Consumer biodiversity increases organic nutrient availability across aquatic and terrestrial ecosystems

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Abstract :

Human land-use intensification threatens arthropod (for example, insect and spider) biodiversity across aquatic and terrestrial ecosystems. Insects and spiders play critical roles in ecosystems by accumulating and synthesizing organic nutrients such as polyunsaturated fatty acids (PUFAs). However, links between biodiversity and nutrient content of insect and spider communities have yet to be quantified. We relate insect and spider richness to biomass and PUFA-mass from stream and terrestrial communities encompassing nine land uses. PUFA-mass and biomass relate positively to biodiversity across ecosystems. In terrestrial systems, human-dominated areas have lower biomass and PUFA-mass than more natural areas, even at equivalent levels of richness. Aquatic ecosystems have consistently higher PUFA-mass than terrestrial ecosystems. Our findings reinforce the importance of conserving biodiversity and highlight the distinctive benefits of aquatic biodiversity.

Main Text:

Earth's biodiversity is decreasing across ecosystems at all trophic levels as a consequence of anthropogenic stressors, especially climate and land-use change (*1–3*). A wealth of studies suggests that biodiversity loss, especially that of primary producers (i.e., plants and algae), can impair key ecosystem functions (e.g., (*4–5*)). The effects of consumer species richness on ecosystem functions remain poorly understood (*6-8*), but is urgently needed in light of major, recent declines in both animal diversity and biomass(e.g., (*3, 9-11*)).

Consumers provide an especially valuable, but underappreciated ecosystem function to one another: they both synthesize and accumulate many important organic nutrients in their bodies (Fig. 1A; (*12–15*)). Importantly, unlike elemental nutrients (e.g., N, P), organic nutrients are ephemeral in that they often quickly oxidize into simpler compounds after organisms die, upon which their value to consumers quickly diminishes. At present, the nutritional functions provided by consumers are poorly-accounted for in currencies other than biomass or elemental nutrients (*16, 17*) and organic dietary nutrients have yet to be widely incorporated into biodiversity-ecosystem function (BEF; i.e., relationships between species and/or functional richness and key ecosystem functions like production or nutrient cycling) research (but see (*18*)). Organic nutrients like long-chain polyunsaturated fatty acids (LC-PUFA) are especially important for consumers, and aquatic ecosystems food webs typically contain more of these key fats than do their terrestrial counterparts (e.g., (*19–20*)). Consequently, consumers that actively move across ecosystem boundaries as part of their life cycles, such as emergent stream insects in riparian terrestrial areas, can serve as sources of LC-PUFA in food webs where these nutrients would otherwise be rare and limit secondary production (e.g., (*20-22*)).

As the most diverse group of consumers on earth (*24*), insects are particularly important to study from a nutritional BEF perspective. Insects and spiders serve as crucial intermediate trophic links within food webs, providing a conduit for the transfer, accumulation, and synthesis of organic nutrients between primary producers and higher trophic levels (e.g., (*20, 25-26*)). Furthermore, insects and other arthropods are experiencing some of the greatest regional population and diversity losses (e.g., (*3, 9, 11, 27*), but see (*9, 38*)), making it especially important to understand the functions that their biodiversity provides. Insect diversity and abundance are particularly threatened by land-use changes, such as urbanization, farming intensification, and wetland draining (*29*), which have the potential to alter BEF relationships (e.g., (*17, 30-32*)).

Here, we examined the relationship between insect and spider biodiversity, and their biomass and organic nutrient production, using two databases of over 577,000 records of observations of 7,675 species of insects and spiders sampled in 419 wadable stream and 323 terrestrial communities across Switzerland (Figure S2; *33-35*). We examined how such relationships varied with human land-use and habitat-type by comparing both stream and terrestrial communities from nine land-use categories ranging from urban city centers to natural grasslands and forests (Fig. 2A-B), asking how anthropogenic and environmental factors influence BEF relationships (*5, 30, 34*) and including those for organic nutrients. We specifically focused our analyses on the availability of omega-3 (n-3) and omega-6 (n-6) PUFA, which are essential organic dietary nutrients for most consumers (*12, 35-36*). Aquatic insects have much higher n-3 LC-PUFA content compared to terrestrial insects, due to the greater n-3 LC-PUFA content of aquatic primary

producers (Figure 1A; (*37-38*)). Aquatic insects, are the main source of n-3 PUFA for a diversity of vertebrate predators, ranging from fish to birds to mammals (*20, 39-40*). In contrast, n-6 PUFA are often readily available throughout both aquatic and terrestrial food webs (*37-38*).

Most work on the effects of land-use on BEF has focused exclusively freshwater or terrestrial ecosystems, and limiting our understanding of how biodiversity sustains food webs across ecosystem boundaries (e.g., (*25, 41*)). Ecotones can be especially important sources of scarce organic nutrients (e.g., (*20*)). We propose that aquatic insect biodiversity likely has especially strong effects on n-3 LC-PUFA availability, providing an important cross-ecosystem function for insectivorous predators. Considering such availability as an ecosystem function allows us to assess the nutritional quality of resources for consumers that forage across riparian meta-ecosystem boundaries, and, using this currency, evaluate the significance of management actions that preserve connectivity between ecosystems.

Total biomass of nutritionally relevant fatty acids increases with species richness

We found that insect and spider species diversity in both stream and terrestrial ecosystems was positively correlated with biomass and organic nutrient (i.e., PUFA) availability (Fig. 2C-H). Species richness varied by at least one order of magnitude in aquatic communities, and by over two orders of magnitude in terrestrial communities (Fig 2). In spite of differences in the range of diversity, we found that overall insect and spider dry biomass, while consistently higher in terrestrial ecosystems, increased by ~11.5% (95% CI [9.8, 13.2]) for every 10% increase in species richness for our consumers (LMM, $R^2M = 0.70$, $R^2C = 0.87$; Fig. 2C; Table S3). More importantly, the mass of the most physiologically-critical n-3 and n-6 PUFA, including LIN, ALA, arachidonic acid (ARA, 20:4n-6), eicosapentaenoic acid (EPA; 20:5n-3), and docosahexaenoic acid (DHA; 22:6n-3), were all positively related to biodiversity across ecosystems (Fig. 2D-H; Table S3). For example, the mass of EPA increased by 12.2% (95% CI [8.9 - 15.5%] for every 10% increase in species richness in both aquatic and terrestrial systems (Table S3). Relationships between species richness and the n-6 and n-3 LCPUFA precursors LIN and ALA were similar for aquatic and terrestrial ecosystems (Fig. 2D-F; Table S3). However, stream LC-PUFA (i.e., ARA, EPA, and DHA) availability was from 10 to 100 times greater than terrestrial LC-PUFA availability depending on the observed level of species richness (Fig. 2G-H; Table S1).

Human land-use intensity explains variation in biodiversity-ecosystem nutritional relationships

Biomass and organic nutrient availability within insect communities was lower in terrestrial environments strongly influenced by human activities. In both stream and terrestrial ecosystems, we found that species richness was negatively associated with human land-use intensity (i.e., , Table S1), and that in terrestrial systems BEF relationships themselves varied with land-use (i.e., Fig. 2; Table S2; Fig. S4-5). Terrestrial insect and spider biodiversity were greatest in forested habitats and likewise aquatic insect diversity was greatest in streams surrounded by forests (Table S2). Biodiversity was lowest in terrestrial agricultural and urban areas as well as in streams surrounded by these land-uses (Table S2). These differences in diversity due to human land-use intensity were particularly pronounced among terrestrial sites: terrestrial diversity was nearly an order of magnitude greater in coniferous and mixed-coniferous forests compared to human-dominated areas (i.e., urban, suburban, and agricultural areas). In addition, while BEF relationships were consistently positive across all habitats and land-uses, we found differences among

land-use categories, especially in terrestrial systems. For instance, within human-dominated areas, higher diversity was associated with higher biomass and PUFA availability (Fig. 2C-H, Fig. S4-5), highlighting the functional importance of biodiversity across all land use types. However, for a given level of species richness, insect and spider communities in more natural terrestrial areas, such as forests, had higher biomass and longer chain PUFA-mass (ARA, EPA, and DHA) compared to communities in human-dominated areas (Fig. 2C-H, Fig. S4-5), demonstrating that the strength of terrestrial BEF relationships varied with land use.

Trophic structure of biodiversity drives patterns of nutrient density and availability

Previous BEF studies have rarely considered how the proportion of predator biomass might increase as a function of species richness, but this relationship has important implications for understanding nutrient accumulation in food webs. Our datasets of multi-trophic communities allowed us to infer the relationship between nutrient density (i.e., mass of PUFA per unit dry biomass) and the proportion of predatory versus prey biomass alongside richness across land use types and habitats. Patterns of predatory insect and spider biomass were particularly important in explaining biodiversity-nutrient density relationships in terrestrial habitats because predators were the main source of terrestrial LC-PUFA, often containing an order of magnitude or more LC-PUFA per dry mass compared to non-predatory taxa (EPA and DHA, Fig. 3D, 3F; ARA, Fig. S6-10). Across terrestrial sites, predator biomass and LC-PUFA-mass initially were higher for a given level of biodiversity compared to those of prey species, before leveling off at higher levels of species richness (Fig. 3A-F). This means that predators had more nutrient-dense biomass, especially at lower levels of species richness. This also explains why biodiversity-EPA and -DHA slopes, but not biodiversity-biomass slopes, of most stream sites were higher than those in terrestrial sites at all species richness levels, but more similar at higher richness levels (Fig. 2C-H). Within terrestrial habitats, at lower levels of richness, heavily human-dominated areas had lower biomasses of both predators and non-predatory taxa compared to more natural land use types (Fig. 3C-D), like forests and grasslands. In contrast, in aquatic food webs, the nutrient density and proportion of total biomass composed of predators varied relatively little with species richness and varied little with land-use or species richness. Stream insect biomass was dominated by prey species regardless of land-use type (Fig. 3A), but because non-predatory aquatic taxa are rich in LC-PUFA, particularly EPA (e.g., (*19-20*)), the nutrient-density of aquatic biomass was consistently much higher than that of terrestrial biomass. Previous studies have demonstrated that EPA and DHA content increase with trophic position (*13-15*) and vary across functional groups (e.g., (*38, 42*)). For instance, predatory arthropods, like spiders, have the capacity to either accumulate LC-PUFA from prey or synthesize them from precursors like ALA and LIN (*40, 43*). Our results reflect this outsized importance of predatory arthropods as sources of LC-PUFA in terrestrial systems, and additionally demonstrate how land-use can modify the role of predators as drivers of BEF relationships through changes in trophic structure.

Availability of n-3 LC-PUFA is an essential ecosystem function

Our results imply that community structure of insect and spider communities has a strong effect on the availability of PUFA across aquatic and terrestrial meta-ecosystems (Fig. 4, Supplemental Tables 4, 5, and 6). Insect and spider taxa vary widely both in their relative biomass and in their nutritional

composition (*20, 38*), such that observed stream and terrestrial communities vary considerably in their nutrient density (Fig. 3C-F). Estimating this nutrient density of communities is a critical step toward quantifying the importance of variation in PUFA availability across ecosystems. To explore this, we quantified the total nutrient content (e.g., EPA and DHA; Fig. 3C-F) of local communities based on either the observed species rank abundance distribution or a uniform rank abundance distribution (i.e., all species across all trophic levels are equally abundant in a community). Comparing these community-wide nutrient content estimates allowed us to assess the importance of both community composition (i.e., the identity of species in a community) and relative abundance of species for our PUFA availability estimates. Importantly, we found that for both stream and terrestrial communities, the observed EPA density of communities was, on average, 45% greater than of communities with a uniform abundance distribution (Fig. 4). In other words, for a given amount of biomass, we found greater n-3 LC-PUFA content than would be expected if all species made an equal contribution to n-3 LC-PUFA. This pattern reveals that those species contributing the most to community biomass tend to have higher than average nutrient density. This also means that accounting for compositional variation in species is important for investigating effects of nutrient availability across riparian meta-ecosystems.

To investigate different scenarios of nutrient availability along hypothetical riparian meta-ecosystem boundaries, we calculated the nutrient density of potential insect and spider-based (i.e., insectivore) diets ranging from being composed of entirely terrestrial to entirely aquatic taxa as described above (i.e., comparing observed rank abundance distributions to uniform distributions). These simulated diets along terrestrial-to-aquatic gradients (*44*) represent a range of potential diets for insectivorous predators including those foraging in inland terrestrial food webs with little connection to aquatic ecosystems (e.g., (*40, 43*)), in riparian zones with a mix of aquatic and terrestrial prey (e.g., (*20, 25, 41*)), and larger lakes and rivers where terrestrial insects contribute little to secondary production (but see (*45*). As diets become more dominated by aquatic taxa, they consistently have higher nutrient density, especially n-3 LC-PUFA (e.g., Fig. 3, Table S4). In addition, the identity and relative abundance of species found in communities has a strong impact on the nutrient density of aquatic as well as most terrestrial communities. The positive nutrient density slope from purely terrestrial to increasingly aquatic diets emerges because the biomass-dominant aquatic taxa dominating have greater nutrient density relative to other species than do the biomass-dominant terrestrial taxa (Table S4). This slope is even greater for EPA than for its shorter-chain precursor ALA (Fig. 4), because such compositional effects are even greater for n-3 LC-PUFA.

Overall, the EPA content of simulated insectivore diets reflected the relative abundances of sampled insect and spider communities and increased by 2.2% per unit of mass for every 10% increase in the proportion of aquatic insects in diet (Fig. 4B). This is the result of aquatic taxa having on average more than 140% higher EPA density than terrestrial taxa and these n-3 LC-PUFA-rich taxa being more abundant in sampled stream compared to sampled terrestrial communities (Table S3, Fig. 4). Terrestrial insects and spiders (Fig. 4: 100% terrestrial diet) contained on average nearly 3.8 times more of the n-3 LC-PUFA precursor ALA per biomass (i.e., greater ALA density, Table S3) than aquatic insects (Fig. 4: 100% aquatic diet). However, across all land uses, simulated dietary ALA content based on relative abundances of sampled insect and spider communities decreased by 2.5% per unit of mass for every 10% increase in the proportion of aquatic insects compared to null expectations (i.e., even species distributions; Fig. 4D, ALA), demonstrating a strong effect of community structure on nutrient availability. In contrast, contents of the n-6 PUFA LIN were more than eleven times greater in terrestrial

insects and spiders compared to aquatic insects (Table S2) and simulated diets based on observed species abundance had only minor effects on LIN availability. LIN content of simulated insectivore diets was greater in terrestrial communities compared to aquatic ones: LIN content decreased by 6.6% for every 10% increase in the proportion of aquatic insects along ecotones (LM, Adjusted R^2 = 0.68, Supplemental Table 4). In contrast, ARA content increased by 1.3% for every 10% increase in the proportion of aquatic insects.

Conclusions

Our study shows that insect and spider diversity is of fundamental importance in both terrestrial and aquatic ecosystems, influencing the availability of biomass as well as nutritionally-relevant fatty acids. Our results confirm those of previous studies of biodiversity-biomass relationships for consumers and primary producers (*8*), while demonstrating that biodiversity also increases the availability of critical organic nutrients across ecosystems encompassing a wide range of human land-uses and habitat types. We observed strong effects of diversity on nutrient availability across land-use categories, highlighting the importance of conserving biodiversity for ecosystem functioning even in human-dominated landscapes. Concerningly, urbanized terrestrial environments with low insect and spider diversity had biomass of substantially lower n-3 LC-PUFA density than more natural environments. There was a clear biomass deficit of insects and spiders in human-dominated terrestrial communities, particularly at low diversity. Additionally, the proportion of predator biomass (i.e., the more LC-PUFA-rich part of the community) to total terrestrial biomass increased at a slower rate with species richness in human-dominated areas. This suggests that predatory taxa like beetles as well as spiders may be especially susceptible to anthropogenic stressors (*11*), which may explain why their own predators, like birds, mammals, and reptiles, are also struggling most in human-dominated habitats (*10*). Compared to terrestrial insect and spider communities, aquatic stream insect communities had a consistently higher n-3 LC-PUFA density and greater insensitivity of nutrient density to variation in species richness and land-use. Encouragingly, this means that streams are a robust source of important fatty acids that can subsidize terrestrial food webs over a broad range of anthropogenic impacts. In urban settings, for example, emergent aquatic insects serve as especially nutrient-dense prey for insectivores, such as birds and bats (e.g., (*20, 39*)). Importantly, however, many contaminants accumulate in aquatic systems and are taken up by juvenile aquatic insects, degrading the otherwise high nutritional quality of aquatic insects, making it especially important to protect and restore freshwaters in human-dominated areas (*46*).

Nutrient availability in ecosystems is strongly determined by how biodiversity is structured within communities and among ecosystems. Our analysis shows that a lack of information about the relative abundance of species can substantially underestimate nutrient availability across both aquatic and terrestrial ecosystems. Predatory insects and spiders, for example, play a keystone role in the overall availability of organic nutrients. Similarly, emergent stream insects can have a large effect on nutrient availability for other consumer populations, such as aerial insectivores (e.g., (*20-22*)) Predators like dragonflies that actively forage and disperse over long distances (*47*) are likely to be more important vectors of these nutrients compared to passively-foraging predators like web-building spiders (e.g., (*40, 43*)).

In light of growing concerns about loss of insect diversity, our results highlight nutrition as an underappreciated dimension of these consumers' contributions to ecosystem functioning. There is growing awareness about the importance of the nutritive diversity of marine and riverine biodiversity for human health (*48, 49*). Similarly, a diversity of consumers in terrestrial food webs likely benefit from the high-quality of organic nutrients produced from aquatic systems, and hence, from restoration efforts that prioritize nutrient fluxes from biodiverse aquatic communities.

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Code and raw data (other than the full BDM and WSL insect datasets) are deposited at Zenodo (50). BDM and NAWA aquatic insect raw data files are publicly available from the Swiss Federal Office for the Environment (BAFU) by request with data usage agreement to Hintermann & Weber AG Ökologische Beratung, Planung und Forschung (51). WSL terrestrial insect data are available at Envidat (52).

Supplementary Materials

Materials and Methods

Figs. S1-S12

Tables S1-S8

References (53-59)

Fig .1. A. Differences in organic nutrient availability at the base of food webs, such as the terrestrial (green) and aquatic (blue) food webs shown, as well as rates of preferential retention (i.e., the content of nutrients retained and incorporated into biomass relative to their content in diet) and internal biosynthesis by consumers (i.e., whether or not nutrients originate from primary producers) influence nutrient density (i.e., nutrient content as a proportion of biomass; intercept). The relationship between nutrient density and trophic level is determined by both the nutrient density in primary producers (intercept) and the rate at which nutrient density increases between trophic levels (slope). This slope incorporates the preferential retention of compounds produced by primary producers as well internal consumer biosynthesis. For example, in food webs with steeper slopes, dietary nutrient content at higher trophic levels is largely a product of synthesis within the food chain rather than accumulation of strictly dietary nutrients from primary producers. B. Most community biomass is typically found at lower trophic levels, and has a pyramid shape as trophic level increases (gray). However, the density of organic nutrients that are selectively retained and undergo enrichment between trophic levels increases with trophic position, comprising a larger proportion of total biomass and creating an inverted pyramid pattern (orange). C. Communities with more species tend to have more consumers, such that the mean trophic position of a food web (i.e., the mean trophic position of all trophic levels from primary producers through any higher order consumers) typically increases with species richness (*23*). Because organic dietary nutrients accumulate and become enriched in biomass at higher trophic levels at varying rates, food webs can differ in their scaling relationship between species richness and mean dietary nutrient content, with some reaching higher levels of nutrient density at lower levels of species diversity.
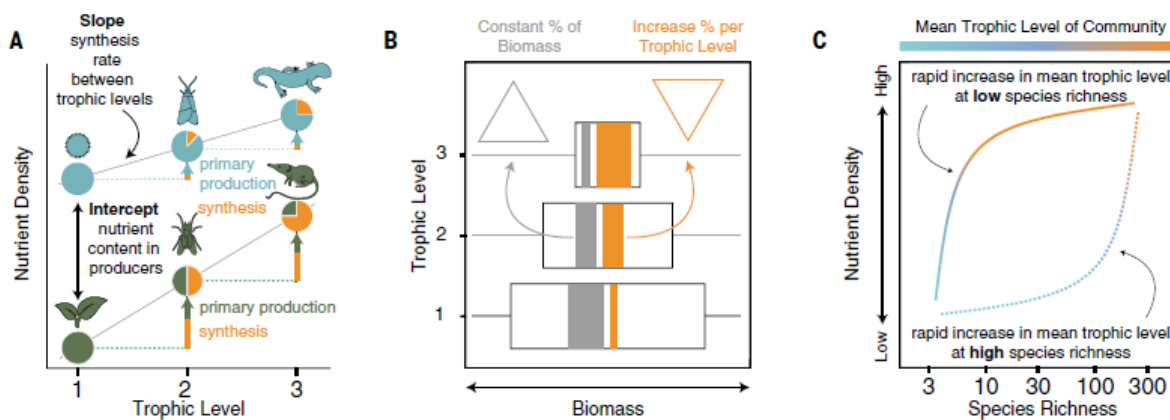
Fig. 2. Scaling relationships between biodiversity and biomass and nutrient availability. A. Distribution of land uses and habitats sampled, spanning from human-dominated habitats to more natural habitats like forests and grasslands. Number of sample sites are provided above each land-use category and the elevation distribution of sampling. B. Elevational distribution of sampling between aquatic and terrestrial sites. C-H. Increasing species richness results in increased (C) dry insect and spider biomass, (D) linoleic acid (LIN), (E) alpha-linolenic acid (ALA), (F) arachidonic acid, (G) eicosapentaenoic (EPA) and (H) docosahexaenoic acid (DHA) biomass across different land use types in both aquatic (blue) and terrestrial (green) ecosystems. There was significant positive relationship (*p<0.05*) between the response (dry biomass and all PUFA) in all models with 89, 74, 71, 64, 71, and 62% of the variance explained for dry biomass, LIN, ALA, ARA, EPA, and DHA respectively in a generalized additive mixed model.
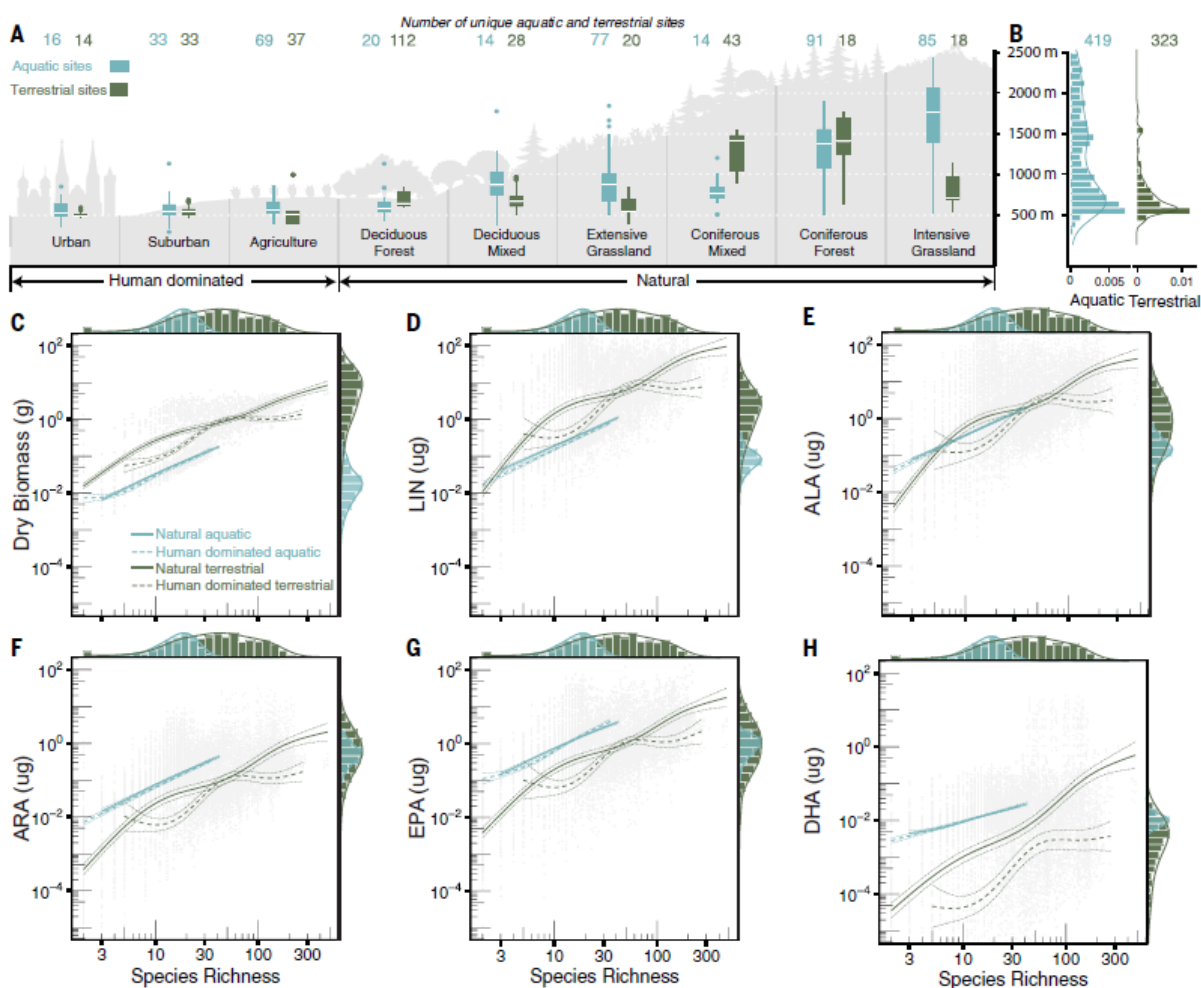
Fig. 3. Scaling relationships between biodiversity and predator or prey biomass (A-B) and between biodiversity and the nutrient density of that biomass (C-F) in aquatic and terrestrial insect and spider communities varying in land-use. There was a significant positive relationship ($p<0.05$) between species richness and dry biomass in aquatic systems explaining on average 87% of the variance, but no significant positive relationship with EPA or DHA density in aquatic systems. In contrast, in terrestrial systems there was a significant positive relationship ($p<0.05$) with species richness explaining on average 84, 44, and 74%% of the variance in dry biomass, EPA density, and DHA density in terrestrial systems, respectively.
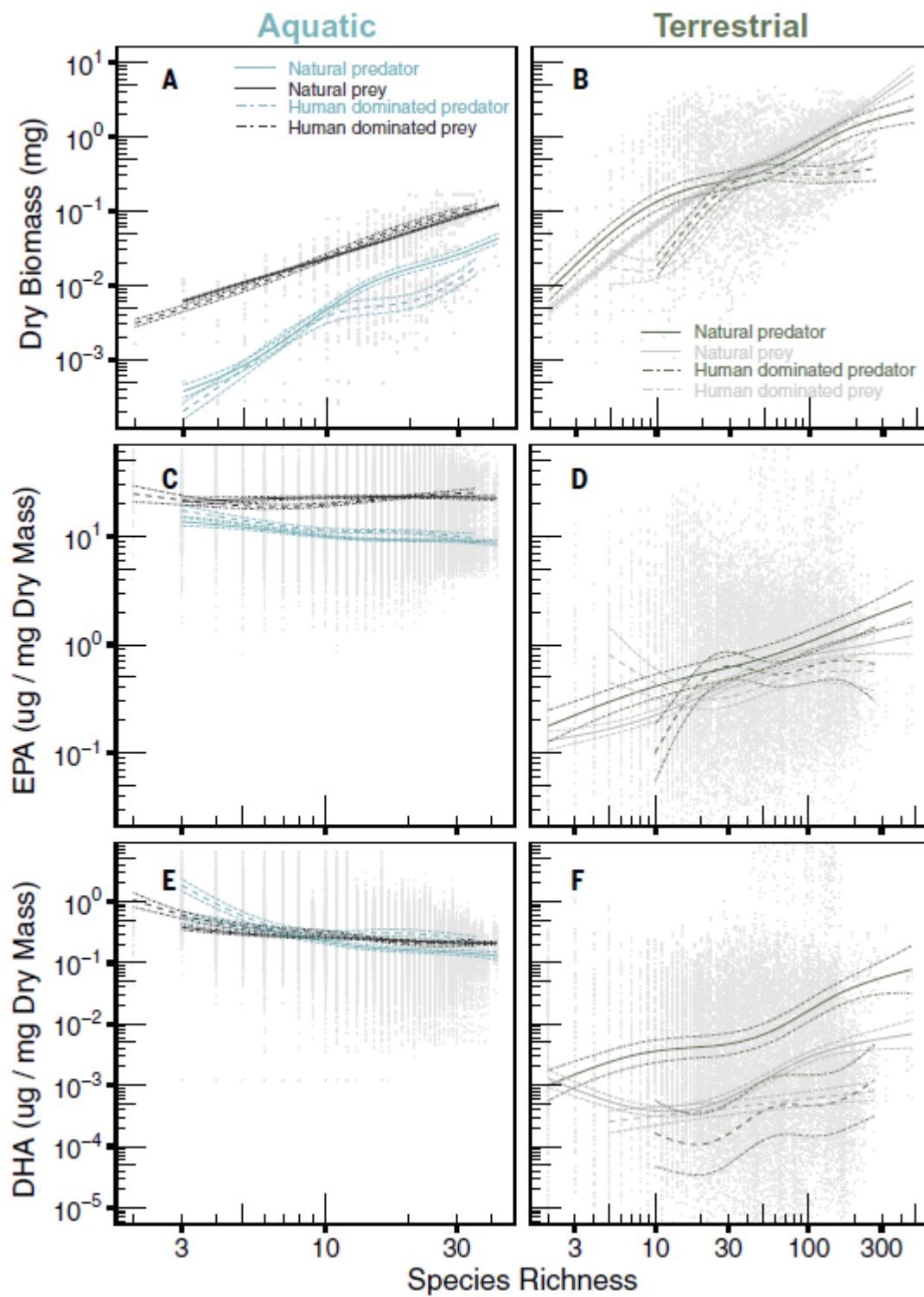
Fig. 4. Effects of insect and spider community composition on nutrient availability for insectivorous predators with diets varying from entirely terrestrial (e.g., an inland-foraging Woodpecker) to mixed aquatic and terrestrial (e.g., a riparian-foraging Swallow) to entirely aquatic (e.g., a benthic-foraging Grebe). A. Insect and spider species vary both in their abundance and nutrient content, which can scale across entire communities and ecosystems. For example, if the most abundant species also are more nutrient-rich, then observed communities should have a greater nutrient density than randomly assembled communities. B. Nutrient density of ALA (the n-3 LC-PUFA precursor) and C. n-3 LC-PUFA (EPA) of simulated insect and spider-based diets varying from 100% terrestrial to 100% aquatic taxa based on either uniform abundance distributions (dashed line) or those based on the relative abundance of sampled communities (solid line). D-E. Relative differences between diets based on sampled communities varying in land use (colored lines) and uniform distribution-based communities (bolded black line). Negative values mean that observed community structure results in lower n-3 PUFA content than in a community with a uniform species distribution, zero values mean that observed community structure has no impact on PUFA content, and positive values mean that observed community structure results in higher n-3 PUFA content than expected if all species were equally abundant.