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Review

Ecosystem-size relationships of river populations and communities

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Knowledge of ecosystem-size influences on river populations and communities is integral to the balancing of human and environmental needs for water. The multiple dimensions of dendritic river networks complicate understanding of ecosystem-size influences, but could be resolved by the development of scaling relationships. We highlight the importance of physical constraints limiting predator body sizes, movements, and population sizes in small rivers, and where river contraction limits space or creates stressful conditions affecting community stability and food webs. Investigations of the scaling and contingency of these processes will be insightful because of the underlying generality and scale independence of such relationships. Doing so will also pinpoint damaging water-management practices and identify which aspects of river size can be most usefully manipulated in river restoration.

Highlights

The fractal-like branching of river networks and connectivity with riparian areas and groundwater mean that rivers have longitudinal, lateral, vertical, and temporal dimensions.

We argue that the development of scaling relationships between ecological properties and river size and investigation of fragmentation effects can improve understanding of this multidimensionality.

Stream metabolic processes scale with river size, driven mainly by downstream accumulation of resources and changes in boundary interface dimensions.

Aspects of predator size, population size, richness, community stability, and food-web structure vary with river size, but scaling relationships are most likely when physical constraints limit body size or movements or when space limits affect community assembly.

Assessment of the occurrence, shape, and universality of ecosystem-size relationships, especially their scaling, will inform river management.

Ecosystem-size influences are integral to rivers

Flowing-water ecosystems (i.e., streams and rivers, and referred to here as 'rivers'), driven by their dendritic branching structure, grow in size downstream, changing ecosystem size [1–3]. Rivers also contract and expand with drying and flooding, driving dynamics that are integral to their biodiversity [4,5]. However, river sizes are being drastically altered by global change drivers including **abstractions** (see Glossary), encroachment, and climate change [6–8], highlighted by devastating droughts and floods costing billions [9,10]. Knowledge of the ecological effects of river ecosystem size will be integral to the balancing of human and environmental needs for water and can inform general understanding of ecosystem-size influences.

Altered attributes of populations and communities and rates of ecological processes linked to ecosystem size changes are to likely underpin critical aspects of riverine ecological structure via biogeochemical, body-size, movement, species-area, and interaction-network **scaling** relationships [11–14]. The scaling of physicochemical processes with river size is comparatively well known [14–16], but many effects on populations and communities remain to be fully appreciated and are complicated by the multiple dimensions of river ecosystems. Filling these gaps is urgent because of global human dependence on fresh water, the imperilled plight of rivers, and their connection to river restoration [6,17].

Here, we focus on the rapidly developing field of river ecosystem-size influences on populations and communities, underpinned by advances in river geomorphology and biogeochemistry [14,18]. We review terminology to better guide progress, summarise mechanisms involved in ecosystem-size effects, and highlight management applications and knowledge gaps. We focus on ecosystem size-related mechanisms integral to the resilience and restoration of rivers, highlighting the value of developing ecosystem-size scaling relationships.

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River ecosystem multidimensionality

The fractal-like processes involved in river network branching [3] and associated alterations in geomorphic properties encompassed in this scaling have wide influence on river habitats [19]. First, the multiple dimensions created by the scale independence of this structure, including connectivity with riparian areas and groundwater, mean there are many ways to characterise river size (Box 1). These encompass the longitudinal, lateral, vertical, and temporal dimensions of rivers, including the aquatic faunas of interstitial, surface, and temporary waters and the associated terrestrial faunas of riparian zones [20]. The development of generalised mathematical scaling relationships (as defined in [21]) between ecological properties and ecosystem size offers great promise because relationships can be transferred across scales and systems. This could enable better translation across contexts and avoid pitfalls associated with a multitude of potential ecosystem-size measures.

Second, dynamic expansion and contraction of wetted river components mean that large proportions of channel length are intermittent [8,22] and that many rivers experience periodic **floodplain** inundation [5]. Humans are modifying these cycles through artificial drying regimes [23], flow fluctuations [24], channel alterations [7], and the addition of non-native plants that affect drying [25]. The development of metrics that better reflect these size dynamics will be integral to a better understanding of river-size influences.

Finally, the diversity of riverine aquatic and terrestrial habitats is likely to increase with habitat area. Given that there are many aspects of geomorphic complexity relevant to riverine biota [26], determining which of these scale with river ecosystem size and which are size independent is also an important challenge [12]. Mapping with side-scan sonar reveals a hierarchy of habitat patchiness in

Box 1. The multiple measures of river ecosystem size

River ecosystems contain **open populations**, and appropriate ecosystem-size measures depend both on where resources come from and where organisms live [18,89,93]. Defining a river ecosystem as a region of strong interactions among and between river-associated organisms and the flux and flow of energy or material in the river' ([18], p. 113) overcomes some of the multidimensionality challenges by connecting geomorphology, processes, and functions, with populations and communities. Size measures can be large-scale like **river network length** or local like **cross-sectional area** or floodplain width (Figure I), but an appropriate measure depends on the question. **Structural boundaries**, based on physical characteristics like shorelines, are most important for population and communities, whereas **functional boundaries**, like catchments or spatial extents of species interactions, are most important for processes [18].

There are also potentially confusing international differences in the terminology used for some large-scale measures, with the area of land draining to a river being its catchment (or **watershed** area or drainage basin) and the boundary between catchments being the watershed (Figure IA). Use of these terms is entrenched in different parts of the world, but referring to catchment or watershed area will help clarity.

Advective water movement defines rivers, and their size is inexorably linked to temporal runoff dynamics. Ecosystem-size measures including a temporal component like discharge or annual runoff production (Figure IA,B) are particularly useful since water availability is a fundamental currency for aquatic organisms [39,46]. However, large-scale measures based on land area may not incorporate the dynamics associated with intermittent flow (Figure IC) or exchange with ground water (Figure ID).

Where exchange between surface water, groundwater, and terrestrial environments occurs, boundary characteristics, including the amount of shoreline, benthic surface area, **hyporheic zone** area, and air–water interface area, will influence rates of exchange [14,18,30,94]. One of the main effects of hydropeaking, for example, is to change the amount of shoreline. Those ratios affect how bounded the ecosystem is and are important in controlling ecosystem connectivity, making multichannel rivers (Figure IE) hotspots of exchange [89].

Finally, drainage configuration is important because branch length (Figure IA) increases ecosystem size [95], but branching per unit river distance, being independent of spatial scale in a fractal structure, involves an orthogonal complexity aspect reflecting habitat diversity per unit area [12]. In river branching, small first-**order** (Figure I) branches are often more isolated than larger rivers [61], so isolation and ecosystem size are linked.

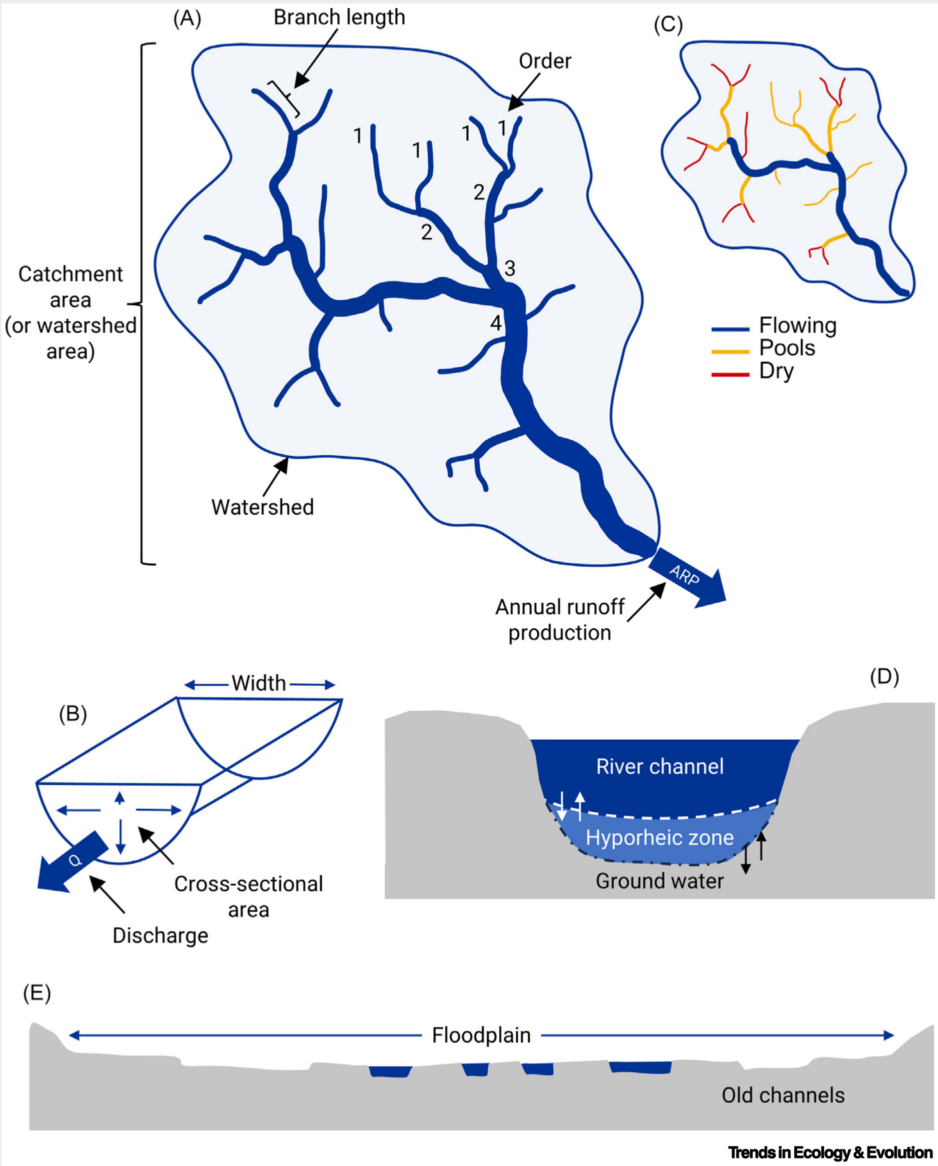

Figure I. Relationships between river ecosystem-size measures ranging from large scale (A) to more local (B) and incorporating intermittence (C), exchange with ground water (D), and area of floodplains (E).

big rivers whereby physical heterogeneity increases with spatial scale [27]. Likewise, multispectral satellite imagery reveals that hyporheic habitat size may peak at intermediate drainage areas [28]. Understanding such relationships is essential to link landscape-scale process with biological structure and function [29,30] and is likely to require more use of new technology and more collaboration [27].

Ecological properties scaling with river ecosystem size

Some ecosystem-size effects, like those predicted by the river continuum concept, are well known and underpin fundamental understanding of river ecosystems [1,31], but the range of mechanisms involved and attributes affected is developing rapidly (Table 1).

Glossary

Abstraction: removal of water from rivers for human use.
Annual runoff production: the portion of annual precipitation that is drained by a river network.
Bounded ecosystem: an ecosystem where strong associations occur among resource flow, community membership, and physical boundaries, as in islands and lakes [18].
Catchment: also known as watershed area or drainage basin; the land area above a specific point on a stream from which water drains towards the stream.
Community size: total abundance across taxa of individuals in a community.
Cross-sectional area: 2D measure (wetted width × depth) of aquatic habitat.
Discharge: the rate at which a volume of water flows through a given cross-section of a river channel.
Floodplain: or braidplain for braided rivers; valley floor adjacent to the stream channel that becomes inundated at high flows. This also encompasses the extent of area occupied by actively moving channels in a multichannel river.
Functional boundaries: define the spatial extents of interactions or processes.
Hyporheic zone: the region of interstitial space beneath and alongside a stream bed occupied by stream organisms, where shallow groundwater and surface water mix.
Open population: population where external processes are relatively more important than internal processes.
Order: or stream order or Strahler stream order; categorisation of river channels based on the hierarchical pattern of branching, with individual branches treated as nodes and the smallest (first order) channels being those that appear on small-scale topographical maps; two first-order streams combine to form a second-order stream and so forth.
River network length: total topological length of river channel.
Scaling: scale-invariant relationship between two quantities (as opposed to scale-dependent relationships [21]).
Structural boundaries: based on physical characteristics.
Watershed: topographical boundary dividing two catchments or drainage basins.

Table 1. Selected examples of processes and attributes demonstrating the variations in relationships with river size

Property	Ecosystem-size measure	Relationship	Refs
Habitat characteristics			
Benthic substrate diversity	Spatial extent	+ve	[27]
Riparian canopy volume	Catchment area	+ve, power	[36]
Hyporheic flow capacity	Contributing drainage area	Hump	[28]
Salmonid habitat quality	Hillslope storage capacity	+ve	[30]
Ecosystem processes			
Cumulative biogeochemical function	Cumulative catchment area	+ve, power	[14]
Net CO_2 emissions	Discharge	–ve	[35]
Riparian foliar $\delta^{13}C$	Catchment area	–ve, power	[36]
Body size			
Maximum predator length	Cross-sectional area	Limit response	[38]
Predator body size	Discharge	+ve, power	[39]
Salmonid length	Stream order	+ve, log	[40]
Invertebrate body mass	Drought intensity	Hump	[43]
Populations			
Macroinvertebrate density	Discharge	No relationship	[39]
Macroinvertebrate density	Drying intensity (coefficient of variation in depth)	+ve	[25]
Macroinvertebrate densities	Drought intensity	Mixed	[43]
Trout density	Reach size	+ve	[47]
Fish carrying capacity	Net annual runoff	+ve	[46]
Measures of minnow survival	Drying rates and pool depths	Mixed	[51]
Mudfish survivorship	Drying intensity (coefficient of variation in depth)	–ve	[25]
Fish recruitment	Flood size	+ve	[53]
Richness			
Taxon richness studies	Multiple	Mixed	[56]
Taxon richness from eDNA	Catchment area	Mixed	[57]
Richness of diatoms, invertebrates, and fish	Landscape polygons	+ve, power	[58]
Fish taxon richness	Catchment area	+ve, power	[12]
Communities			
Assembly processes	Headwaters vs. mainstems	Varied	[62]
Fish composition	Low flows	Increase non-native	[68]
Community traits	Drought intensity	Thresholds	[69]
Community stability	Discharge	+ve	[66]
Food webs			
Food-chain length	Cross-sectional area	+ve	[73]
Food-chain length	Catchment area	+ve	[72]
Maximum trophic position	Cross-sectional area	+ve	[76]
Food-chain length	Flow variation	–ve	[75]
Food-chain length	Catchment area	No relationship	[74]
Fish trophic position ($\delta^{15}N$)	Drying intensity (coefficient of variation in depth)	+ve	[25]
Prey flux	Drying intensity (coefficient of variation in depth)	+ve	[25]

Ecosystem processes

There are unlikely to be universal scaling 'laws' of cumulative river network function [14], but the scaling of ecosystem processes with river ecosystem size can tell us much about the activities of organisms and their energy supplies [32]. Important drivers like light, temperature, and carbon subsidies all scale with network length, benthic surface area, or air–water surface area, leading to strong relationships of key ecosystem processes with river size (Table 1) [14,16,30,33]. These include scaling of ecosystem respiration and gross primary production with cumulative **catchment** area [34], so that large catchments contribute disproportionately to production [14]. Because of their close connectivity with terrestrial environments, small streams emit proportionally more terrestrially derived CO_2 than large streams, and the percentage of aquatically derived CO_2 emitted increases with river size [35]. Nutrients are typically taken up in proportion to benthic surface area, but areal scaling of cumulative process rates associated with substrates (like nutrient assimilation and denitrification) also depends on flow rates [14]. Water supply is also a primary driver – from surface and subsurface (i.e., groundwater, hyporheic) environments – but particularly in arid areas; so, for example, in Sycamore Creek, AZ, USA, stream network configuration controls riparian vegetation structure by mediating plant–water interactions [36]. Overall, these relationships point to strong dependence of river metabolism on: (i) the configuration of boundaries between water and air, water and benthic substrates, and water and the riparian zone; and (ii) downstream accumulation of upstream, laterally derived, and vertically derived (i.e., from groundwater) resources (Figure 1) [15].

The derivation of these scaling relationships has been game changing for the understanding of drivers of river functioning, but global changes altering rivers pose further challenges. For example, flow changes and alteration of associated rates mean that catchment sizes are poor predictors of nutrient export to oceans, and human modification of riparian zones alters primary production scaling [16,37]. Such contingencies complicate predictions of the effects of ecosystem process scaling on river populations and communities, but understanding of their causes will reveal important influences (Box 2).

Body sizes of individuals

Like the direct influences on ecosystem functions, physical dimensions related to channel area also directly limit some organism characteristics. Predatory fish body size is limited by channel width or **discharge** and is reduced when channel size is experimentally restricted (Table 1) [38–40]. Such constraints are linked to the allometry of home-range sizes and habitat use [41] and mean that larger-body-size fish are more likely to emigrate from shrinking habitats [42]. Moreover, because body size is connected to individual metabolic rates, this can affect the capacity of food webs to support predatory fish [39]. Thus, direct constraints on predator body size are likely to be some of the most important influences of river ecosystem size. These effects will be modified by pressures like fishing, but assessment of such impacts could be aided by utilising null models of body size distributions expected based on river size. Effects are also more complicated when habitat drying traps large predatory organisms in remnant habitats, potentially driving instability [43].

Populations

Downstream increases in river dimensions could influence population sizes if, for example, total food resource availability expands due to increased productive space [18], but evidence for this is mixed (Table 1). Links between macroinvertebrate abundance per unit area and measures of ecosystem size have hardly been examined but appear uncommon so far [39,44]. Few effects of reduced ecosystem size on total population sizes have also been observed in other ecosystems [45] and many other factors like flow-related disturbances are also important in driving total population sizes of macroinvertebrates in rivers. Nevertheless, aquatic habitat availability

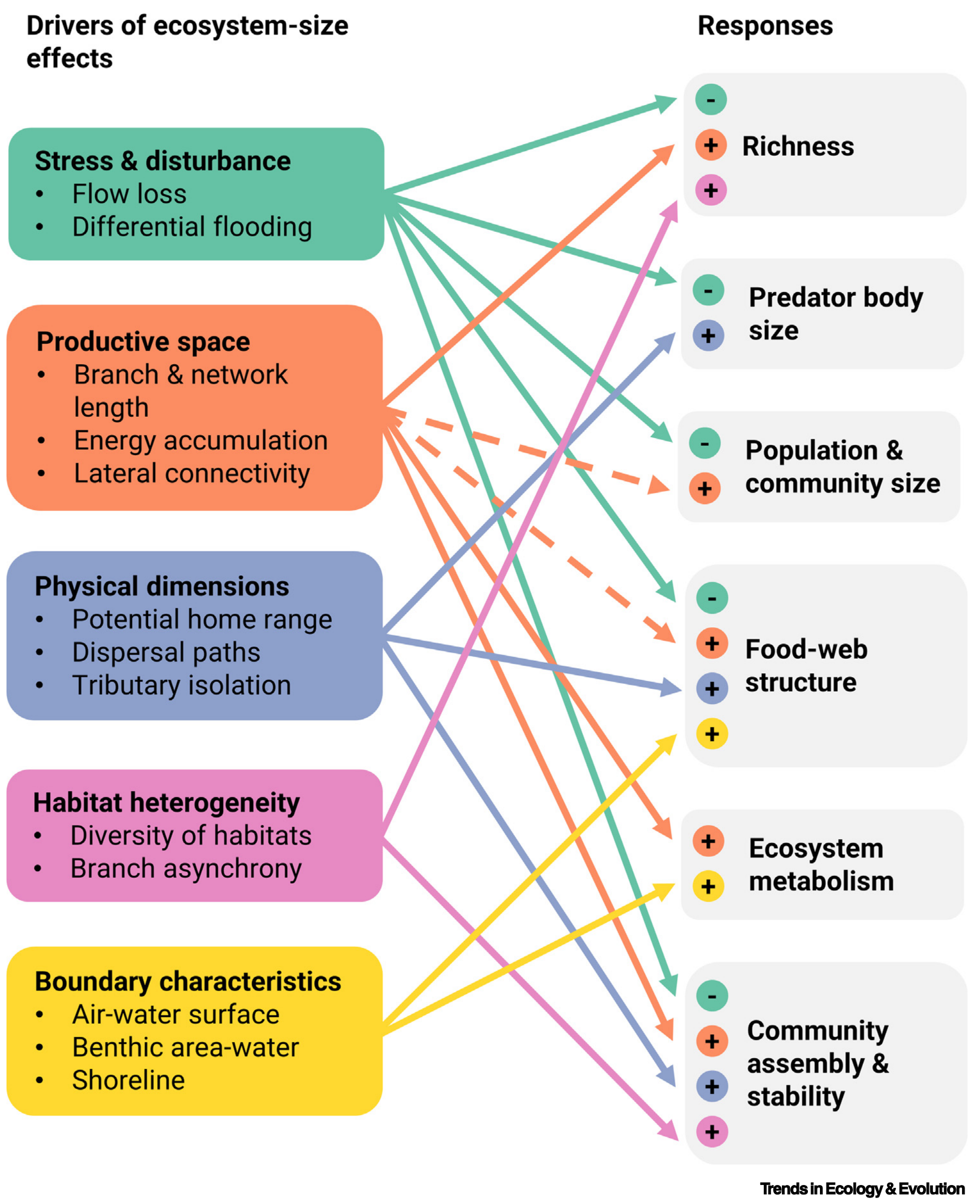

Figure 1. Drivers of ecosystem-size influences on river ecosystems, including positive and negative effects and variation in their strength (broken lines, weaker).

throughout catchments should influence total population sizes, so how scaling of habitat availability combines with other influences to affect population sizes, and which ecosystem-size measures work best, are important issues to resolve (Box 2).

Given direct habitat-size constraints on predator size in rivers, the effects of space availability are likely to be particularly important for tertiary consumers like predatory fish. Muneepeerakul and colleagues [46] successfully used average **annual runoff production** as a measure of fish habitat availability, arguing that water availability over the year was a reasonable indicator of carrying capacity. Others show that brown trout (*Salmo trutta*) density increases with habitat patch size (flowing water area) and decreases with reach isolation [47]. Moreover, bigger and less isolated

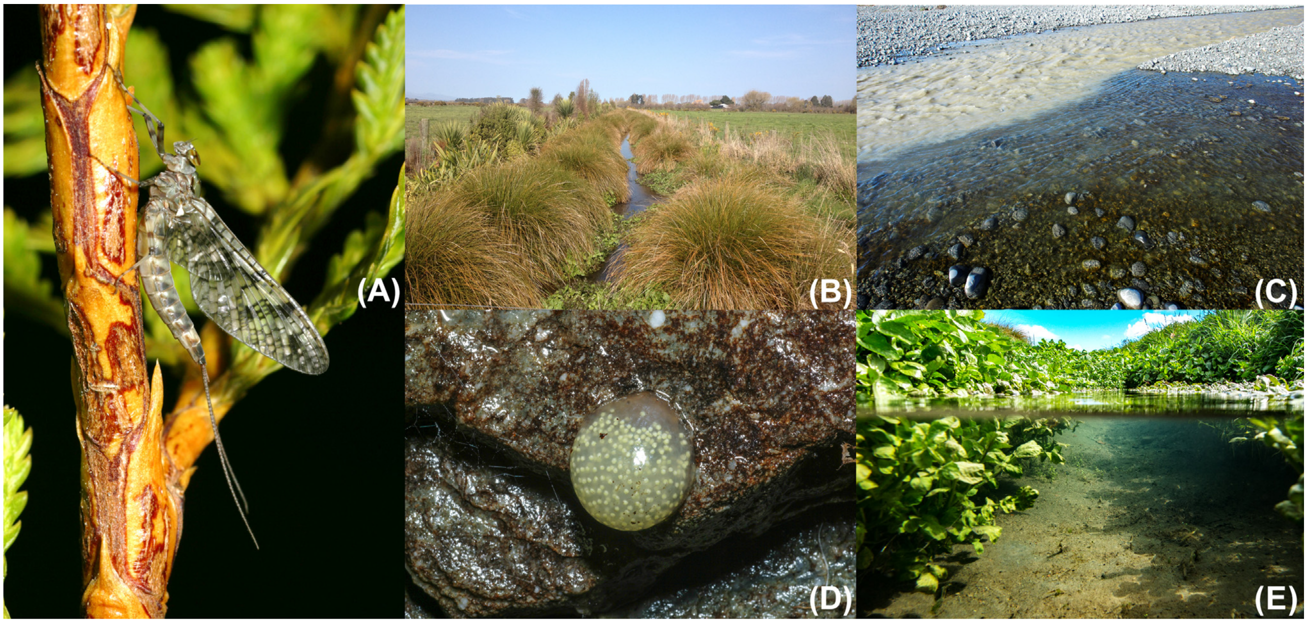

Figure 2. The importance of boundary properties in controlling the rates of processes in rivers means that disruptions to the lateral and vertical dimensions of rivers will be particularly influential. Examples of lateral influences include the effects of riparian zone size on the survival and movements of adult aquatic insects (A) (*Nesameletus* sp. mayfly subimago) [93], the effectiveness of contaminant filtering by riparian zones (B) [99], and the positive influences of the diversity of lateral habitat types (C) on community stability [29,84]. Vertical influences include the water depth on rocks affecting the accessibility of key oviposition substrates like emergent rocks to adult caddisflies and the vulnerability of egg masses to drying (D) [100] and the reduction in niche diversity caused by the sedimentation of interstitial habitats (E). Images, A.R. McIntosh.

brown trout populations were also less variable, and edge effects occurred whereby proximity to pool habitat reduced density [47]. These findings match expectations that edge effects should occur in river habitats and that ecological drift will be associated with smaller populations [44]. Thus, for organisms whose home range is constrained by river dimensions, ecosystem size is likely to be an important driver of population size, in combination with river network configuration and connectivity (Box 2).

The most influential effects of river ecosystem size on populations are linked to ecosystem contraction and expansion. Discharge variation can affect the permeability of boundaries between river habitat types for dispersing fish [48]. This is important when ontogenetic changes in habitat requirements require fish to move between river habitat types like mainstems, tributaries, and floodplains, and is affected by river regulation, which limits both movement and habitat availability [42,49]. Time series, especially those from arid areas, report dramatic collapse and changes in fish populations associated with drought-induced mortality and reduced recruitment (Table 1) [25,50,51]. Many of these effects are caused by human-driven habitat deterioration, including the loss or alteration of flow, fragmentation to pools, and increases in environmental harshness associated with poor water quality [52]. Thus, the stress associated with low flow is a major driver of these effects (Figure 1). However, increased ecosystem size, particularly when associated with spring snow melt or floodplain inundation, can increase recruitment [53] and the availability of drifting food [54] (Table 1). Moreover, the capacity of hillslopes to store and release groundwater is likely to be important in buffering populations of fish like salmonids from the detrimental effects of ecosystem size fluctuations [30]. Since the availability of key spaces is a fundamental driver of fish population sizes [55], more investigation of the scaling of population responses should be fruitful.

Box 2. Important contingencies in river scaling relationships

Ever since the River Continuum Concept was proposed [1], factors that modify the effects of size-related drivers in rivers have been identified. These factors provide both insights that enrich understanding of how size-related drivers work and further challenges regarding how river size interacts with other drivers. These contingencies affect key river-size scaling relationships and greater consideration of them will be insightful.

The multiple influences on macroinvertebrate populations

Despite primary production increasing with catchment area, relationships with macroinvertebrate secondary production are typically much weaker [37]. This is unsurprising given the general disassociation of local per-unit-area density with river size, driven by the many other influences, especially disturbance, on macroinvertebrate populations [39]. However, few studies have evaluated how total population sizes (i.e., per-unit-area density × habitat area) change with river size or have attempted to disentangle the ecosystem size-related effects from non-size-related drivers.

The effects of river network topology on community assembly

The fractal nature of stream network topology not only drives aquatic habitat size but also constrains aquatic dispersal and affects the isolation of habitats [3]. Such limitations can underpin neutral community dynamics, whereby given local carrying capacities, dispersal kernels constrained by dendritic topological structure explain fish diversity [46] and potentially many other processes [11]. This means that the configuration of branches, as well as their size, is important. Because within-branch characteristics are typically more homogeneous than between-branch characteristics, the former can stabilize populations by preventing among-branch synchronization [96]. By comparison, because branch size increases population sizes, branch-size heterogeneity will tend to reduce extinction risk by reducing relative fluctuations [95]. Moreover, because disturbance progresses downstream in an advective dendritic network, relatively undisturbed headwater branches may underpin resilience [97]. The occurrence of such refuges could be a product of either branching complexity (more branches) or ecosystem size (a large catchment contains more branches), with the relative importance of mechanisms depending on how synchronised perturbations are across branches [95].

Mobile predators and cross-ecosystem subsidies involving rivers

Mobile or cross-boundary predators are particularly important because they move energy beyond traditional ecosystem boundaries, decoupling demographic feedback between predator and prey populations and their resources [98]. Wading or raptorial birds, diadromous fish, and other predators that move over vast spatial scales are not influenced by river size in the same way as resident species or those confined to river channels [93]. For river systems with large amounts of shoreline, like multichannel bed or 'braided rivers', the amounts of exchange across the water–riparian boundary can be huge, greatly extending the influence of the river ecosystem [89,93]. For those situations, relevant ecosystem sizes will encompass whole landscapes. However, better understanding of how the scaling of river ecosystem boundaries, both longitudinal and lateral, scales with exchange rates could be integral to meta-ecosystem stability [84,98].

Richness

Compared with other influences, ecosystem-size effects on river taxon richness appear modest and variable (Table 1) [56,57] but may also reflect less refined understanding of how river size influences richness. Species-area scaling is a cornerstone of ecology [58], but only 53% of 165 evaluations utilising a swath of ecosystem size metrics revealed positive relationships for rivers [56]. This situation may reflect a less mature understanding of how river size influences diversity.

First, the lack of strong relationships is likely to point to the inadequacy of classical frameworks for predicting richness in branching networks, signalling the need for new theory [59]. The success of models combining both network topology and habitat size in explaining fish community composition [12,46] points to the importance of branch topology as well as habitat-size-related drivers (Box 2). Second, it will be difficult to disentangle the various direct and indirect effects of river size, like niche diversity and productive space, on richness if they act in opposing or multiplicative ways [56]. Finally, strong species-area relationships have been identified using landscape polygons as units of habitat size [58]. Being land based, such measures do not explicitly measure freshwater ecosystem extent, but instead are likely to combine the effects of branching complexity, ecosystem size, and biogeography in a large-scale spatial measure. Thus, there is much to be uncovered regarding the drivers of riverine species-area relationships, but productive space and habitat heterogeneity are both likely to be involved (Figure 1).

Community assembly

If smaller **community sizes** are subject to higher ecological drift [44,60] and space limitations correspond to smaller community sizes, communities in smaller headwater habitats might be subject to heightened instability. However, headwaters are also relatively isolated compared with mainstems, and the mix of processes involved in community assembly is hypothesised to differ depending on network position [61]. Experiments support elements of this hypothesis [62], but considerable variability has also been observed [60,63]. Further advances in understanding of river ecosystem-size effects on community assembly will involve disentangling the relative influences of space, isolation, and branching (Box 2).

Community stability

Multiple connections are being established between river size and disturbances (Table 1). First, matching evidence of population collapses in contracted streams, surveys indicate that communities of small streams are more impacted by a range of disturbance types than larger rivers [64,65]. An experimental flood-simulating disturbance applied across a river-size gradient also showed that community stability increases with ecosystem size, driven by heightened resistance in larger rivers [66]. Larger rivers may be more resistant to perturbation if increased space facilitates the stabilising effects of mobile predators or greater compensation via portfolio effects [66].

Second, alterations to river flows that reduce aquatic habitat size are particularly influential. When this is seasonal and predictable, large temporal changes in community composition can occur that increase regional diversity because the taxa present during wet and dry phases are different [67]. However, reductions in flow associated with systemic and intensifying drought leading to habitat deterioration are causing dramatic shifts in fish and invertebrate assemblages [68–71]. Human alterations of flow regimes that create stressful conditions also have strong effects on invertebrates, with abundance, density, and richness all reduced, whereas algal abundance is increased [52]. Groundwater influences are likely to be an important stabilising force, with the largest changes in community composition occurring when flow becomes intermittent, with more severe change associated with human-driven intermittence [23]. Overall, these relationships suggest that small rivers are particularly susceptible to flow-related disturbance, with the most severe effects likely to occur when that disturbance modifies the natural flow regime and results in intermittence (Figure 1).

Food webs

Space, and productive space, are hypothesised to be fundamental drivers of food-web configuration because of their connection to habitat and resource availability [72]. Positive correlations between river size and food-chain length (Table 1) are associated with predatory fish absence from the smallest habitats and restrictions on fish body size, and therefore trophic level, in small rivers [72,73], but become less important in big rivers where body-size constraints are relatively unimportant [74]. However, such constraints on predator body size are probably underappreciated because of the under-sampling of very large rivers. In the largest rivers, habitat heterogeneity may promote stable food-web configurations [29], but the logistical challenges of sampling at such scales are just being overcome. Beyond those effects, alteration in flow dynamics associated with either dampening of discharge variation through flow regulation or increased flood disturbance leads to lengthening or shortening, respectively, of food chains via effects on trophic omnivory [72,73,75]. Thus, overall, both physical habitat availability constraints and flow-related environmental disturbance drive size-related influences on food webs (Figure 1), but considering ecosystem-size relationships from first principles with flow changes layered on top is helpful.

Habitat-availability effects are strongest where extreme flow reduction leads to food-web collapse in drying rivers [72,76]. Drought simulation experiments, although they typically do not include fish, also show that the largest organisms, predators, are most impacted [77]. Relatively small changes in ecosystem size can elicit large changes in trait combinations [69], revealing break-points in food-web collapse [43]. For example, increased densities of predators in contracted fragments can drive strong destabilising species interactions resulting in unexpected changes in communities [43]. Thus, although compensatory dynamics affecting the topology of food-web connections are important in maintaining stability in the face of shrinking habitat size, the effects of flow loss on food webs remain substantial [78]. Better understanding of these (de)stabilising forces, and the scaling of relationships, will be important in avoiding the negative consequences, particularly lingering legacies, of drought-induced riverine food-web collapse [76].

Managing river size

Humans are altering river ecosystem size [6,7,23]. Some modifications are intentional and well known, like flow regulation and abstraction. However, many, like groundwater reductions and floodplain encroachment [7], are underappreciated and are likely to lead to unintentional fragmentation effects, which will be important to manage. Management needs to recognise the inevitable connection of rivers and human society and the likely association of river size with the stable provision of ecosystem services.

Evaluating fragmentation, homogenization, and edge effects in rivers

Habitat loss, such as that associated with reduced river size, is typically accompanied by fragmentation, homogenization, and edge effects [45], but these influences, as well as the scaling relationships that might constrain them, are poorly understood. Longitudinal fragmentation due to drying and migratory obstacles [23,79] and temporal homogenization caused by flow regulation [52] are detrimental, but the influence of changes in lateral and vertical dimensions are poorly known, as are edge effects and the influences of spatial homogenization (Figure 2). Such fragmentation is important because new landscape-scale evaluations of heterogeneity reveal its role in underpinning river stability [29]. Second, spatial homogenization of river branches via flow regulation could undermine an important stabilising influence driven by spatial insurance mechanisms [80]. Finally, idiosyncratic fragmentation of rivers involving isolated and unnatural drying caused by abstraction, and diversion of water, which alters branching [23], could also lead to edge effects.

Managing river size in human-dominated landscapes

The multidimensionality of river ecosystems and their inevitable, and inescapable, integration into human-dominated landscapes means that traditional responses to habitat loss, like reserve creation, are less useful for rivers. Thus, plans for retaining or restoring river size need to be implementable in human-dominated landscapes [81]. This will start with legal definitions of rivers that reflect their multidimensionality, especially their longitudinal and lateral connections [82]. This also needs approaches that balance the needs of all ecosystem components with human demands for water [83], mitigate flood risks to adjacent communities while maintaining key lateral habitats [7,84], overcome connectivity barriers [85], and reflect relational approaches by Indigenous peoples [81]. Overcoming these challenges requires work across the boundary between policy and science [86].

Connection of vulnerability and restorability with river size

The linkage of river discharge to ecological community stability [66] has further implications for both the differential vulnerability of rivers to disturbances and potential restoration opportunities. The intertwined character of resistance and resilience to both community disassembly and reassembly [87] mean that any influences of ecosystem size on stability will be inexorably linked to restoration potential. Because small rivers (in terms of discharge) are likely to be more vulnerable to disturbance than large rivers, they ought to be prioritised in protection. River size could provide an important indication of the feasibility of or amount of effort required for restoration success. Moreover, if community assembly processes vary according to river size, river size could indicate the types of restoration approaches that will be successful [88]. Although large rivers might have more stable communities, they are disproportionately important for many ecosystem processes and delivery of services [16,89] and suffer faster regime shifts [90]. Thus, restoration efforts can benefit from the developing understanding of ecosystem-size influences on rivers.

Concluding remarks

River size has influential effects and underlies fundamental parts of contemporary mechanisms explaining patterns in river populations and communities [12,23,39,69]. The multiple measures of ecosystem size that have been applied in rivers, in addition to the variety of relationships with populations and communities and the associated contingencies, can be seen two ways. They could be unhelpful context dependence or they could lead to unifying concepts. Recent advances revealing strong scaling of physical properties and biogeochemical processes highlight the potential helpfulness of scaling relationships in answering fundamental questions with global implications. To develop the much-sought cohesive framework for forecasting effects of river ecosystem size changes, many aspects of ecosystem size scaling need to be more thoroughly investigated (see Outstanding questions).

Our evaluation suggests that river ecosystem size is most important for river populations and communities when associated with physical constraints limiting body size or movements, when boundary conditions such as surfaces areas or shorelines affect rates of processes, or where contraction severely limits habitat space. Where river-size effects are associated with co-varying riparian conditions, productive space, or branch configuration, effects are likely to be more context dependent. However, many of the landscape-scale influences are only beginning to be appreciated and could be very important. In total, these relationships mean that human alteration of river ecosystem-size scaling will have far-reaching implications, so further investigation of the generality and contingencies affecting these scaling relationships will be particularly important.

Rationalization of theoretical insights into biodiversity drivers with observations that the patterns of river flow, their lateral and vertical dimensions, and even their patterns of branching are being altered will be necessary. This potentially involves many poorly understood fragmentation-, homogenization-, and edge-effect issues, which have large potential to affect scaling relationships. Thus, there is a danger that just as we discover better ways to model the dynamics of river populations and communities, they are redundant because rivers are now so heavily modified by human influence. This quandary means that some of the most important outstanding questions relate to how best to characterise changes in river ecosystem size [7,29] and how to restore those dimensions [17].

Finally, river ecosystems are at the open end of a continuum of ecosystem types varying in the extent to which they are '**bounded ecosystems**' [18]. Ecosystem size-related mechanisms that generate biodiversity, regulate populations, and stabilize communities are likely to be qualitatively similar across these ecosystem types [13,91,92], but assessing how ecosystem-size effects are influenced by the boundary characteristics and dimensionality characteristics of these different ecosystems is likely to yield useful insights about those general mechanisms.

Outstanding questions

What are the shapes, universality, and spatial domains of scaling relationships between river size and their populations and communities, and what contingencies affect those scaling relationships? Characterising these relationships, determining which size measures are most useful, and revealing causal connections will aid limit-setting to avoid further damage to river ecosystems and help in devising ways to balance human and ecological needs for water.

How are all the dimensions of river ecosystems changing and how can fragmentation, homogenisation, and edge effects be measured in all river dimensions? Logistical challenges mean that large rivers and groundwater influences are being under-sampled. Solving this requires a change of focus as well as better collaboration between hydrologists, geomorphologists, and ecologists and the use of new technologies.

How do total population sizes (i.e., per-unit-area density × habitat area) change with river size? Few studies have attempted to disentangle ecosystem size-related effects from non-size-related drivers.

Which dimensions of river ecosystems are the most important to restore and how does ecosystem size affect the restorability of a river? Since many aspects of river impairment are linked to aspects of their size, determining which aspects of river size can be best manipulated to enhance restoration success will be important.

How do the size-scaling relationships that characterise the relatively open but highly dynamic and boundary-dependent ecosystems of rivers differ across ecosystem types varying in boundedness? Here, comparisons across lake, river, island, and reef ecosystems will be fruitful.

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Declaration of interests

No interests are declared.

References

1. Vannote, R.L. *et al.* (1980) The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37, 130–137
2. Campbell Grant, E.H. *et al.* (2007) Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol. Lett.* 10, 165–175
3. Rodriguez-Iturbe, I. *et al.* (2009) River networks as ecological corridors: a complex systems perspective for integrating hydrologic, geomorphologic, and ecologic dynamics. *Water Resour. Res.* 45, W01413
4. Stanley, E.H. *et al.* (1997) Ecosystem expansion and contraction in streams. *BioScience* 47, 427–435
5. Jardine, T.D. *et al.* (2015) Does flood rhythm drive ecosystem responses in tropical riverscapes? *Ecology* 96, 684–692
6. Tonkin, J.D. *et al.* (2019) Prepare river ecosystems for an uncertain future. *Nature* 570, 301–303
7. Brierley, G.J. *et al.* (2023) Reanimating the strangled rivers of Aotearoa New Zealand. *WIREs Water* 10, e1624
8. Datry, T. *et al.* (2023) Non-perennial segments in river networks. *Nat. Rev. Earth Environ.* 4, 815–830
9. Lal, P. *et al.* (2020) Evaluating the 2018 extreme flood hazard events in Kerala, India. *Remote Sens. Lett.* 11, 436–445
10. Martin, J.T. *et al.* (2020) Increased drought severity tracks warming in the United States' largest river basin. *Proc. Natl. Acad. Sci. U. S. A.* 117, 11328–11336
11. Rinaldo, A. *et al.* (2020) *River Networks as Ecological Corridors: Species, Populations, Pathogens*, Cambridge University Press
12. Terui, A. *et al.* (2021) Emergent dual scaling of riverine biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2105574118
13. Galiana, N. *et al.* (2022) Ecological network complexity scales with area. *Nat. Ecol. Evol.* 6, 307–314
14. Wollheim, W.M. *et al.* (2022) Superlinear scaling of riverine biogeochemical function with watershed size. *Nat. Commun.* 13, 1230
15. Segatto, P.L. *et al.* (2021) The metabolic regimes at the scale of an entire stream network unveiled through sensor data and machine learning. *Ecosystems* 24, 1792–1809
16. Battin, T.J. *et al.* (2023) River ecosystem metabolism and carbon biogeochemistry in a changing world. *Nature* 613, 449–459
17. Palmer, M. and Ruhi, A. (2019) Linkages between flow regime, biota, and ecosystem processes: implications for river restoration. *Science* 365, eaaw2087
18. Post, D.M. *et al.* (2007) The problem of boundaries in defining ecosystems: a potential landmine for uniting geomorphology and ecology. *Geomorphology* 89, 111–126
19. Benda, L. *et al.* (2004) The network dynamics hypothesis: how channel networks structure riverine habitats. *BioScience* 54, 413–427
20. Ward, J.V. *et al.* (1998) The boundaries of river systems: the metazoan perspective. *Freshw. Biol.* 40, 531–569
21. Terui, A. (2023) Revisiting scale invariance and scaling in ecology: river fractals as an example. *Popul. Ecol.*, Published online August 7, 2023. https://doi.org/10.1002/1438-390X.12163
22. Messager, M.L. *et al.* (2021) Global prevalence of non-perennial rivers and streams. *Nature* 594, 391–397
23. Datry, T. *et al.* (2023) Causes, responses, and implications of anthropogenic versus natural flow intermittence in river networks. *BioScience* 73, 9–22
24. Abernethy, E.F. *et al.* (2021) Hydropeaking intensity and dam proximity limit aquatic invertebrate diversity in the Colorado River Basin. *Ecosphere* 12, e03559
25. Meijer, C.G. *et al.* (2021) Disentangling the multiple effects of stream drying and riparian canopy cover on the trophic ecology of a highly threatened fish. *Freshw. Biol.* 66, 102–113
26. Wohl, E. (2016) Spatial heterogeneity as a component of river geomorphic complexity. *Prog. Phys. Geogr. Earth Environ.* 40, 598–615
27. Scholl, E.A. *et al.* (2021) Uncovering process domains in large rivers: patterns and potential drivers of benthic substrate heterogeneity in two North American riverscapes. *Geomorphology* 375, 107524
28. Dralle, D.N. *et al.* (2023) Mapping surface water presence and hyporheic flow properties of headwater stream networks with multispectral satellite imagery. *Water Resour. Res.* 59, e2022WR034169
29. Scholl, E.A. *et al.* (2023) Landscape diversity promotes stable foodweb architectures in large rivers. *Ecol. Lett.* 26, 1740–1751
30. Dralle, D.N. *et al.* (2023) The salmonid and the subsurface: hillslope storage capacity determines the quality and distribution of fish habitat. *Ecosphere* 14, e4436
31. Junk, W.J. *et al.* (1989) The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 106, 110–127
32. Bernhardt, E.S. *et al.* (2022) Light and flow regimes regulate the metabolism of rivers. *Proc. Natl. Acad. Sci. U. S. A.* 119, e2121976119
33. Finlay, J.C. *et al.* (2011) Light-mediated thresholds in stream-water nutrient composition in a river network. *Ecology* 92, 140–150
34. Koenig, L.E. *et al.* (2019) Emergent productivity regimes of river networks. *Limnol. Oceanogr. Lett.* 4, 173–181
35. Hotchkiss, E.R. *et al.* (2015) Sources of and processes controlling CO_2 emissions change with the size of streams and rivers. *Nat. Geosci.* 8, 696–699
36. Sponseller, R.A. and Fisher, S.G. (2006) Drainage size, stream intermittency, and ecosystem function in a Sonoran desert landscape. *Ecosystems* 9, 344–356
37. Finlay, J.C. (2011) Stream size and human influences on ecosystem production in river networks. *Ecosphere* 2, art87
38. Jellyman, P.G. *et al.* (2014) Increases in disturbance and reductions in habitat size interact to suppress predator body size. *Glob. Chang. Biol.* 20, 1550–1558
39. McIntosh, A.R. *et al.* (2018) Capacity to support predators scales with habitat size. *Sci. Adv.* 4, eaap7523
40. Al-Chokhachy, R. *et al.* (2022) Stream size, temperature, and density explain body sizes of freshwater salmonids across a range of climate conditions. *Can. J. Fish. Aquat. Sci.* 79, 1729–1744

41. Woolnough, D.A. *et al.* (2009) Fish movement and habitat use depends on water body size and shape. *Ecol. Freshw. Fish* 18, 83–91
42. Walker, R.H. *et al.* (2022) Should I stay or should I go: hydrologic characteristics and body size influence fish emigration from the floodplain following an atypical summer flood. *Ecol. Freshw. Fish* 31, 607–621
43. Aspin, T.W.H. *et al.* (2019) Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment. *Freshw. Biol.* 64, 750–760
44. Siqueira, T. *et al.* (2020) Community size can affect the signals of ecological drift and niche selection on biodiversity. *Ecology* 101, e03014
45. Haddad, N.M. *et al.* (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, e1500052
46. Muneepeerakul, R. *et al.* (2008) Neutral metacommunity models predict fish diversity patterns in Mississippi–Missouri basin. *Nature* 453, 220–222
47. Tamario, C. *et al.* (2021) Size, connectivity and edge effects of stream habitats explain spatio-temporal variation in brown trout (*Salmo trutta*). *Proc. Biol. Sci.* 288, 20211255
48. Schlosser, I.J. (1995) Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* 76, 908–925
49. Roberts, H.C. *et al.* (2023) Tributary streams provide migratory fish with access to floodplain habitats in a regulated river: evidence from alligator gar, *Atractosteus spatula*. *Can. J. Fish. Aquat. Sci.* 80, 393–407
50. Perkin, J.S. *et al.* (2019) Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. *Ecohydrology* 12, e2120
51. Archdeacon, T.P. and Reale, J.K. (2020) No quarter: lack of refuge during flow intermittency results in catastrophic mortality of an imperiled minnow. *Freshw. Biol.* 65, 2108–2123
52. Sabater, S. *et al.* (2018) Effects of human-driven water stress on river ecosystems: a meta-analysis. *Sci. Rep.* 8, 11462
53. Jenney, C.J. *et al.* (2022) Increased juvenile native fish abundance following a major flood in an Arizona river. *J. Freshw. Ecol.* 37, 1–14
54. Caldwell, T.J. *et al.* (2018) Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance. *River Res. Appl.* 34, 965–976
55. Freeman, M.C. *et al.* (2022) Toward improved understanding of streamflow effects on freshwater fishes. *Fisheries* 47, 290–298
56. Vander Vorste, R. *et al.* (2017) Does stream size really explain biodiversity patterns in lotic systems? A call for mechanistic explanations. *Diversity* 9, 26
57. Carraro, L. *et al.* (2023) Modelling environmental DNA transport in rivers reveals highly resolved spatio-temporal biodiversity patterns. *Sci. Rep.* 13, 8854
58. Passy, S.I. *et al.* (2023) On the shape and origins of the freshwater species–area relationship. *Ecology* 104, e3917
59. Rinaldo, A. *et al.* (2018) River networks as ecological corridors: a coherent ecohydrological perspective. *Adv. Water Resour.* 112, 27–58
60. Green, M.D. *et al.* (2022) Rethinking biodiversity patterns and processes in stream ecosystems. *Ecol. Monogr.* 92, e1520
61. Brown, B.L. and Swan, C.M. (2010) Dendritic network structure constrains metacommunity properties in riverine ecosystems. *J. Anim. Ecol.* 79, 571–580
62. Brown, B.L. *et al.* (2018) Experimentally disentangling the influence of dispersal and habitat filtering on benthic invertebrate community structure. *Freshw. Biol.* 63, 48–61
63. Schmera, D. *et al.* (2018) Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshw. Biol.* 63, 74–85
64. Greenwood, M.J. *et al.* (2012) Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *J. Appl. Ecol.* 49, 213–222
65. Campbell, R.E. and McIntosh, A.R. (2013) Do isolation and local habitat jointly limit the structure of stream invertebrate assemblages? *Freshw. Biol.* 58, 128–141
66. Greig, H.S. *et al.* (2022) Habitat size influences community stability. *Ecology* 103, e03545
67. Tonkin, J.D. *et al.* (2017) Seasonality and predictability shape temporal species diversity. *Ecology* 98, 1201–1216
68. Ruhí, A. *et al.* (2016) Declining streamflow induces collapse and replacement of native fish in the American Southwest. *Front. Ecol. Environ.* 14, 465–472
69. Aspin, T.W.H. *et al.* (2019) Extreme drought pushes stream invertebrate communities over functional thresholds. *Glob. Chang. Biol.* 25, 230–244
70. Nelson, D. *et al.* (2021) Energy pathways modulate the resilience of stream invertebrate communities to drought. *J. Anim. Ecol.* 90, 2053–2064
71. Saffarinia, P. *et al.* (2022) Effects of experimental multi-season drought on abundance, richness, and beta diversity patterns in perennially flowing stream insect communities. *Hydrobiologia* 849, 879–897
72. Sabo, J.L. *et al.* (2010) The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* 330, 965–967
73. McHugh, P.A. *et al.* (2010) Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecol. Lett.* 13, 881–890
74. Warfe, D.M. *et al.* (2013) Productivity, disturbance and ecosystem size have no influence on food chain length in seasonally connected rivers. *PLoS One* 8, e66240
75. Ruhí, A. *et al.* (2016) Flow regulation increases food-chain length through omnivory mechanisms in a Mediterranean river network. *Freshw. Biol.* 61, 1536–1549
76. McHugh, P.A. *et al.* (2015) Habitat size influences food web structure in drying streams. *Ecography* 38, 700–712
77. Ledger, M.E. *et al.* (2013) Drought alters the structure and functioning of complex food webs. *Nat. Clim. Chang.* 3, 223–227
78. Lu, X. *et al.* (2016) Drought rewires the cores of food webs. *Nat. Clim. Chang.* 6, 875–878
79. Anderson, E.P. *et al.* (2018) Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Sci. Adv.* 4, eaao1642
80. Boddy, N.C. and McIntosh, A.R. (2021) Could spatial heterogeneity in flow disturbance drive temporal stability of native–invasive species co-occurrence in riverscapes? *Freshw. Biol.* 66, 902–913
81. Febria, C. *et al.* (2022) Pluralistic approaches in research aim to advance farming and freshwater restoration in the Great Lakes basin. *Adv. Ecol. Res.* 66, 201–241
82. Vosloo, R. *et al.* (2022) Braided rivers: between land and water, between law and science – "Canterbury Regional Council v Dewhirst Land Company.". *N. Z. J. Environ. Law* 26, 255–269
83. Tonkin, J.D. *et al.* (2021) Designing flow regimes to support entire river ecosystems. *Front. Ecol. Environ.* 19, 326–333
84. Harris, H.A.L. *et al.* (2023) Multi-scale ecological resilience in braided rivers. In *Resilience in Riverine Landscapes* (Thoms, M.C. and Fuller, I.C., eds), pp. 157–176, Elsevier
85. Verhelst, P. *et al.* (2021) Toward a roadmap for diadromous fish conservation: the big five considerations. *Front. Ecol. Environ.* 19, 396–403
86. Goodrich, K.A. *et al.* (2020) Who are boundary spanners and how can we support them in making knowledge more actionable in sustainability fields? *Curr. Opin. Environ. Sustain.* 42, 45–51
87. Lake, P.S. (2013) Resistance, resilience and restoration. *Ecol. Manag. Restor.* 14, 20–24
88. Patrick, C.J. *et al.* (2021) The application of metacommunity theory to the management of riverine ecosystems. *WIREs Water* 8, e1557
89. Hauer, F.R. *et al.* (2016) Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. *Sci. Adv.* 2, e1600026
90. Cooper, G.S. *et al.* (2020) Regime shifts occur disproportionately faster in larger ecosystems. *Nat. Commun.* 11, 1175
91. McWilliams, C. *et al.* (2019) The stability of multitrophic communities under habitat loss. *Nat. Commun.* 10, 2322
92. Matthews, T.J. *et al.* (2021) *The Species–Area Relationship: Theory and Application*, Cambridge University Press

93. Muehlbauer, J.D. *et al.* (2014) How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. *Ecology* 95, 44–55
94. Strayer, D.L. *et al.* (2003) A classification of ecological boundaries. *BioScience* 53, 723–729
95. Ma, C. *et al.* (2020) Spatial variation in branch size promotes metapopulation persistence in dendritic river networks. *Freshw. Biol.* 65, 426–434
96. Terui, A. *et al.* (2018) Metapopulation stability in branching river networks. *Proc. Natl. Acad. Sci. U. S. A.* 115, E5963–E5969
97. Lowe, W.H. *et al.* (2006) Linking scales in stream ecology. *BioScience* 56, 591–597
98. Recalde, F.C. *et al.* (2020) Allochthonous aquatic subsidies alleviate predation pressure in terrestrial ecosystems. *Ecology* 101, e03074
99. Champagne, E.J. *et al.* (2022) Riparian buffers maintain aquatic trophic structure in agricultural landscapes. *Biol. Lett.* 18, 20210598
100. Lancaster, J. *et al.* (2021) Hydrological controls on oviposition habitat are associated with egg-laying phenology of some caddisflies. *Freshw. Biol.* 66, 1311–1327