.3
10	PKS	Andraso, Gregory	2005	same	quanti	neighboring	old	24			0.4
8	PKS	Gondinho, Francisco	1997	same	quanti	foreign	NA	294			0.3
9	PKS	Locke, Sean	2013	same	quanti	same	recent	99	rich	intermediate	0.9
19	RBT	Jeppson, Paul	1959	same	quanti	same	old	32			0.6
32	RBT	Jodar, DNN	2020	same	quanti	foreign	new	40			0.3
18	RBT	Marsden, Ellen	2022	Lake Trout	quanti	neighboring	recent	114			0.5
33	RBT	Mumby, James	2018	same	quanti	foreign	new	21			0.3
30	RKB	George, Elinor	1979	same	quanti	foreign	old	20			0.3
29	RKB	Keast, Allen	1968	same	quanti	neighboring	old	10			0.4
38	RKB	Paterson, Gordon	2006	same	quanti	foreign	old	20			0.3
25	RSC	Correia, Alexandra	2002	same	quanti	foreign	old	224			0.3
24	RSC	PerezBote, J	2005	same	quanti	foreign	old	1248			0.3
27	SC	Ercoli, Fabio	2021	same	quanti	foreign	recent	13			0.3
26	SC	Guan, RuiZhang	1998	same	quanti	foreign	old	75			0.3

PaperID	**Taxa**	**First Author (Last, First)**	**Pub_Year**	**Species**	**Method**	**Ecosystem**	**Period**	**N_Samples**	**Quanti Samp Des**	**Quali Samp Des**	**Pedigree**
28	SC	Vedia, Ivan	2019	same	quanti	foreign	recent	85			0.3
15	SCP	Johnson, James	2017	same	quanti	neighboring	recent	174			0.5
17	SCP	Tabor, Roger	2016	same	quanti	same	recent				0.6
14	SMB	Liao, H	2002	same	quanti	neighboring	old	>100			0.4
37	SMB	Olson, Mark	2003	same	quanti	neighboring	old	20			0.4
16	SMB	Weidel, Brian	2000	same	quanti	neighboring	old	230			0.4
13	YLP	Fullhart, Howard	2002	same	quanti	same	old	389			0.6
14	YLP	Liao, H	2002	same	quanti	neighboring	old	>100			0.4
31	YLP	McIntyre	2006	same	quanti	same	new	66	rich	intermediate	0.9

Table A6: Simple linear regression results for effective number of prey items. Significance values corrected for seven multiple comparisons within species α = 0.0072 (. $p < 0.05$; * $p < 0.0072$).

Taxon	Variable	Beta	coef	p.val	
YLP	LitCvrQ_d	(Intercept)	3.002	0.0000	*
		LitCvrQ_d	-3.186	0.0040	*
	LitRipCvQ_10Bd	(Intercept)	3.112	0.0021	*
		LitRipCvQ_10Bd	-2.513	0.1236	
	RVegQ_10B	(Intercept)	1.896	0.0538	
		RVegQ_10B	0.027	0.9845	
	n.nodes	(Intercept)	2.198	0.0525	
		n.nodes	-0.030	0.7734	
	Docks_per_km	(Intercept)	1.790	0.0210	.
		Docks_per_km	0.004	0.8438	
	Primary production	(Intercept)	2.047	0.0027	*
		Chl-a concentration	-0.024	0.8450	
	Area	(Intercept)	1.022	0.0358	.
		Area	0.013	0.0435	.
PKS	LitCvrQ_d	(Intercept)	2.767	0.0015	*
		LitCvrQ_d	-0.916	0.5783	
	LitRipCvQ_10Bd	(Intercept)	3.233	0.0070	*
		LitRipCvQ_10Bd	-1.597	0.4056	
	RVegQ_10B	(Intercept)	3.283	0.0086	*
		RVegQ_10B	-1.332	0.4043	
	n.nodes	(Intercept)	0.878	0.4178	
		n.nodes	0.170	0.1546	
	Docks_per_km	(Intercept)	2.042	0.0271	.
		Docks_per_km	0.015	0.6088	
	Chl-a concentration	(Intercept)	2.608	0.0023	*
		Chl-a concentration	-0.046	0.7795	
	Area	(Intercept)	1.569	0.0234	.
		Area	0.013	0.1376	
LMB	LitCvrQ_d	(Intercept)	1.232	0.3394	
		LitCvrQ_d	3.531	0.2660	
	LitRipCvQ_10Bd	(Intercept)	-0.685	0.6695	
		LitRipCvQ_10Bd	6.066	0.0770	
	RVegQ_10B	(Intercept)	-1.284	0.4733	
		RVegQ_10B	5.528	0.0629	
	n.nodes	(Intercept)	4.357	0.0866	
		n.nodes	-0.192	0.4022	
	Docks_per_km	(Intercept)	5.861	0.0041	*
		Docks_per_km	-0.149	0.0315	.
	Chl-a concentration	(Intercept)	1.985	0.2281	
		Chl-a concentration	0.135	0.6889	
	Area	(Intercept)	4.354	0.0502	
		Area	-0.032	0.3146	
BGL	LitCvrQ_d	(Intercept)	3.248	0.0452	.
		LitCvrQ_d	-1.724	0.4806	
	LitRipCvQ_10Bd	(Intercept)	3.178	0.1627	
		LitRipCvQ_10Bd	-1.130	0.7262	
	RVegQ_10B	(Intercept)	2.219	0.3540	
		RVegQ_10B	0.443	0.8817	
	n.nodes	(Intercept)	0.197	0.8640	
		n.nodes	0.234	0.1053	

Taxon	Variable	Beta	coef	p.val	
	Docks_per_km	(Intercept)	2.606	0.1545	
		Docks_per_km	-0.003	0.9616	
	Chl-a concentration	(Intercept)	2.319	0.1230	
		Chl-a concentration	0.050	0.8381	
	Area	(Intercept)	1.335	0.5099	
		Area	0.020	0.5385	
DRG	LitCvrQ_d	(Intercept)	2.0533	0.1444	
		LitCvrQ_d	4.4189	0.3194	
	LitRipCvQ_10Bd	(Intercept)	0.9494	0.6460	
		LitRipCvQ_10Bd	5.1880	0.2741	
	RVegQ_10B	(Intercept)	1.7244	0.4291	
		RVegQ_10B	2.5112	0.4615	
	n.nodes	(Intercept)	0.0866	0.9320	
		n.nodes	0.3342	0.0187	
	Docks_per_km	(Intercept)	3.1892	0.0729	
		Docks_per_Km	0.0039	0.9450	
	Chl-a concentration	(Intercept)	3.3059	0.0383	
		Chl-a concentration	-0.0294	0.9098	
	Area	(Intercept)	4.0716	0.0058	*
		Area	-3.0696	0.3605	
DAM	LitCvrQ_d	(Intercept)	4.3900	0.0099	.
		LitCvrQ_d	-2.6702	0.4041	
	LitRipCvQ_10Bd	(Intercept)	3.8650	0.0799	
		LitRipCvQ_10Bd	-0.8845	0.8048	
	RVegQ_10B	(Intercept)	2.8986	0.1498	
		RVegQ_10B	0.7595	0.7743	
	n.nodes	(Intercept)	-0.1910	0.9008	
		n.nodes	0.3690	0.0458	.
	Docks_per_km	(Intercept)	4.2965	0.0148	.
		Docks_per_Km	-0.0311	0.4826	
	Chl-a concentration	(Intercept)	2.2142	0.0986	
		Chl-a concentration	0.4075	0.3068	
	Area	(Intercept)	3.9889	0.0285	
		Area	-2.3595	0.6727	

Table A7: Logistic regression model results for diet evenness. Significance values corrected for seven multiple comparisons within species α = 0.0072 (. $p < 0.05$; * $p < 0.0072$).

Taxon	Variable	Variable	coef	p.val
YLP	LitCvrQ_d	(Intercept)	2.0587	0.2194
		LitCvrQ_d	-5.2081	0.2529
	LitRipCvQ_10Bd	(Intercept)	2.2832	0.3772
		LitRipCvQ_10Bd	-4.1878	0.4195
	RVegQ_10B	(Intercept)	0.4727	0.8486
		RVegQ_10B	-0.3306	0.9327
	n.nodes	(Intercept)	-0.7615	0.7939
		n.nodes	0.1095	0.7185
	Chl-a concentration	(Intercept)	-0.3907	0.7782
		Chl-a concentration	0.1998	0.5853
	Area	(Intercept)	-0.5685	0.7180
		Area	0.0127	0.5692
	Docks_per_km	(Intercept)	0.2916	0.8752
		Docks_per_km	-0.0008	0.9902
PKS	LitCvrQ_d	(Intercept)	0.5517	0.7127
		LitCvrQ_d	0.6893	0.8569
	LitRipCvQ_10Bd	(Intercept)	1.0161	0.6599
		LitRipCvQ_10Bd	-0.4312	0.9222
	RVegQ_10B	(Intercept)	1.6114	0.5204
		RVegQ_10B	-1.2613	0.7355
	n.nodes	(Intercept)	-0.9632	0.7333
		n.nodes	0.1962	0.5304
	Chl-a concentration	(Intercept)	0.4912	0.7252
		Chl-a concentration	0.1066	0.7793
	Area	(Intercept)	-0.6962	0.6881
		Area	0.0247	0.3831
	Docks_per_km	(Intercept)	-0.1869	0.9196
		Docks_per_km	0.0379	0.5806
LMB	LitCvrQ_d	(Intercept)	1.8891	0.5152
		LitCvrQ_d	-0.7336	0.9081
	LitRipCvQ_10Bd	(Intercept)	1.0692	0.7988
		LitRipCvQ_10Bd	0.9298	0.9002
	RVegQ_10B	(Intercept)	0.3039	0.9418
		RVegQ_10B	1.8546	0.7567
	n.nodes	(Intercept)	1.8226	0.7218
		n.nodes	-0.0275	0.9617
	Chl-a concentration	(Intercept)	2.7439	0.3863
		Chl-a concentration	-0.2447	0.6812
	Area	(Intercept)	3.3248	0.5058
		Area	-0.0325	0.7107
	Docks_per_km	(Intercept)	2.2726	0.6473
		Docks_per_km	-0.0341	0.8856
BGL	LitCvrQ_d	(Intercept)	1.3635	0.5716
		LitCvrQ_d	-0.8457	0.8689
	LitRipCvQ_10Bd	(Intercept)	1.4287	0.7141
		LitRipCvQ_10Bd	-0.7360	0.9106
	RVegQ_10B	(Intercept)	1.0651	0.8096
		RVegQ_10B	-0.0780	0.9896
	n.nodes	(Intercept)	-1.5892	0.6896
		n.nodes	0.2725	0.5179
		(Intercept)	0.5538	0.8139

Taxon	Variable	Variable	coef	p.val
	Chl-a concentration	Chl-a concentration	0.1063	0.8343
	Area	(Intercept)	-0.9245	0.8299
		Area	0.0325	0.6531
	Docks_per_km	(Intercept)	1.2200	0.6817
		Docks_per_km	-0.0098	0.9394
DRG	LitCvrQ_d	(Intercept)	0.2132	0.9370
		LitCvrQ_d	3.8853	0.6937
	LitRipCvQ_10Bd	(Intercept)	0.5094	0.9100
		LitRipCvQ_10Bd	1.6680	0.8673
	RVegQ_10B	(Intercept)	1.5287	0.7175
		RVegQ_10B	-0.4409	0.9466
	n.nodes	(Intercept)	-0.8147	0.8249
		n.nodes	0.2255	0.5778
	Docks_per_km	(Intercept)	1.0826	0.6977
		Docks_per_Km	0.0069	0.9485
	Chl-a concentration	(Intercept)	1.1141	0.5683
		Chl-a concentration	0.0215	0.9613
	Area	(Intercept)	2.0234	0.3149
		Area	-2.8485	0.6515
DAM	LitCvrQ_d	(Intercept)	1.2446	0.6122
		LitCvrQ_d	0.7896	0.9013
	LitRipCvQ_10Bd	(Intercept)	0.5870	0.8679
		LitRipCvQ_10Bd	1.8604	0.7860
	RVegQ_10B	(Intercept)	0.5528	0.8667
		RVegQ_10B	1.4995	0.7627
	n.nodes	(Intercept)	0.5129	0.9026
		n.nodes	0.1063	0.8066
	Docks_per_km	(Intercept)	2.4436	0.4076
		Docks_per_Km	-0.0306	0.7353
	Chl-a concentration	(Intercept)	1.0172	0.6527
		Chl-a concentration	0.1842	0.8183
	Area	(Intercept)	2.4646	0.3898
		Area	-3.6505	0.7216

Table A8: Negative binomial regression model results for betweenness centrality. Table A2: Logistic regression model results for diet evenness. Significance values corrected for seven multiple comparisons within species α = 0.0072 (. p < 0.05; * p < 0.0072).

Taxon	Variable	Beta	coef	p.val	
DAM	LitCvrQ_d	(Intercept)	0.7833	0.6177	
		LitCvrQ_d	0.6091	0.8771	
	LitRipCvQ_10Bd	(Intercept)	1.6803	0.0361	
		LitRipCvQ_10Bd	-1.3208	0.3985	
	RVegQ_10B	(Intercept)	1.6544	0.4434	
		RVegQ_10B	-1.0077	0.7477	
	n.nodes	(Intercept)	2.2268	0.3983	
		n.nodes	-0.1260	0.6317	
	Chl-a concentration	(Intercept)	0.8731	0.4656	
		Chl-a concentration	0.0949	0.8068	
	Area	(Intercept)	-0.1246	0.9410	
		Area	0.0174	0.4974	
	Docks_per_km	(Intercept)	0.6436	0.3187	
		Docks_per_km	0.0125	0.5361	
PKS	LitCvrQ_d	(Intercept)	0.5052	0.5818	
		LitCvrQ_d	-2.0318	0.4249	
	LitRipCvQ_10Bd	(Intercept)	1.8214	0.1825	
		LitRipCvQ_10Bd	-4.3420	0.1477	
	RVegQ_10B	(Intercept)	2.0099	0.1267	
		RVegQ_10B	-3.7345	0.1009	
	n.nodes	(Intercept)	2.1449	0.2089	
		n.nodes	-0.2687	0.1780	
	Chl-a concentration	(Intercept)	-1.4161	0.0583	
		Chl-a concentration	0.3266	0.0208	.
	Area	(Intercept)	-1.1196	0.2319	
		Area	0.0133	0.2576	
	Docks_per_km	(Intercept)	0.2264	0.8439	
		Docks_per_km	-0.0156	0.7089	
YLP	LitCvrQ_d	(Intercept)	0.4858	0.5788	
		LitCvrQ_d	-1.8046	0.4830	
	LitRipCvQ_10Bd	(Intercept)	-0.6107	0.6786	
		LitRipCvQ_10Bd	1.0619	0.7158	
	RVegQ_10B	(Intercept)	-2.0218	0.1756	
		RVegQ_10B	2.9723	0.1652	
	n.nodes	(Intercept)	0.6671	0.6985	
		n.nodes	-0.0822	0.6534	
	Chl-a concentration	(Intercept)	-1.1498	0.2165	
		Chl-a concentration	0.2700	0.1768	
	Area	(Intercept)	1.2158	0.1347	
		Area	-0.0223	0.1198	
	Docks_per_km	(Intercept)	1.8112	0.0464	.
		Docks_per_km	-0.0789	0.0495	.
BGL	LitCvrQ_d	(Intercept)	-2.1594	0.2493	
		LitCvrQ_d	3.4529	0.2976	
	LitRipCvQ_10Bd	(Intercept)	-1.9501	0.4479	
		LitRipCvQ_10Bd	2.4211	0.5481	
	RVegQ_10B	(Intercept)	-0.1071	0.9650	
		RVegQ_10B	-0.5666	0.8665	
	n.nodes	(Intercept)	2.1854	0.3010	
		n.nodes	-0.3017	0.2350	

Taxon	Variable	Beta	coef	p.val	
	Chl-a concentration	(Intercept)	-0.8326	0.5535	
		Chl-a concentration	0.0709	0.7950	
	Area	(Intercept)	0.6471	0.7841	
		Area	-0.0196	0.6260	
	Docks_per_km	(Intercept)	0.2080	0.9073	
		Docks_per_km	-0.0351	0.6841	
DRG	LitCvrQ_d	(Intercept)	1.9085	0.0006	*
		LitCvrQ_d	-2.0805	0.3028	
	LitRipCvQ_10Bd	(Intercept)	2.3659	0.0164	.
		LitRipCvQ_10Bd	-2.3060	0.3033	
	RVegQ_10B	(Intercept)	1.9573	0.0340	.
		RVegQ_10B	-0.9910	0.5071	
	n.nodes	(Intercept)	0.5199	0.5125	
		n.nodes	0.0831	0.2681	
	Chl-a concentration	(Intercept)	0.8778	0.0560	
		Chl-a concentration	0.1019	0.2704	
	Area	(Intercept)	1.5314	0.0002	*
		Area	-0.0030	0.6229	
	Docks_per_km	(Intercept)	0.7587	0.2305	
		Docks_per_km	0.0230	0.3111	
LMB	LitCvrQ_d	(Intercept)	0.3195	0.9101	
		LitCvrQ_d	-7.8664	0.4838	
	LitRipCvQ_10Bd	(Intercept)	384.2007	0.9996	
		LitRipCvQ_10Bd	-1086.0167	0.9996	
	RVegQ_10B	(Intercept)	11.6347	0.6562	
		RVegQ_10B	-26.2858	0.6347	
	n.nodes	(Intercept)	3.2066	0.5493	
		n.nodes	-0.6481	0.3884	
	Chl-a concentration	(Intercept)	-1.8380	0.4700	
		Chl-a concentration	-0.0261	0.9636	
	Area	(Intercept)	39.2297	0.9998	
		Area	-1.5384	0.9998	
	Docks_per_km	(Intercept)	-1.1204	0.7448	
		Docks_per_km	-0.0386	0.8094	

Table A9: Logistic regression model results for connectance. Significance values corrected for seven multiple comparisons $\alpha = 0.0072$ (. $p < 0.05$; * $p < 0.0072$).

Response Variable	**Explanatory Variable**	**Beta**	**coef**	**p.val**	
Connectance	LitCvrQ_d	(Intercept)	-0.4467	0.7617	
		LitCvrQ_d	-0.7078	0.8504	
	LitRipCvQ_10Bd	(Intercept)	-0.2923	0.8969	
		LitRipCvQ_10Bd	-0.8230	0.8513	
	RVegQ_10B	(Intercept)	-0.4091	0.8630	
		RVegQ_10B	-0.4610	0.8988	
	n.nodes	(Intercept)	-0.5244	0.8424	
		n.nodes	-0.0194	0.9451	
	Chl-a concentration	(Intercept)	-0.5582	0.6794	
		Chl-a concentration	-0.0419	0.9063	
	Area	(Intercept)	-1.0247	0.4976	
		Area	0.0049	0.8132	
	Docks_per_km	(Intercept)	-0.9035	0.6229	
		Docks_per_km	0.0075	0.9068	
Mean Link Strength	LitCvrQ_d	(Intercept)	-2.2541	0.2798	
		LitCvrQ_d	1.0588	0.8306	
	LitRipCvQ_10Bd	(Intercept)	-2.5684	0.4223	
		LitRipCvQ_10Bd	1.3928	0.8143	
	RVegQ_10B	(Intercept)	-2.4471	0.4718	
		RVegQ_10B	0.9120	0.8559	
	n.nodes	(Intercept)	-0.3766	0.9206	
		n.nodes	-0.1682	0.6961	
	Chl-a concentration	(Intercept)	-1.4367	0.5608	
		Docks_per_Km	-0.0161	0.8589	
	Area	(Intercept)	-1.8411	0.2948	
		Chl-a concentration	-0.0051	0.9914	
	Docks_per_km	(Intercept)	-1.6065	0.4406	
		Area	-0.0040	0.8969	
Mean Degree	LitCvrQ_d	(Intercept)	4.9071	0.0000	*
		LitCvrQ_d	-2.2286	0.1324	
	LitRipCvQ_10Bd	(Intercept)	4.6290	0.0005	*
		LitRipCvQ_10Bd	-1.0639	0.5616	
	RVegQ_10B	(Intercept)	3.6739	0.0038	*
		RVegQ_10B	0.6645	0.6642	
	n.nodes	(Intercept)	2.2121	0.0341	
		n.nodes	0.2075	0.0571	
	Chl-a concentration	(Intercept)	3.8720	0.0004	*
		Docks_per_Km	0.0084	0.7577	
	Area	(Intercept)	4.4888	0.0000	*
		Chl-a concentration	-0.1199	0.4008	
	Docks_per_km	(Intercept)	3.5706	0.0001	*
		Area	0.0081	0.3565	

Table A10: Zooplankton reliance for yellow perch logistic regression model results. Significance values corrected for seven multiple comparisons within species $\alpha = 0.0072$ (. $p < 0.05$; * $p < 0.0072$).

Variable	**Beta**	**coef**	**p.val**
LitCvrQ_d	(Intercept)	-2.8452	0.1263
	LitCvrQ_d	5.3567	0.2379
LitRipCvQ_10Bd	(Intercept)	-3.6722	0.2274
	LitRipCvQ_10Bd	5.6150	0.3340
RVegQ_10B	(Intercept)	-1.7799	0.5246
	RVegQ_10B	1.4238	0.7426
n.nodes	(Intercept)	0.4126	0.8982
	n.nodes	-0.1405	0.6819
Docks_per_km	(Intercept)	-0.7908	0.6953
	Docks_per_km	-0.0039	0.9554
Chl-a concentration	(Intercept)	-0.1810	0.8991
	Chl-a concentration	-0.2248	0.5893
Area	(Intercept)	1.0102	0.6059
	Area	-0.0311	0.3341