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AQUATIC ECOSYSTEM SERVICES

REVIEW PAPER

Ecosystem services provided by small streams: an overview

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Abstract Small streams constitute the majority of the water courses in a catchment and have specific characteristics that distinguish them from larger streams and rivers. Despite their small size and frequently remote locations, small streams contribute to ecosystem services that are important for humans. Here, we have identified 27 ecosystem services that small streams provide: seven supporting services, eight regulating services, five provisioning services and seven cultural services. Small streams are especially important for the maintenance of biodiversity, which is the basis of many ecosystem services. Small streams also support ecosystem services provided by larger streams and rivers due to longitudinal connectivity resulting in the downstream transference of energy, water, sediments, nutrients, organic matter and organisms. Small streams are, however, highly vulnerable to disturbances, which can compromise the ecosystem services they supply. We see a global need to effectively protect small streams to safeguard biodiversity and human wellbeing.

Keywords Supporting services · Regulating services · Provisioning services · Cultural services · Longitudinal connectivity · Threats

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Small streams and headwaters: definitions, characteristics and legislation

The definitions of “small streams” and “headwater streams” are not consensual and they are often used

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interchangeably (Biggs et al., 2017). Richardson (2019) makes a distinction between both terms, defining "headwater streams" as 1st order streams, i.e., the smallest streams with a defined channel, and "small streams" as 2nd order streams, i.e., streams that result from the confluence of two 1st order streams (Strahler, 1957). Here we will use the term "small streams" to refer to 1st and 2nd order streams together (Meyer et al., 2007; Wohl, 2017), as they are all relatively small and share similarities in many aspects, and we will use the term "headwaters" to refer to small streams at higher elevations (Fig. 1; Table 1). There are cases where 1st order streams emerge at the surface already with considerable width and high discharge, but this often results from geologic peculiarities, e.g., outflows in karst regions (Paiva et al., 2016). Most often, 1st and 2nd order streams are up to a few meters wide and have low discharge (up to a few—tens of—liters per second; Ferreira et al., 2006; Rosemond et al., 2015). Despite their small size, and consequently small drainage areas, many small streams are perennial, i.e., they flow year-round in a typical year, especially in humid regions. In arid regions, however, a large percentage of small streams are temporary: intermittent streams that stop flowing or dry out at some point over their length and for some time, generally in the warmer months, and ephemeral streams that only flow as a consequence of heavy rainfall or snow melt (Hill et al., 2014; Messager et al., 2021). Here we address ecosystem services provided by flowing small streams considering perennial streams and temporary streams together as both stream types share many characteristics when flowing (for reviews dedicated to ecosystem services specifically provided by temporary streams (all hydrological phases) and dry rivers please see Datry et al., 2018; Stubbington et al., 2020; Gutiérrez et al., 2022). The number of small streams in hydrographic networks is generally underestimated as they are too small to display on large scale maps, and may also not display on small-scale maps, especially if intermittent (Meyer et al., 2007). Still, small streams are the most numerous in total number and contribute the most to total stream length in hydrographic networks (Horton, 1945; Leopold et al., 1964). For instance, small streams comprise > 70% of water course length in European catchments (Kristensen & Globevnik, 2014) and ~ 75% of total water course length at a global scale (Downing et al., 2012).

Despite their large number and cumulative length in hydrographic networks, small streams are generally disregarded; they are often not included in legislation, not considered in official bioassessment programs, and consequently not protected. The European Water Framework Directive (enforced by the 27 European Union member states), in its size typology for rivers, defines the smallest size class as having a catchment area between 10 and 100 km^2, which excludes many 1st and 2nd order streams that have catchment areas < 10 km^2 (EC, 2000; Kristensen & Globevnik, 2014). The US Clean Water Act (CWA) from 1972 does not specifically protect small streams, although they were partially considered due to their important contribution to the health, productivity and navigability of larger (i.e., navigable) streams and rivers; however, the US Supreme Court SWANCC decision in 2001 limited small stream protection only to those streams that are directly connected to or influence navigable waters (Nadeau & Rains, 2007). The Obama Administration's Waters of the US (WOTUS) Rule in 2015 placed small streams under CWA jurisdiction, but an executive order by the Trump Administration in 2017 counteracted the WOTUS Rule (Colvin et al., 2019), which itself was again overturned late in 2021, reasserting pre-2015 definitions (https://www.epa.gov/wotus). These back-and-forth decisions about the legal protection of small streams indicate that the relevance of small streams is not yet consensual at governmental scales.

Also, in many African countries, there is no specific legislation for the protection of small streams as this is done as part of protected areas (e.g., national reserves, national parks) and relevant legislations and regulations. In Kenya, for instance, protection of forested streams falls under the Water Act (2016) and as vulnerable water sources they can be protected by declaring the catchment area they drain as a protected area. Owing to rampant deforestation and declining water resources in Kenya, the government also established the Water Towers Agency in 2012 to coordinate and oversee the protection, rehabilitation, conservation and sustainable management of all the critical water towers, i.e., high elevation Afromontane landscapes in Kenya, such as the Aberdares, Mau Forests, Mt. Elgon and Mt. Kenya, which are sources of many streams and rivers that supply water to millions of people.

Fig. 1 Small streams in different regions. Larrainsoroeta (**A**) and Agauntza (**B**) are 2nd order streams, both in mixed deciduous forests dominated by beech (*Fagus sylvatica* L.) in the Basque Country, northern Spain. An unnamed tributary of Ribeira do Catarredor (**C**) and Ribeira do Candal (**D**) are 2nd order perennial streams in mixed deciduous forests dominated by oaks (*Quercus* spp.) and chestnuts (*Castanea sativa* Mill.) in Serra da Lousã, central Portugal. Arroyo Caracolito is a 1st order intermittent stream in a monospecific deciduous beech (*Nothofagus pumilio* (Poepp. & Endl.) Krasser) forest that forms the upper tree belt in southern Andes (**E**) and Arroyo Ottowest is a 1st order perennial stream in a mixed forest (**F**), both in the Cordillera de los Andes, Patagonia, Argentina. An unnamed 1st order perennial stream in Kaptagat Forest, Kerio Escarpment, western Kenya (**G**). Snyder Cove Creek (**H**) is a 2nd order perennial stream in western Washington, US, which is a spawning site for several species of salmon (*Oncorhynchus* spp.). A 1st order perennial reach of Rio Preto at Parque Estadual do Rio Preto (**I**) and Córrego Taiobas, a 2nd order perennial stream at Serra do Cipó (**J**), both in the Cerrado (Brazilian savanna) biome in Minas Gerais, SE Brazil. Córrego São Bartolomeu is a 2nd order perennial stream in Minas Gerais (**K**) and Córrego Luxemburgo is a 2nd order perennial stream in Espírito Santo (**L**), both in the Atlantic Forest biome, SE Brazil. Photo credits: **A**, **B** Aitor Larrañaga; **C**, **D** Verónica Ferreira; **E**, **F** Ricardo Albariño; **G** Christine Owade; **H** Carri LeRoy; **I**, **J**, **K**, **L** Marcelo Moretti

Table 1 Generic characteristics that distinguish small streams (1st and 2nd order streams) from downstream larger streams and rivers, and their drivers (adapted from Lowe & Likens, 2005; Meyer et al., 2007; Wohl, 2017; Richardson, 2019)

Stream characteristic	Characteristic driver
Hydromorphology	
Small size (narrow, shallow)	Defining characteristic
Small water volume	Defining characteristic
Close linkage to the terrestrial environment	Large aquatic-terrestrial interface due to large perimeter-to-volume ratio
Hydrological independence (isolation)	No (in the case of 1st order streams) or few (in the case of 2nd order streams) tributaries due to their head position in the hydrographic network
Reduced surface storage zones	No large valley bottoms or floodplains
Reduced subsurface storage zones	Small hyporheic zones or alluvial aquifers
High spatial and temporal hydrological variability	Small drainage areas and small surface and subsurface water storage capacities increase susceptibility to storms and droughts
High susceptibility to local disturbances/High morphological instability	Small size increases susceptibility to landslides, wildfires, thunderstorms, which may promote bank collapse, inputs of large amounts of sediment, or inputs of large wood
High longitudinal variation	Fast decrease in elevation (in high-relief regions); Variation in channel geometry resulting from e.g., large wood blockages, bank collapse
Longitudinal disconnectivity	Waterfalls (in high-relief regions); Low subsurface flow
Hydrologically rough boundaries and coarse substrates (in high-relief regions)	Waterfalls (in high-relief regions); Low erosional power
Riparian vegetation	
Shaded (in forested landscapes)	Closed riparian canopies due to small size
Heterotrophic (mostly in forested landscapes)	Input of large amounts of coarse particulate organic matter from direct litter fall and lateral litter inputs; Low solar radiation, low temperatures and dissolved nutrient availabilities limit instream primary production
Water characteristics	
Water chemistry highly influenced by geology, soil characteristics and atmospheric inputs	Water sources from groundwater inputs and overland flow; Small buffering capacity due to small water volume
Well oxygenated	Cool water temperatures hold higher dissolved oxygen; High surface-to-volume ratio allows atmospheric interchange; High turbulence can increase dissolved gas concentration
Cool temperatures	Shading from riparian forests (in forested landscapes); Closed valleys; High elevations
High or low thermal variation	Low thermal buffering capacity due to small water volume; But, thermal stability if groundwater fed; Thermal stability if shaded

These characteristics partially determine the services provided by small streams and their vulnerability to environmental changes (see also Tables 2 and 4)

Additionally, in Argentina, small streams are protected under different national and provincial laws, which establish the preservation and management of surface and subsurface water resources. Among the laws sanctioned by the Argentine National Congress, the Water Environmental Management Act (Law 25688, 2002), the Native Forest Protection Act (Law 26331, 2007) and the Civil and Commercial Code (Law 26994, 2014) provide some protection. National and provincial water departments and inter-jurisdictional Water Bureaus set the rules and/or administer water usage and pollution control. This does not mean that small streams are protected against human related impacts, e.g., from agriculture, livestock or urbanization, because in developing or low/middle income countries, such as

Argentina, limited economic resources go more frequently to other projects instead of being used for environmental management and control.

Finally, in Brazil, a country with huge hydrographic networks, environmental laws do not adequately address small streams. The Forest Code (Law 12.651; Brasil, 2012) establishes riparian forests as Areas of Permanent Preservation. However, impacts that occur beyond the banks of small streams, such as deforestation to create areas for agriculture and livestock, road building, and construction, are not addressed in the actual legislation. Although these are only several examples of the types of legislation that pertain to small streams, these examples are widely distributed over four continents and include both developed and developing regions. This shows that small streams being disregarded in legislation is not a localized issue and is not dependent on a region's developmental state.

The protection of small streams can, nevertheless, help achieve several of the United Nations' Sustainable Development Goals (https://sdgs.un.org/goals). In particular, Goal 6, which aims to "ensure availability and sustainable management of water and sanitation for all", in its Target 6.3 aims to "improve water quality by reducing pollution, eliminating dumping and minimizing release of hazardous chemicals and materials" and in its Target 6.6 aims to "protect and restore water-related ecosystems". Also, Goal 15, which aims to "protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss", in its Target 15.1 aims to "ensure the conservation, restoration and sustainable use of terrestrial and inland freshwater ecosystems and their services" and in its Target 15.5 aims to "take urgent and significant action to reduce the degradation of natural habitats, halt the loss of biodiversity".

In this review, we aim to (i) highlight the importance of small streams in providing ecosystem services by making an exhaustive compilation of these services (including cultural services), (ii) describe the contributions of small streams to ecosystem services provided by downstream waters, and (iii) emphasize the vulnerability of small streams and their ecosystem services by identifying specific threats to these ecosystems.

Ecosystem services provided by small streams

Definition of ecosystem services

The term "ecosystem services" was coined by Ehrlich and Ehrlich (1981) and popularized by Gretchen Daily (1997) and the Millennium Ecosystem Assessment (MEA) report as "benefits people obtain from ecosystems" (MEA, 2003, 2005), and this is the definition we are using here. According to the MEA, ecosystem services are distributed into four categories: supporting, regulating, provisioning and cultural services (MEA, 2003, 2005). Supporting services are those "that are necessary for the production of all other ecosystem services", and include primary production, oxygen production, soil formation and retention, nutrient, and water cycling and provisioning of habitat. Regulating services are "the benefits obtained from the regulation of ecosystem processes", and include, for instance, air quality maintenance, water regulation and purification and erosion control. Provisioning services are "the products obtained from ecosystems", such as food, fiber, fuel, energy, fresh water, genetic resources, biochemical, and ornamental resources. Finally, cultural services are "the non-material benefits people obtain from ecosystems" through, for instance, esthetic enjoyment, inspiration, recreation and nature-based tourism (Fig. 2).

As defined by the MEA, ecosystem services are seen from an anthropogenic perspective ("benefits *people* obtain") and, therefore, their recognition depends on people's use, i.e., a given ecosystem service is only recognized as such if and when people take advantage of it. For instance, small streams are a source of freshwater (provisioning service) and inspiration (cultural service) only where they are accessible to people; in remote areas, small streams may not provide these (or other) ecosystem services, although they contribute to the services provided by downstream rivers. Also, ecosystem services are assumed as "*benefits* people obtain," which is to some degree subjective. For instance, a small stream can be seen by some people as improving the esthetic appeal of a forested landscape (cultural service), while people with locomotion difficulties may see it as an obstacle and, in this case, the stream could be providing a "disservice" (von Döhren & Haase, 2015). Therefore, not all small streams are capable of providing *all* the ecosystem services addressed below, as these

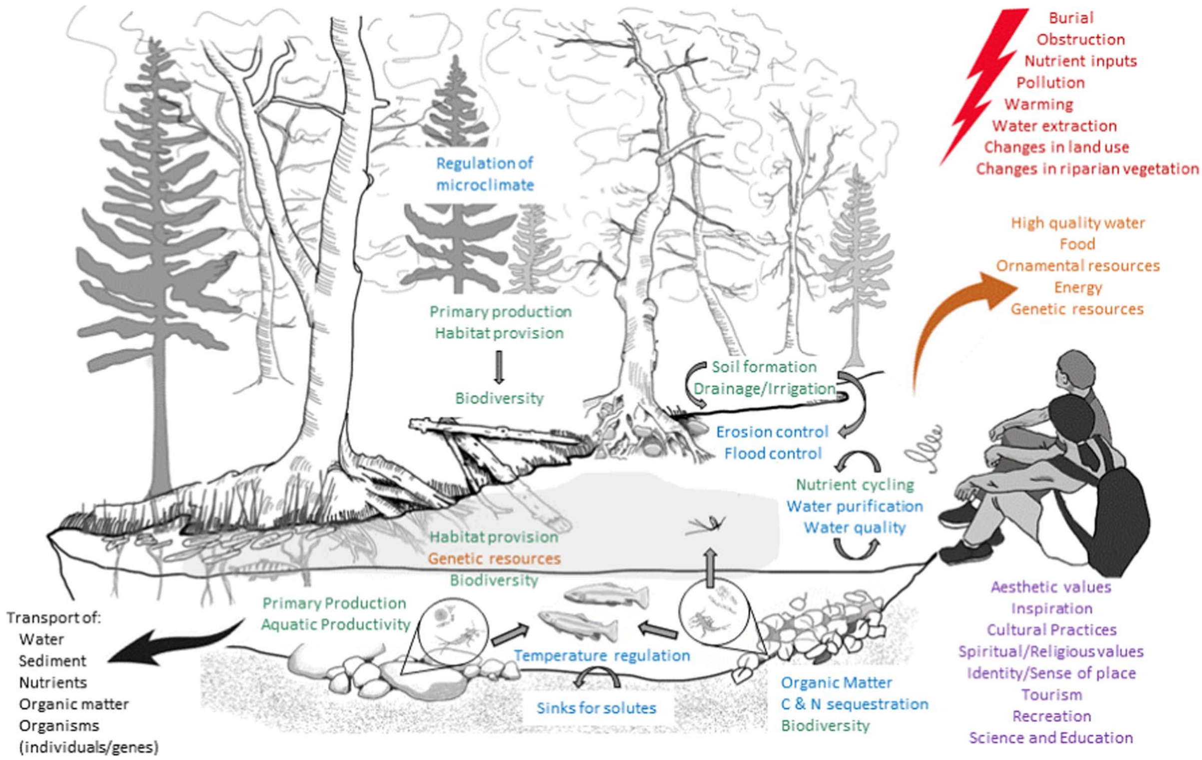

Fig. 2 Ecosystem services provided by small streams: supporting services (in green), regulating services (in blue), provisioning services (in orange) and cultural services (in purple). In addition, contribution of small streams to downstream larger streams and rivers (in black) and some of the major threats to small streams (in red) are also shown. Original artwork by Carri LeRoy

services depend on the presence of people and on their positive perceptions regarding the services being provided. However, we will assume that most small streams *can potentially provide* the services discussed below (Fig. 2; Table 2).

It is also important to note that many ecosystem services are provided at the expense of others. For instance, hydropower generation (provisioning service), with the establishment of transversal barriers (dams), is provided at the expense of several other ecosystem services, including habitat provisioning, nutrient cycling, and biodiversity (supporting services) (Martínez et al., 2013, 2017) or even the reduction on their contribution to services provision by downstream ecosystems caused by alteration of the fluvial connectivity (regulating and provisioning services). Also, a given stream does not provide all ecosystem services simultaneously. For instance, temperature regulation, regulation of microclimate (regulating services), and recreation (cultural service) are mostly provided in summer, while flood control and erosion control (regulating services) are mostly provided in winter. Finally, not all ecosystem services are provided with the same magnitude by small streams, especially if they result from somehow opposite mechanisms. For instance, erosion control (regulating service) likely has higher relevance than soil/sediment formation (supporting service) in small streams. Therefore, tradeoffs between different ecosystem services, their timing and magnitude need to be considered in the management of streams and their catchments.

Because of longitudinal variation in the abiotic and biotic characteristics along hydrographic networks, there is great spatial variability in the importance of different ecosystem services (Bastian et al., 2012; Bagstad et al., 2013). In general, small streams provide more regulating and supporting ecosystem services while larger streams and rivers are more associated with provisioning services. Also, small

Table 2 Ecosystem services provided by small streams, their benefits for humans and the stream characteristics that support them (see Table 1 for characteristics that are specific to small streams)

Ecosystem service	Benefits for humans	Supporting stream characteristics
Supporting services		
Water cycling	Water source	Water storage in the hyporheic zone/sediments; Hydrological connectivity; Shading
Nutrient cycling	Clean water; Food resources for organisms beneficial to humans (e.g., fish)	Nutrient assimilation by decomposers/ biofilms/ plants; Primary production; Secondary production; Biogeochemical transformations in the hyporheic zone; Organic matter processing by decomposers and detritivores; Accumulation of organic matter
Primary production	Food resources for organisms beneficial to humans (e.g., fish)	Availability of nutrients and dissolved organic carbon for microbial and primary production
Soil/sediment formation	Alluvial deposition and fertilization of floodplains and riparian lands; Production of biomass	Accumulation of allochthonous materials enabled by the steep slopes; Erosion and deposition processes; Alluvial deposition
Habitat provisioning and maintenance	Biodiversity; Maintenance of endemic species; Support for other ecosystem services	Conducive environment (fast flows, highly oxygenated cool water, etc.) for adapted species; Habitat complexity
Maintenance of biodiversity	Biota-driven ecosystem processes	High productivity at all trophic levels; Robust autotrophic and heterotrophic food webs; Habitat complexity
Maintenance of aquatic and riparian productivity	Maintenance of aquatic species; Support for terrestrial species; Alluvial deposition and fertilization riparian lands; Food production	Strong terrestrial-aquatic connectivity; Reciprocal flows of energy; Robust autotrophic and heterotrophic food webs; Erosion and deposition processes; Alluvial deposition; Longitudinal and lateral connectivity
Regulating services		
Flood control	Minimizing the frequency and magnitude of floods; Protection of human lives and properties	Rainfall interception and evapotranspiration of the riparian forest; Presence of large substrates and permeability of the streambed; Bank stabilization
Erosion control	Low bank and channel erosion; Maintenance of water quality	Sediment retention on the streambed; Bank stabilization by the root system; Lower flood magnitudes
Sinks for potentially harmful solutes	Control of metal and organic pollutants; Minimizing eutrophication and other human impacts on stream water and biota	Nutrient and litter fall retention on the forest floor; Atmospheric deposition of metals
Temperature regulation	Maintenance of biodiversity and ecosystem processes; Downstream water cooling	Radiation and wind interception by the riparian forest; Shading the stream channel; Low fluctuations in water and air temperatures
Regulation of microclimate	Biodiversity; Maintenance of terrestrial and aquatic species	Riparian forest transpiration and shading; Stream channel evaporation
Drainage and natural irrigation	Water collection and supply; Water quantity and quality	Rainfall interception and evapotranspiration of the riparian forest; Soil properties; Stream topography
Water purification and quality	Clean drinking water; Uncontaminated food	Riparian buffers; Wetlands; Debris dams; Woody debris
Carbon and nitrogen sequestration	Lowered concentrations of CO_2; Lower eutrophication	Organic material; Debris dams; Burial of organic material

Table 2 (continued)

Ecosystem service	Benefits for humans	Supporting stream characteristics
Provisioning services		
High quality water	Water source	Lower pollution levels; Recharge of aquifers
Food	Fish, crustaceans	Spawning and rearing habitat; Resources exported to larger rivers
Ornamental resources	Trading, economic benefit	Repositories of biodiversity, and thus, diverse in morphology and color
Genetic resources	Maintenance of aquatic species; Metabolites	Conducive environment (fast flows, highly oxygenated cool water, etc.) for adapted species; Habitat complexity; Strong terrestrial-aquatic connectivity; Good water quality; Biodiversity
Energy	Sustainable energy source	Steep slopes; Rainy areas
Cultural services		
Esthetic values	Enjoyment of scenery	Water availability; Biodiversity; Geomorphology
Inspiration (cultural and artistic values)	Use as motive and inspiration for cultural and artistic activities; Inspiration for given names, surnames, place names	Water availability; Biodiversity; Geomorphology
Spiritual and ritual values	Use of stream water for baptism (Christians) and as "holy water" for performing special rituals; During circumcision, diving in the cold water by initiates helps reduce bleeding; Source of clean water for the circumcised initiates during the period of isolation	Clean and cold water
Identity and sense of place	Names, surnames and place names	Geomorphology
Nature-based tourism	Enjoyment of scenery; Outdoor activities	Water availability and quality; Biodiversity; Geomorphology
Recreation	Swimming, bathing	High water availability and quality
Science and education	Use for research and education	All characteristics support education

streams are important for the generation of many ecosystem services that are not necessarily utilized or consumed locally but may benefit other parts of the catchment due to the strong longitudinal connection along hydrographic networks. Additionally, many of the ecosystem services we present here are not restricted to the streams themselves, but also extend into the hyporheic zone (saturated sediments extending below and to the sides of streams) and riparian areas (streamside-vegetated areas) due to strong vertical and lateral connections between streams and surrounding areas (Fig. 2; Table 2).

Supporting services

Water cycling

Small streams are often located at higher elevations in hydrographic networks, where they are a crucial element of the global water cycle by collecting and concentrating the atmospheric water that ultimately feeds into and maintains the flows of larger rivers through hydrological connectivity. This connectivity facilitates the exchange of mass, energy, and organisms across the four dimensions of riverine ecosystems: longitudinally, vertically, laterally, and temporally (Ward, 1989; Moore & Wondzell, 2005). Because of the large channel surface area-to-volume ratio of small streams, and the close contact between the water and the streambed, small streams are important locations for water storage in hydrographic networks (Alexander et al., 2000; Peterson et al., 2001). Moreover, the relatively coarse substrate in headwater streams offers more frictional resistance than other locations in the hydrographic network allowing time for interstitial water infiltration (Harvey & Wagner, 2000; Harvey et al., 2003). The riparian area along forested streams also enhances groundwater recharge. Additionally, the shading effect offered by riparian vegetation limits the solar radiation that reaches the streambed, minimizing water loss through evaporation.

Nutrient cycling

Small forested streams are hotspots for the processing of coarse particulate organic matter (CPOM) produced by riparian vegetation, which enters streams mainly in the form of leaf litter (Fischer & Likens, 1973; Vannote et al., 1980; Wallace et al., 1997). Processing of CPOM is carried out by microbial decomposers and invertebrate shredders, who integrate it into their own biomass, and convert it into fine particulate organic matter (FPOM; e.g., small litter particles, feces, fungal spores), dissolved organic carbon (DOC), inorganic nutrients (mainly nitrogen and phosphorus), and CO_2 (Marks, 2019), which are integrated into food webs locally and downstream (Vannote et al., 1980; Wipfli & Gregovich, 2002).

Small streams are important areas for the transport and transformation of nutrients in fluvial networks (Mulholland 1992). Nitrogen and phosphorus input to small streams is mainly through litterfall, runoff, and groundwater flow. Because of the intimate connection between water and sediments and the numerous of debris dams, small streams play important roles in nitrogen and phosphorus cycling by controlling rates of sedimentation (mainly for phosphorus), transformation (mainly for nitrogen), and uptake by plants. Phosphorus removal from streams is mainly through sedimentation and uptake by photosynthetic organisms, while nitrogen removal is mainly by uptake and denitrification. Although the biomass of photosynthetic organisms, such as macrophytes and algae, is low in small forested streams, and hence, their uptake of nitrogen and phosphorus may be low, they indirectly affect nitrogen cycling by supplying limiting organic carbon and nitrate to denitrifying bacteria, and in the process create favorable conditions for denitrification (Weisner et al., 1994; Birgand et al., 2007).

Primary production

Primary production is another important process that influences the processing, retention, and export of carbon and nutrients in ecosystems. In small streams, primary producers are generally associated with benthic substrates, and include algae, cyanobacteria, bryophytes, and vascular macrophytes. Small forested streams, however, are not active areas for primary production in hydrographic networks because of the often-high canopy cover from riparian vegetation that limits solar radiation reaching the streambed (i.e., there is light limitation of primary production; Hill et al., 1995; Friberg et al., 1997; Larned, 2010). Therefore, forested stream food webs are postulated by the River Continuum

Concept to rely heavily on detritus or allochthonous organic matter for secondary production (Vannote et al., 1980). However, the Riverine Productivity Model (Thorp & Delong, 2002) emphasizes the importance of microalgae as the main source of energy that sustains animal production, as well as the significance of the microbial loop that processes the majority of allochthonous material. The exudates of primary producers, such as periphytic algae, can induce the mineralization of recalcitrant organic matter via priming effects in small forested streams (Danger et al., 2013). Because of the growing recognition of the importance of microalgae and/or periphyton in streams, despite its small biomass compared to allochthonous organic matter, studies have sought to evaluate the relative importance of autochthonous production for food webs in small forested streams using stable-isotope techniques and gut content analyses. Indeed, several studies have shown that autochthonous production can be a major source of energy for food webs in tropical (March & Pringle, 2003; Lau et al., 2009; Neres-Lima et al., 2016) and temperate (Rosi-Marshall et al., 2016) forested streams.

Soil/sediment formation

The formation of soil/sediment is probably not a significant in situ feature of small streams. Small streams, however, act as sediment retention hotspots by entrapping hillslope sediments from landslides and chronic erosion (Terweh et al., 2021). In small forested streams, wood jams form retentive devices that trap sediment (Seixas et al., 2020), which results directly in habitat provisioning as it increases hyporheic habitats for specific invertebrates/microbes and facilitates nutrient cycling processes (Storey et al., 2004; Harjung et al., 2019). Additionally, small streams receive substantial inputs of CPOM (i.e., dung, leaves, twigs, seeds, fruits, etc.) and large wood from riparian forests through physical (erosion, landslides), biological (litter fall, defecation by animals), and hydrological processes (flooding, aggradation) and the decomposition of this CPOM by bacteria, fungi, and detritivores (Marks, 2019) releases organic and inorganic fractions, which together with the inorganic materials resulting from entrapment and substrate erosion constitute the bulk of sediments ultimately carried downstream.

Habitat provisioning and maintenance

Small streams have unique habitat characteristics that are not found elsewhere in the hydrographic network. These characteristics include fast flows, highly oxygenated water, cooler temperatures, stable substrates and, if forested, high standing stocks of CPOM (Table 1). As a consequence, forested streams harbor species that have preferences for these environmental characteristics, such as stenotherm and rheophile species, as well as shredders that feed on CPOM. For instance, forested headwaters have a higher diversity of macroconsumers (fish, freshwater decapods, and semi-aquatic cockroaches; Mendes et al., 2017), shredders and other invertebrates, some endemic to these streams, than any other river sections or land-use types (Yule et al., 2009; Masese et al., 2014; Yegon et al., 2021). Small forested streams also receive a large supply of wood (Naiman et al., 2002; Elosegi & Johnson, 2003; Gregory et al., 2003), which is an important structural element and influences hydraulics, sediment stability, organic matter retention, channel form, and habitat across a wide range of spatial and temporal scales (Gurnell, 2012). Wood is an important instream habitat feature for both invertebrates and fish, often associated with increased biodiversity (Hoffmann & Hering, 2000). Dead wood and logjams are areas of active physical, chemical, and biological processes such as the retention and processing of organic matter, nutrient cycling, and denitrification (Elosegi et al., 2007). It is because of these benefits that many restoration efforts in forested streams emphasize the retention or introduction of dead wood to provide cover and increase habitat complexity for aquatic organisms (Beechie & Sibley, 1997; Moore et al., 2005; Flores et al., 2017).

Maintenance of biodiversity

Small streams can provide threatened species with critical refuge habitat allowing them to escape from exotic species invading downstream reaches or from downstream waters that are becoming warmer (Robison & Buchanan, 1988; Zale et al., 1994; Magoulick & Lynch, 2015). Also, small streams vary in their hydrological regime (i.e., they can be perennial or temporary), which allows for greater taxa heterogeneity among streams (i.e., great β-diversity) (Falke et al., 2012; Hutson et al., 2018). Additionally, small streams provide dispersal corridors along which aquatic organisms can move across the landscape (Jaeger et al., 2014).

Small streams have distinct biodiversity patterns depending on taxonomic groups and spatial scales, which contrast with patterns in other positions of the fluvial network. Small streams harbor higher species richness (α-diversity) of benthic microbes than mid-sized streams, probably due to the higher aquatic-terrestrial interface in small streams that allows for higher inputs of terrestrial microbes (e.g., phyllosphere communities) into the aquatic environment (Besemer et al., 2013). There is also high variability in diversity among small streams (i.e., high β-diversity), which further contributes to making small streams important pools of regional microbial diversity (i.e., γ-diversity) (Besemer et al., 2013). In contrast, for diatoms and macroinvertebrates, species richness increases with increasing stream order (i.e., lower α-diversity in low-order streams), but β-diversity is highest in small streams, making them important contributors to regional diatom (Jyrkänkallio-Mikkola et al., 2018) and macroinvertebrate (Clarke et al., 2008; Finn et al., 2011) diversity. Likely, a combination of high habitat heterogeneity and many species with limited dispersal capabilities lead to high variation in community composition among small streams, which results in high γ-diversity (Clarke et al., 2008; Finn et al., 2011; Jyrkänkallio-Mikkola et al., 2018). Many endemic fish species survive in geographically isolated headwater streams (Junk et al., 2007). Even for semi-aquatic organisms, such as herpetofauna, headwater streams have a higher biodiversity than larger rivers (Welsh & Hodgson, 2011).

Biological diversity is also higher in small forested streams when compared with similar-sized human-altered streams. This can be due to various drivers that interact with each other. First, there is higher hydromorphological heterogeneity in forested streams compared to agricultural and urban streams (Ramião et al., 2020). Second, due to inputs of organic matter, tree diversity of forests influences leaf litter decomposition and all associated aquatic communities (bacteria, fungi, invertebrates) in forested streams (Gessner et al., 2010; Ferreira et al., 2016a; LeRoy et al., 2020). There is carryover from terrestrial ecosystems to aquatic communities, with phyllosphere communities in forests influencing fungal diversity in streams (Koivusaari et al., 2019). Finally, detrital inputs drive heterotrophic food webs within which energy is more conserved and recycled and so can lead to higher efficiencies than in autotrophic food webs (Cebrian & Lartigue, 2004; Evans-White & Halvorson, 2017) as well as support increased biomass and diversity of higher trophic levels (e.g., birds, spiders, bats, lizards, and mammals).

Maintenance of aquatic and riparian productivity

Interactions between small streams and forests through allochthonous inputs of woody debris, leaves, flowers, fruits, and falling insects (Nakano & Murakami, 1999; Garthwaite et al., 2021) drive instream food webs and can provide increased productivity for both local and downstream aquatic ecosystems. One side effect of increased organic material in small forested streams can be the increased export of DOC (Wahl et al., 1997). Although this can result in lowered water quality in some cases, DOC can also drive increased instream productivity, particularly for microbial communities (Williams et al. 2010). CPOM is generally not directly used by higher consumers such as fish and amphibians (Vannote et al., 1980; Wallace et al., 1997); however, the inputs of terrestrial invertebrates from riparian forests (Nakano et al., 1999; Jefferies, 2000) are a high-quality food source that can be foraged directly by fish (Mason & MacDonald, 1982), and, thus, increase their productivity (Kawaguchi et al., 2003). Therefore, forested streams can maintain larger-than-expected populations of fish by facilitating foraging on large quantities of terrestrial invertebrates (Allen, 1951).

Reciprocally, forested streams can subsidize terrestrial food webs through insect emergence (Murakami & Nakano, 2002; Sabo & Power, 2002). Studies have shown that riparian forests generally support greater species diversity and population abundances of terrestrial consumers than adjacent upland habitats (McGarigal & McComb, 1992; Knopf & Samson, 1994; Glass & Floyd, 2015). Riparian consumers, such as birds, bats, lizards, and spiders, can benefit from energy transfer gained by feeding on adult aquatic insects that have emerged from streams, contributing 25–100% of the energy or carbon to these species (Gray, 1993; Power, 1995; Baxter et al., 2005), and also by feeding on aquatic specimens, as dippers and semi-aquatic spiders do (Baba et al., 2019; Hong et al., 2019).

Emergence of aquatic insects can make substantial contributions to soil fertility in riparian areas due to their high numbers and high body nitrogen concentrations (~ 10%); aquatic insect-derived nitrogen deposition in the soil can reach 12.5 mg/m^2/d in some areas, which exceeds the daily atmospheric nitrogen deposition in some regions (Raitif et al., 2019). In lowland coastal catchments of North America, spawning migrations of anadromous salmonids represent another important vector for transfer of nutrients and organic matter from streams to riparian forests. Large numbers of dead fish are deposited in adjacent riparian forests by scavenging mammals, including raccoons, otters, and bears (Gende et al., 2002; Fellman et al., 2008). Studies have shown that salmon-borne, marine-derived nutrients are incorporated into terrestrial vegetation adjacent to spawning streams (Hilderbrand et al., 1999; Helfield & Naiman, 2002; Naiman et al., 2002; Bilby et al., 2003; Morris & Stanford, 2011).

Riparian fertility is also enhanced through the deposition of organic matter and nutrients by animals through excretion and egestion. Several attributes of riparian forests make them hotspots of animal biodiversity, such as proximity to water, food availability, diverse vegetative structures, low light incidence and stable temperatures (Sabo et al., 2005; McClure et al., 2015; Cabette et al., 2017). These conditions allow many animals to move from upland areas into riparian areas seasonally, and by doing so they transfer nutrients and organic matter leading to increased fertility and productivity in riparian areas (Doughty et al., 2016).

Regulating services

Flood control

Small streams are generally surrounded by forests that intercept a significant proportion of the precipitation (Zaimes et al., 2006) and release it slowly into the stream channel, reducing variability in stream discharge (Bhattacharjee & Behera, 2017). Small streams have large substrates (e.g., cobbles, boulders, and large wood) that also delay water movement. As a result of these characteristics, small forested streams generally have lower mean and peak discharges than non-forested streams with similar catchment areas (Stott, 1997). Changing land cover, i.e., decreasing forest cover and increasing impervious surfaces in the catchment of small streams, can increase flow rates and chances for floods in hydrographic networks, both in rural and urban areas (Wissmar et al., 2004; Karagül & Çitgez, 2019). The morphology and lithology of the stream channel can also contribute to flood control in small streams. In mountainous catchments, the magnitude of floods is related to stream width at the apex of a bend and overflows are less frequent around wide apexes (Scorpio et al., 2018). In this context, the increased bank and stream channel stabilization provided by the riparian vegetation in small streams helps to reduce water velocity. Small forested streams are also important for restricting flood damage and, consequently, protecting human lives and property (Santos & Reis, 2018). Because of the important role of small forested streams in flood control, their protection is even more relevant in regions with frequent seasonal rainstorms. In Taiwan, for instance, permeable soils and high evapotranspiration in riparian areas contribute to reduced stream flows in small forested streams during the rainy season (Cheng et al., 2002).

Erosion control

Small forested streams, through interactions with riparian woody plants, minimize soil erosion and trap sediments on the streambed, slowing sediment input and export to downstream reaches (Stott, 1997). Also, the reduced water quantity reaching the stream channel and the lower flood magnitudes in these streams contribute to reduced stream bank erosion (Beeson & Doyle, 1995). Riparian trees can reduce erosion through mechanical strengthening and binding of the banks by roots (Laubel et al., 1999). Bank erosion rates in small forested streams can be influenced by differences in bank material, climate and topography, but also by stream flow, as well as the taxonomic composition of tree species (Zaimes et al., 2006). While bank material with a high percentage of fine particles and the powerful flows that occur in steep catchments increase bank retreat (Lawler et al., 1999), the root systems of large tree species provide structural support to the stream bank and reduce erosion (Hughes, 2016). Additionally, large wood can have a significant impact on channel form and processes in small forested streams (Schuller et al. 2010). Log steps effectively trap coarse sediment in these ecosystems and act as a series of check dams that inhibit channel erosion, but may be less effective at trapping fine sediment (e.g., sand and small gravel) (Ryan et al., 2014). The restoration of natural wood standing stocks in wood-depleted streams greatly increases erosion control and sediment retention, and the benefits of these services surpass the costs of active restoration (Acuña et al., 2013).

Sinks for potentially harmful solutes

Small forested catchments are effective at improving water quality in streams by controlling the transport of both metals (Landre et al., 2010) and organic pollutants (Bergknut et al., 2011). While lithogenic metals (e.g., Al, Co, Fe, Mn, Zn) primarily resulting from rock weathering are generally exported from these catchments, substantial amounts of metals contained in atmospheric pollution (e.g., As, Cd, Cu, Ni, Pb) can be taken up by riparian trees and retained as litterfall on the forest floor (Landre et al., 2010). Consequently, riparian areas of small streams, by storing litter inputs, can act as sinks for atmospheric deposited metals (Kaste et al., 2003). Additionally, riparian forests can reduce pulses of nitrogen and phosphorus moving from the groundwater or agricultural drainage systems into stream water (Welsh et al., 2021).

Temperature regulation

Stream water temperature is mostly regulated by vegetation cover, air temperature, rainfall, surface runoff and subsurface storage (Subehi et al., 2009). In particular, riparian forests influence the incidence of solar radiation, slow wind speeds and reduce exposure to air advected from open areas, thus, regulating stream water temperatures and increasing relative air humidity (Moore et al., 2005). Headwater streams generally have high cooling rates, and these rates increase with an increase in forest cover (Coats & Jackson, 2020).

Regulation of microclimate

Small forested streams have cool and humid microclimates and these conditions contribute to habitat heterogeneity and biodiversity (Hannah et al., 2008). The higher relative humidity levels within riparian areas of small streams can be due to evapotranspiration from the vegetation immediately adjacent to the stream and to evaporation from the stream channel (Danehy & Kirpes, 2000), and is essential for many plant and wildlife species that are dependent on these microclimates (Eskelson et al., 2013). The gradient of relative humidity, as a function of lateral distance from the stream, can determine the spatial structure of riparian communities. In addition, the complex, steep topography of small forested streams also results in vertical gradients of humidity above the stream (Pabst & Spies, 1998). Small streams have a dynamic area of riparian influence on microclimate that fluctuates daily and seasonally (Rambo & North, 2008). During the winter, daily ranges of temperature and vapor pressure deficit tend to be dampened near the stream and increase with distance from it, while in summer daily ranges are greater near the stream and decrease with distance (Rambo & North, 2008).

Drainage and natural irrigation

The pattern and arrangement of natural stream channels determine the efficiency of the drainage system because the time required for water to flow a given distance is directly proportional to the cumulative stream length (Gray, 1965). In headwaters, catchment runoff generation depends on canopy interception, evapotranspiration rates, and throughfall volume (Dung et al., 2012). Because dominant hydrological processes may differ along stream catchments in association with differences in vegetation type and age, the hydrological responses to precipitation are strongly scale-dependent (Gomi et al., 2008). The natural recharge rates of small streams are dependent on catchment characteristics, such as vegetation cover, soil properties, topography, and land use (Maréchal et al., 2009).

The soils of forested catchments feature layers of leaf litter and soil organic matter, both of which contribute to an abundant and diverse micro- and macrofauna and root systems of riparian trees that are extensive and relatively deep (Jana et al., 2017). These conditions create soils with high macroporosity, low bulk density, highly saturated hydraulic conductivities and high infiltration rates that facilitate more prolonged baseflows (Neary et al., 2009). Sustainable management of small forested catchments is essential for the continuous supply of good quality freshwater and protection against natural hazards such as long low flow periods and desertification (Dudley & Stolton, 2003).

Water purification and quality

Small forested streams act as the finest scale connections between the landscape and the river system and, as such, provide the greatest lotic surface area for water purification. These streams can help to remove pollutants and nutrients through filtration, nutrient remineralization and assimilation into biomass. When comparisons are made between forested streams and urban streams of similar size, forested streams transport lower sediment loads (Wahl et al., 1997), show a greater propensity to reduce nitrate-nitrogen concentrations in groundwater (Osborne & Kovacic, 1993) as well as stream water (Wahl et al., 1997; Schoonover & Lockaby, 2006; Ramião et al., 2020) and also tend to have higher dissolved oxygen concentrations (Ramião et al., 2020). The reasons for these differences are several, including higher woody debris inputs, which can slow flows and increase water purification (Acuña et al., 2013), and increase interactions between terrestrial and instream processes (Lowe & Likens, 2005). Taken in sum, the water purification abilities of small forested streams can be of considerable economic benefit in both temperate (Wang et al., 2017) and tropical regions (Vincent et al., 2016; Piaggio & Siikamäki, 2021).

Through processes of water purification, but also due to complex interactions among forests, parent material (the geology of the catchment), soils, and organisms, small forested streams can have an overwhelming influence on the chemical composition of the water flowing through each catchment. More specifically, dissolved minerals, nutrients, and organic matter make their way through terrestrial landscapes and together determine the physical and chemical conditions of stream water (White et al., 1971; Likens & Bormann, 1974). The geology of the catchment interacts with land use to alter stream water chemistry (Bricker & Rice, 1989; Thornton & Dise, 1998), likely across most forested biomes.

Carbon and nitrogen sequestration

Due to the high reliance on organic matter inputs and high channel complexity, small forested streams can become locations on the landscape where both carbon and nitrogen sequestration can occur. Often located in steep canyons at high elevations, small forested streams receive large quantities of organic material from adjacent riparian areas. Because of their high channel surface-to-water volume ratio, high stream bottom roughness, and low water flows, small streams are more retentive of CPOM than larger streams and rivers (Richardson et al., 2005). Organic debris dams, which are created more frequently in small forested streams, can store large volumes of organic matter (Flores et al., 2011) and reduce the export of dissolved organic matter (DOM) as well as the export of both FPOM and CPOM, leading to increased carbon sequestration (Bilby, 1981). In fact, when organic debris dams are removed from small streams, 6% increases in DOM and 500% increases in FPOM and CPOM export to downstream reaches can occur (Bilby, 1981).

Provisioning services

High quality water

Small streams are often located at higher elevations that can receive higher precipitation than lowland rivers and are, thus, important contributors to long term drinking water reservoirs, such as aquifers or lakes. For instance, headwater areas provide clean water to one third of the US population (USEPA, 2009). Moreover, the new symbolic concept of "water towers" has been coined in Kenya to emphasize the role of mountain regions including headwater streams for providing freshwater to downstream regions (Viviroli et al., 2007). Recharge of aquifers has been shown to depend on land use, with natural vegetation (but also certain crops) supporting the largest recharge rates (Zomlot et al., 2015). As natural landscapes are more commonly found in headwater areas, they are especially important for the recharge of aquifers. In fact, the recharge of mountain aquifers in headwater catchments is now recognized to be critical for supporting streamflow during low discharge periods (Somers & McKenzie, 2020). When the elevation or latitude is high enough, precipitation in the headwaters can be accumulated as snow or ice that is gradually released as seasonal temperatures rise, providing high-quality water when precipitation is low (Liljedahl et al., 2017).

Food

Small streams support lower fish biomass than downstream larger streams and rivers; however, they provide spawning and rearing habitat for migratory species, some of which are commercially exploited (Quinn, 2005; Schindler et al., 2010). For instance, production of important anadromous fish, such as salmon, depend on headwater streams as they need well-oxygenated waters and a relatively limited range of gravel sizes for spawning (Baum, 1997; NMFS, 2009). Small streams, especially forested ones, harbor large densities of freshwater crabs and other decapods like crayfish and shrimp that are delicacies in some communities (Dobson, 2004; Padghane et al., 2016).

Ornamental resources

Humans collect various items from headwater streams that are used as ornamental resources, but here we will focus on those examples that have offered business opportunities. One of the most well-known examples is ornamental fish. They account for a meaningful export value in some parts of the world, such as Colombia, Brazil, and Peru (Olivier, 2001). As 50% of all fish species in the catchment of the Amazon are restricted to headwater streams (Junk et al., 2007), these ecosystems have become an important source for ornamental fish exports. Another small-scale business model that is inextricably linked to small streams is jewelry produced with caddisfly (Trichoptera) cases (Macadam & Stockan, 2015; Prommi, 2018). Coldwater caddisfly taxa are collected from the field and reared in aquaria with gemstones that they assemble to create their protective case. Once the larva emerges, the case is fixed, incorporated into a jewelry piece and sold as a fashion accessory. Caddisfly cases made of natural mineral elements (coarse sand) are also used for the same purpose. Other examples of biological materials that are widely used as ornamental resources include skeletonized leaves, which represent the litter decomposition process, which is most relevant in small forested streams.

Genetic resources

Due to their location and topographic condition (e.g., remote areas, high elevation and terrain slope), and through deliberate efforts geared toward their protection and conservation, small forested streams are usually among the least disturbed ecosystems in the world. Forested streams tend to have stable water quality (e.g., temperature, dissolved oxygen, dissolved solids) due to the protective canopy cover offered by the riparian vegetation, and stable large substrates maintained by high elevations/gradients (Table 1). For these reasons, forested streams are major habitats for threatened aquatic species such as freshwater crabs (Dobson, 2004; Cumberlidge, 2011) and anadromous salmonids that return from the sea to spawn (Beschta & Platts, 1986). Also, forest streams receive large amounts of litter inputs and are privileged locations for aquatic hyphomycetes (a polyphyletic group of fungal decomposers), which can be used as source for a large number of metabolites (Seena et al., 2022).

Energy

Humans have used moving water as a source of energy for more than 5000 years (Smith, 1971; WCD, 2000). Hydropower generation has slowly increased its presence throughout the twentieth century, but the demand for energy from renewable sources is increasing, leading to increases in new dam projects (Zarfl et al., 2015). Most of the hydropower plants are small in terms of the energy they produce. In Europe, for instance, 91% of the existing hydropower plants produce less than 10 MW (WWF, 2019), and most of these plants are located on small streams (EVE, 1995).

Cultural services

Esthetic values

People highly appreciate aquatic elements in landscapes (Hammitt et al., 1994; White et al., 2010; Eroglu et al., 2018). Additionally, the sound of water flowing in streams is commonly a favorite natural

Fig. 3 Illustration of some cultural ecosystem services provided by small streams: Esthetic values and nature-based tourism illustrated with a waterfall in a 2nd order stream (Ribeira do Candal, central Portugal; **A**); Cultural and artistic values illustrated with paintings (**B** "Stream in the forest" by Ivan Shishkin; **C** "Forest stream" by Arseny Meshchersky; **D** "Stream in the forest winter" by Thomas Hill; **E** "The forest stream" by Stanislav Zhukovsky) and advertisements (**F** muppi of the 2017 advertising campaign of bottled-water company Águas das Pedras®, Portugal; **G** outdoor of the 2012 advertising campaign of the company of outdoor clothes company Schöffel®, Germany); Spiritual and religious values illustrated with a shrine of the most popular pagan saint in Argentina, the Difunta Correa (the Deceased Correa) raised near a small stream, and a detail showing bottled water left as votive offerings "to calm her eternal thirst" (South Andes, Argentina, **H**); Recreation illustrated with a "swimming pool" in a 1st order stream (unnamed tributary of Ribeira da Cerdeira, central Portugal, **I**); Science illustrated with whole-stream manipulations (**J** nutrient enrichment at a 1st order stream (unnamed tributary of Ribeira da Margaraça, central Portugal); **K** organic matter exclusion at a 1st order stream (unnamed tributary of Arroyo de Salderrey, northern Spain); **L** warming at a branch of a 2nd order stream (Ribeira do Candal, central Portugal)); Education illustrated with creeking in a 1st order stream (unnamed tributary of Ribeira do Catarredor, central Portugal, **M**). Photo credits: **A**, **I**, **J**, **M** Verónica Ferreira; **B**, **C**, **D**, **E** Ann.; **F** Água das Pedras®; **G** Schöffel®; **H** Ricardo Albariño; **K** Arturo Elosegi; **L** João Rosa

sound, as shown in studies aimed at identifying preferred natural sounds to improve urban acoustic quality (Jeon et al., 2010; Hong et al., 2020). Therefore, streams increase the appeal of forests for visitors by enhancing the landscape as well as the soundscape. Streams with waterfalls are especially regarded as attractive, as the latter contain elements of the beautiful and the sublime, and often help compose a picturesque scene (Hudson, 2000) (Fig. 3A).

Inspiration (cultural and artistic values)

Small forested streams have long caught the attention of artists, and during the nineteenth century, they were often the central element in paintings portraying forested landscapes (Fig. 3B–E). Small forested streams are also pictured in many wallpapers, as an online search will show, further supporting the notion that they contribute to pleasant surroundings. Streams are often associated with the idea of purity in nature, and this association has been exploited in advertisements to convey the message of a natural product or of a product that creates a connection to nature (Fig. 3F–G).

Streams have also inspired writers. Miguel Torga, one of the greatest Portuguese writers of the twentieth century, wrote "Eclogue," one of the most famous Portuguese pastoral poems, about a small stream that unexpectedly runs dry. Streams are also present in traditional folk music, as in the case of "When crossing the little stream," a popular song in Alentejo (south Portugal; https://vimeo.com/86905639), which integrates the repertoire of innumerous traditional folk groups in the region, and is part of the repertoire of Cante Alentejano, a musical genre recognized by UNESCO as an intangible cultural heritage of humanity. More widely, a search on a specialized global website (https://www.lyrics.com/) retrieves > 18,000 English-language song lyrics including the word "stream."

Spiritual and ritual values

In many religious societies, streams and other water sources have many symbolic meanings. Christians use them for baptizing the newly converted, and some denominations like Legio Maria in western Kenya consider water from some springs as "pi hawi" or holy water and use it in performing special rituals (Obiero et al., 2012). In Argentina, shrines of the most popular pagan saint, La Difunta Correa (the Deceased Correa), are occasionally raised near small streams "to calm her eternal thirst" (Mrs. Correa died in 1840 while walking with her baby in search of her sick husband after her food and water ran out, and was found with her baby still alive and breast-feeding, which was taken as her first miracle) (Fig. 3H). Additionally, streams play an important role in the rites of passage of members of many communities. Among the Kalenjin peoples of Kenya, streams were important areas for construction of isolation shelters for circumcised boys as they provided water for drinking and cleaning. These isolation shelters were areas of educating the circumcised on their new roles and responsibilities as community warriors or protectors. Similarly, in many communities, recruits for circumcision had to swim in these streams very early in the morning before being circumcised as this was meant to reduce bleeding after the cut. For indigenous and traditional communities in Brazil, small streams are considered abundant divine gifts, and therefore, their disappearance means the end of the society. In the culture of these communities, stream waters are a symbol of life. Streams are inhabited by supernatural beings that protect them, such as "Oxum," the queen of freshwaters in Afro-Brazilian cults, and "Mãe d'Água" (Mother of Water) of the Caboclos of the Amazon. For the riverside populations of the Amazon and Pantanal, waters of small streams symbolize purity and innocence and, therefore, must be especially respected, under penalty of serious punishment (Diegues, 1996).

Identity and sense of place

Streams are important elements in providing identity and a sense of place. An example is their use as a surname in different languages. For instance, "Ribeiro" ("stream" in Portuguese) is the 18th most common surname in Portugal and the 12th in Brazil, where it is used by > 1.5 million people (Sociedade Portuguesa de Informação Económica, 2004; Campacci, 2012). The word "Ribeiro" originates from the Latin "ripariu", which means "small stream", making the surname "Ribeiro" a toponymic surname, i.e., a name derived from a place. Also, the names "Brook" and "Brooke" (syn. for "stream") are in the top 1000 first names in the US (https://www.ssa.gov/cgi-bin/babyname.cgi). Another example is their use in the name of villages, towns and cities, as a search in Google Maps by the terms "Ribeiro", "Ribeirinho" (small stream), and variations of these, will show for Portugal.

Nature-based tourism

Streams increase landscape heterogeneity and the attractiveness of forests for outdoor activities (e.g., walking, trekking, orienteering, appreciation of scenery). This is especially true when streams have waterfalls, which are often regarded as natural scenic attractions (Hudson, 1998). Although small stream waterfalls have low discharge, they can still be impressive in their height and complexity (Fig. 3A). Canyoneering is a major tourist activity in the US desert Southwest, often in slot canyons carved by ephemeral streams.

Recreation

In mountainous regions distant from littoral areas, populations often turn to freshwaters for bathing and swimming during summer. In small streams this is generally accompanied by human "improvements" to the stream, such as the widening of stream sections, the paving of the streambed and the construction of small temporary dams to create small "swimming pools" of accumulated water (Fig. 3I). The number of these swimming pools is difficult to estimate as they are often constructed out of individual or popular initiative. In small streams that have naturally high slopes or barriers (e.g., waterfalls), these reaches may be fishless, and the hydromorphological alterations in the swimming pool area (i.e., increased depth during summer, homogenization of substrate) are likely to have only local and/or seasonal effects on aquatic communities.

Science and education

Small forested streams allow for unique opportunities for scientific research and education. Owing to their small size and reduced discharge, small streams are amenable to whole-stream experimental manipulation, which is generally not feasible in larger streams and rivers. In whole-stream manipulations, the variable of interest can be examined at the most relevant ecosystem scale, which allows for assessment of the effects of environmental changes on aquatic communities and ecosystem processes including all interactions among species and with other environmental characteristics that may show diel, seasonal or interannual variation (Nakano & Murakami, 2001). Therefore, whole-stream manipulation is the most realistic experimental approach allowing for the establishment of causal relationships by comparison with a similar stream or stream reach not exposed to manipulation. Examples of whole-stream manipulations include whole-stream litter exclusion to assess the importance of allochthonous organic matter to stream communities and functioning (Wallace et al., 1997), litter input manipulations to assess the effects of eucalyptus litter inputs (mimicking those of eucalyptus monocultures) vs. native litter inputs (mimicking those of native temperate deciduous broadleaf forests) on stream communities and functioning (Larrañaga et al., 2014), nutrient enrichment to assess the effects of increases in nutrient availability on organic matter processing and associated communities (Gulis & Suberkropp, 2003; Ferreira et al., 2006; Rosemond et al., 2015), insecticide additions to quantify the role of invertebrates on organic matter processing (Cuffney et al., 1990) and water warming to assess the effects of global warming on stream communities and processes (Hogg & Williams, 1996; Ferreira & Canhoto, 2014) (Fig. 3J, K, L).

Small streams are also ideal places for introducing children, school groups, and families to stream ecosystems, due to their reduced safety risks (i.e., they are shallow), abundance in the landscape and high environmental heterogeneity and biodiversity. Creeking, i.e., "exploring a stream and picking up rocks to see what is on or under them" as defined by Suter & Cormier (2015), is ideally performed in small streams (Fig. 3M).

Contribution of small streams to ecosystem services provided by downstream waters

A common characteristic of many ecosystem services is that areas of service supply and demand are spatially dislocated due to the separation between natural or semi-natural ecosystems and human-dominated environments (Bagstad et al., 2013; Schirpke et al., 2019). Mountain regions are potential hotspots of ecosystem services, whereas high demand areas are mostly associated with lowland urbanized or agricultural areas (Schirpke et al., 2019). Small streams perform ecological functions (i.e., biological, geochemical and physical processes) that are critical for ecosystem services provided throughout their catchments (Hill et al., 2014; Colvin et al., 2019) and connect mountainous regions to lowlands. Moreover, when small streams directly flow into larger rivers, they provide sediments and resources that shape large river communities and make them more productive ecosystems (Rice et al., 2001; Kiffney et al., 2006). Longitudinal connectivity is one of the fundamental dimensions linking streams with downstream habitats and ecosystems (Townsend, 1989; Ward, 1989) and it is the basis of different conceptualizations to enhance our understanding of the functioning of fluvial systems (e.g., Vannote et al., 1980; Thorp et al., 2010; Wohl et al., 2015; Raymond et al., 2016). While connectivity between headwaters and downstream reaches is bidirectional, the upstream–downstream direction, ruled by gravity, overrides in importance. Such characteristics determine the transportation of materials, including water, when surface flow occurs (MacDonald & Coe, 2007; Datry et al., 2014; Allan et al., 2021) (Fig. 2). The linear connection between small streams and downstream reaches may, however, be discontinued by natural and manmade lentic ecosystems (e.g., dam-produced reservoirs), which regulate hydrological regimes, water temperature and the export of dissolved and particulate material (Ward & Stanford, 1983; Jones, 2010; Covino, 2017). This fluvial discontinuity alters the spatial and temporal expression of ecosystem service provisioning because lentic water bodies alter the timing and magnitude of water and other material fluxes.

Water drained by small streams is the foundation of fluvial connectivity and, as a good itself, is predominantly taken up and used downstream; small streams contribute ~ 80% of mean annual flow volume to downstream reaches (estimation for 7th order hydrographic networks of the north-eastern US; Alexander et al., 2007) (Table 3). Human populations are distributed heterogeneously on Earth, preferably inhabiting lowlands (Kummu et al., 2016), and future population dependency on runoff from mountain landscapes (39% of land mass) for water provisioning (e.g., direct human consumption, animal growing and irrigation) has been estimated at ~ 1.4 billion people (23% of world's population) by 2050 compared to ~ 0.2 billion (~ 8%) in the 1960s (Viviroli et al., 2020). Water exported from small forested streams is also important for maintaining water quality in larger streams and rivers. Cool stream water flowing from shaded environments into open areas helps in downstream cooling (Moore et al., 2005) and, by containing low concentrations of nitrogen and phosphorus, small stream contributions can dilute nutrients drained from pastures and other land uses that predominate in lowlands, limiting eutrophication in downstream reaches (Chiwa et al., 2015).

Sediment export to downstream reaches is slowed due to channel complexity, further reduced by large wood dams (Wohl & Beckman, 2014; Sklar et al., 2017). However, sediments arriving to downstream reaches may become suitable habitats for fish reproduction (Riebe et al., 2014) (Table 3). Also, the adsorption of trace elements, phosphorus and DOM to clays, silts, and sand grains, makes them natural soil fertilizers (Lottig & Stanley, 2007; Ward et al., 2017) (Table 3). These nutrient-rich sediments may deposit in floodplains of large streams and rivers when water overflows, contributing nutrients to landscapes, and supporting high biodiversity and productive soils for agriculture and livestock (Tockner & Stanford, 2002; Chapman et al., 2016). An endpoint of sediments transported from headwaters is the dynamic formation of deltaic riverscapes at the mouth of inland water bodies and ocean

Table 3 Contribution of small streams to ecosystem services (provisioning and supporting categories) provided by downstream larger streams and rivers

Contribution of small forested streams to downstream waters		Role in downstream waters	Ecosystem services provided by downstream waters
Water	Quantity and quality	Resources	Water for domestic, agricultural and industrial use
		Resources	Energy production
Sediments	Sediments	Substrate	Fish production
	Trace elements, phosphorus and DOM adhered to clay and silt	Resources	Agricultural and livestock production; Biodiversity
Nutrients	Nitrogen, phosphorus, salts	Resources	Productivity of food webs
Organic matter	Dissolved and particulate organic matter	Resources	Productivity of food webs
	Large wood	Resources; Substrate	Productivity of food webs; Biodiversity
Organisms	Mass, energy, nutrients and genes	Resources	Productivity of food webs; Biodiversity

estuaries, areas that also support high biodiversity and provide many other ecosystem services (Tockner & Stanford, 2002; Adger et al., 2018; Richardson et al., 2021). In this regard, dam construction along watercourses obstructs these dynamic ecosystem services, resulting in river "sediment starvation" and in generalized strong reductions in delta formation (Tockner et al., 2008). In contrast, excess sediment production and transportation to lowland streams and rivers, as happens when land use or wildfire increases catchment erosion, is also a problem (Grabowski & Gurnell, 2016). Fine sediments in transport are erosive to biota and are also trapped within channel bottoms embedding larger substrates by filling interstices, which causes habitat loss for sensitive benthic biota, especially invertebrates (Jones et al., 2012), and may undermine ecosystem services dependent on habitat heterogeneity and benthic biota (Table 2).

In general, dissolved nutrients and DOM exported from small streams travel further downstream than particulate organic matter, which mainly moves down episodically via rainstorms and snowmelt (Battin et al., 2008; Bernal et al., 2013; Bunte et al., 2016; Rowland et al., 2017). Spates produce massive movement of dissolved and particulate materials (e.g., FPOM, leaf litter and wood substrates) (Bernal et al., 2013; García et al., 2015; Raymond et al., 2016; Turowski et al., 2016), but it is during base flow conditions that the fluvial ecosystem is most bioreactive (Battin et al., 2008; Raymond et al., 2016). Dissolved and suspended materials are biophysically removed and mineralized by microbes in biofilms and aggregates in the water column (Battin et al., 2008, 2016), although physical processes also take part (e.g., adsorption, flocculation, and photodegradation). Downstream processing results in more recalcitrant, small-sized substances; however, even such substances can be photo- and biodegraded (Battin et al., 2008; García et al., 2018). As part of the carbon and nutrient cycles, these materials boost the productivity of food webs in downstream lowland streams, rivers, wetlands (e.g., floodplains, deltas and estuaries), and further into the ocean environment (Cole et al., 2007; Ward et al., 2017; Bergström, 2020). It has been shown that 30 to 45% of DOM exported by small streams may be removed and mineralized on its way to the sea resulting in important CO_2 outgassing (Cole et al., 2007; Battin et al., 2008; Mineau et al., 2016). Leaf litter and FPOM, which only travel long distances during spates, are also exploitable resources for downstream food webs (Wipfli et al., 2007) (Table 3). Finally, large driftwood pieces become important when sunk in lowland rivers, deltas and sea coasts. In particular, wood exported into marine environments can amount to 4.7 million m^3/year (Wohl & Iskin, 2021). Wood inputs to the seafloor create an oasis of habitat and food in the barren ocean benthos comparable to coral reef habitats, supporting distinctive communities of fungi, mollusks, and crustaceans (Wohl & Iskin, 2021) (Table 3).

Living organisms move up- and downstream along hydrographic networks, exchanging mass, energy, nutrients, and genes (Meyer et al., 2007; Wipfli et al., 2007; Pond et al., 2016) (Table 3). In particular, invertebrate drift is a natural phenomenon in fluvial systems. Drift is defined as individuals escaping from unfavorable conditions or being transported incidentally downstream during spates (Brittain & Eikeland, 1988; Naman et al., 2016). Therefore, drift contributes to species dispersion. While catastrophic events can result in drift (passive drift), the effects can include population mortality and the whole system is under stress during spates. More controlled behavioral drift constitutes an essential strategy for invertebrates to colonize new reaches downstream and is also a resource for drift-feeding fish (Naman et al., 2016). Many small streams are fishless, mostly because they are isolated by natural barriers, such as waterfalls, and the surface flow is seasonally more variable than in downstream reaches, which results in a riskier habitat for strictly aquatic biota (Gomi et al., 2002; Richardson, 2019). In these situations, drifting invertebrates exported from small streams constitute a potential net input of food to downstream fish populations inhabiting larger streams and rivers (Wipfli & Gregovich, 2002; Wipfli et al., 2007; Pond et al., 2016). Headwater streams hold biota that are spread along hydrographic networks and may maintain genetic fluxes by dispersion of both aquatic and terrestrial stages to downstream reaches (Meyer et al., 2007). This contributes to a striking pattern in organisms, which display higher intraspecific genetic diversity in downstream reaches, in part because of asymmetrical longitudinal dispersal success due to unidirectional water flow (Paz-Vinas et al., 2015; Blanchet et al., 2020).

The ability of small streams to contribute to ecosystem service provision to downstream reaches may, however, be constrained by the in situ acquisition and delivery of certain goods and services provided by small streams and their catchments. For instance, water abstraction from small streams for human use or energy generation can reduce the volume of water transported downstream, consequently limiting the transportation of sediments, organic matter and organisms. Also, human activities, such as mining, small hydropower dam and reservoir construction, agriculture, and forestry (Lindberg et al., 2011; Deitch et al., 2013; Couto & Olden, 2018; de Vries et al., 2019; Erdozain et al., 2021), may alter the hydrology and chemistry of small streams (e.g., dewatering and pollution, see below), reducing their contributions to ecosystem services provided to downstream reaches.

Threats to small stream ecosystem services

Headwaters are likely the most unpolluted water courses in a catchment given their relative isolation and often high elevation, which makes them individually drain small areas of low human occupation. This generally translates into better water quality at the headwaters of hydrographic networks than in lowland areas (Ferreira et al., 2004; Mou et al., 2004). However, small streams are also the most vulnerable watercourses to environmental changes owing to their small size, reduced water volumes, strong aquatic-terrestrial connections, strong dependency on the riparian forest and isolation (Table 4). Consequently, even relatively small changes to catchment and instream characteristics can affect the services provided by small streams (Fig. 2; Table 2).

For instance, because of their size, small streams are vulnerable to burial (Meyer et al., 2005). The proportion of stream length buried (e.g., through road building, piping, and channeling through culverts) is higher for 1st and 2nd order streams than for higher-order streams (Stammler, 2011). Stream burial impairs the connection between the stream and its riparian forest, impeding direct (i.e., from the canopy) and indirect (i.e., from the stream margins) litter inputs from the riparian vegetation, and leading to significant decreases in coarse and fine benthic organic matter standing stocks, and lower ecosystem respiration (Beaulieu et al., 2014; Pennino et al., 2014). Stream burial also virtually eliminates the penetration of solar radiation into the stream bed, which limits instream primary production (Beaulieu et al., 2014; Pennino et al., 2014). Additionally, stream burial leads to decreases in habitat heterogeneity and to simplified hydromorphology, which results in increased current velocity (Beaulieu et al., 2014; Pennino et al., 2014). As a consequence, nitrate uptake length is longer and nitrate uptake velocity is lower in buried than in open streams, which suggests lower nitrate retention capacity in buried streams (Beaulieu et al., 2014, 2015; Pennino et al., 2014). Lower benthic organic matter, ecosystem respiration, primary production, and nutrient retention capacity in buried streams alters carbon and nutrient export, potentially impairing the water quality of downstream reaches, especially for high levels of stream burial (Beaulieu et al., 2014, 2015; Pennino et al., 2014). Stream burial, with all consequent alterations in stream structure and functioning, potentially impacts all ecosystem services (Table 4).

The size and high elevation of small streams make them susceptible to obstruction by landslides. Landslides are natural events contributing important sediment and large wood inputs to streams, and are caused by natural phenomena, such as heavy rainfall, that decrease slope stability (Geertsema et al., 2009). Landslides can, however, be promoted by human activities and their frequency has been shown to increase with logging-related activities and road density, both of which remove vegetation and, therefore, promote changes to the root cohesion of the soil and soil moisture regimes (Guthrie, 2002; Sidle, 2005; Imaizumi et al., 2008). Forest fires, by removing vegetation, can also promote landslides (Cannon & Gartner, 2005). The predicted increase in the frequency of storms and wildfires and the foreseen expansion of planted forests for timber production (with associated road building and periodic harvesting) will likely increase the frequency of landslides into small streams (Krawchuk et al., 2009; Payn et al. 2015; Prein et al., 2017). Stream obstruction by landslides can have strong influences on supporting services (mostly water cycling and habitat provisioning), regulating services (mostly flood control and erosion control), and cultural services (mostly esthetic values, nature-based tourism, recreation) (Table 4).

Table 4 Threats to small streams as a function of stream characteristics (see Table 1), and their major direct consequences

Stream characteristics	Threats	Major direct consequences	Affected ecosystem services
Small size	Burial (e.g., piping, road building)	Loss of aquatic-terrestrial connectivity; Reduction of litter inputs; Loss of habitat; Loss of light	Potentially impacts all ecosystem services
Small size and close linkage to the terrestrial environment	Obstruction by landslides; Wildfires; Logging	Loss of habitat; Reduction in downstream transport of water, sediments, organic matter and organisms	Supporting services (e.g., water cycling and habitat provisioning); Regulating services (e.g., flood control and erosion control); and cultural services (e.g., esthetic values, nature-based tourism, recreation)
Small water volume and reduced storage zones	Replacement of native forests by dense fast-growing tree plantations and climate change, which increase evapotranspiration leading to reductions in water availability	Loss of habitat; Reduction in downstream transport of water, sediments, organic matter and organisms	Potentially impacts all ecosystem services
Close linkage to the terrestrial environment, shaded and heterotrophic	Changes in the riparian vegetation that affect shading and litter inputs (e.g., clearcuts, replacement by tree monocultures, invasion by exotic species)	Change in the relative importance of basal food sources (i.e., decrease in litter inputs and increase in instream primary production) and consequent changes in the relative importance of the heterotrophic (decrease) and autotrophic (increase) energetic pathways; Changes in litter characteristics; Water warming	Potentially all ecosystem services
Small water volume	Inputs of nutrients and pollutants	Deterioration of water quality (e.g., eutrophication, pollution)	Supporting services (e.g., nutrient cycling, primary production, maintenance of aquatic and riparian productivity and maintenance of biodiversity); Regulating services (e.g., sinks for potentially harmful solutes, water purification and quality, carbon and nitrogen sequestration); Provisioning services (e.g., high-quality water and genetic resources); Cultural services (e.g., esthetic values, nature-based tourism, and recreation)
Isolation	Warming and changes in land use	Extinction of local species that do not have upstream refugees and have limited dispersal capabilities	All biological-driven ecosystem services, e.g., primary production (supporting service), carbon and nitrogen sequestration (regulating service), and food (provisioning service)

Small water volumes and reduced storage zones of small streams make them highly vulnerable to the increased evapotranspiration associated with the replacement of native forests, or to the afforestation of grassland catchments, by dense, fast-growing, tree plantations, which can cause discharge reductions (Jackson et al., 2005; Lara et al., 2009). Also, unregulated water abstraction for domestic and agricultural use can lead to drastic reduction in stream flows (Ashworth & Vizuete, 2017). Additionally, the boom of small hydropower plants deployed in small catchments as part of renewable energy and climate mitigation strategies (Kelly-Richards et al., 2017; Couto & Olden, 2018; Crnobrnja-Isailović et al., 2021), by promoting water diversion, can severely impact streams depending on the stream length dewatered and the amount of streamflow abstracted. Small streams are also at high risk of undergoing drought during the longer, warmer and drier summers forecasted under climate change scenarios, which will increase evapotranspiration and water demand by both riparian forests and human populations in many parts of the world (Reynolds et al., 2015). Decreases in water availability in small streams will lead to the loss of aquatic habitat, loss of longitudinal connectivity with consequent reductions in water, sediment, nutrients, organic matter, and organism transport to downstream reaches, and decreases in water quality resulting from increases in temperature and conductivity and decreases in dissolved oxygen, all of which will negatively influence stream biota and ecosystem processes (Rolls et al., 2012). Decreases in water availability, especially when considering perennial streams, potentially impacts all ecosystem services discussed above (Table 4).

The strong connections between small streams and their riparian forests, which provide shade and litter inputs that sustain heterotrophic food webs, make them highly susceptible to forest changes. Forest clearcutting, by removing riparian vegetation, promotes changes in the relative importance of basal food resources to aquatic communities (i.e., decreases in litter inputs and increases in instream primary production) and consequently changes the relative importance of heterotrophic (decreased) and autotrophic (increased) energetic pathways (Göthe et al., 2009), which can be long lasting (Burrows et al., 2021; Frainer & McKie, 2021). Replacement of native forests by tree monocultures or their invasion by exotic species can also change shade patterns (e.g., when native forests and replacing species differ in deciduousness, stand abundance and/or canopy density), or alter instream primary production and the characteristics of litter inputs (Hladyz et al., 2011; Larrañaga et al., 2021; Ferreira et al., 2021). Reduction in shading with forest clearing increases water temperatures (up to 15ºC) (Johnson & Jones, 2000; Kiffney et al., 2003; Reiter et al., 2015). Warming has strong influences on aquatic biota adapted to cool water, and stimulates biofilm activity and litter decomposition, as shown by whole-stream warming experiments and correlative studies along geothermal gradients (Hogg & Williams, 1996; Friberg et al., 2009; O'Gorman et al., 2012; Ferreira & Canhoto, 2014; Ylla et al., 2014). Litter inputs become less diverse and are often dominated by recalcitrant litter, as when mixed deciduous forests are replaced by eucalyptus or conifer plantations (Molinero & Pozo, 2004; Inoue et al., 2012; Larrañaga et al., 2021), which can influence aquatic communities and processes (Larrañaga et al., 2009; Ferreira et al., 2016b; Monroy et al., 2017). Different forest changes (e.g., afforestation with native or exotic monocultures, invasion by exotic species, clearing) differ in the type and magnitude of their effects on stream structure and functioning (Larrañaga et al., 2021; Ferreira et al., 2021), but they can potentially affect all ecosystem services (Table 4).

Small water volumes, and consequently small dilution capacities, make small streams vulnerable to inputs of nutrients and pollutants, which leads to the deterioration of water quality. In shaded streams with high heterotrophic activity (i.e., high nutrient uptake capacity), effects of mild nutrient enrichment (e.g., from small-scale agriculture) on water quality may be detectable only for a short distance after which dissolved nutrient concentrations return to ambient levels (Ferreira et al., 2006). However, if nutrient inputs surpass the ecosystem nutrient uptake capacity, then there will be an increase in nutrient concentrations in stream water (Gulis et al., 2006), and eutrophication may take place if light and temperature are not limiting (Hagen et al., 2010). Eutrophication affects supporting services (mostly nutrient cycling, primary production, maintenance of biodiversity, and maintenance of aquatic and riparian productivity), regulating services (mostly sinks for potentially harmful solutes, water purification and quality, carbon and nitrogen sequestration), provisioning services (mostly

Table 5 Ecosystem services provided by small streams (see Table 2) in comparison with ecosystem services identified in MEA (2003, 2005)

Ecosystem services identified in MEA	Ecosystem services attributed to small streams
Supporting services	
Water cycling	Water cycling
Nutrient cycling	Nutrient cycling
Primary production	Primary production
Soil formation and retention	Soil/sediment formation
Provisioning of habitat	Habitat provisioning and maintenance
	Maintenance of aquatic and riparian productivity
	Maintenance of biodiversity
Oxygen production	
Regulating services	
Storm protection	Flood control
Erosion control	Erosion control
	Sinks of potentially harmful solutes
Climate regulation	Temperature regulation
Air quality maintenance	Regulation of microclimate
Water regulation	Drainage and natural irrigation
Water purification and waste treatment	Water purification and quality
	Carbon and nitrogen sequestration
Regulation of human diseases	
Biological control	
Pollination	
Provisioning services	
Fresh water	High quality water
Food	Food
Ornamental resources	Ornamental resources
Fuel	Energy
Genetic resources	Genetic resources
Fiber	
Biochemicals, natural medicines and pharmaceuticals	
Cultural services	
Aesthetic values	Aesthetic values
Inspiration	Inspiration
Spiritual and religious values	Spiritual and cultural values
Sense of place	Identity and sense of place
Ecotourism	Nature-based tourism
Recreation	Recreation
Educational values	Science and education
Cultural diversity	
Knowledge systems	
Social relations	
Cultural heritage values	

Highlighted in gray are services identified in MEA for which small streams do not presently contribute much; as knowledge on these systems accumulates, additional ecosystem services may be identified in the future

high-quality water), and cultural services (mostly esthetic values, nature-based tourism, and recreation) (Table 4).

Headwaters are isolated due to their higher position in the hydrographic network, which makes them vulnerable to environmental changes that lead to local species extinctions (e.g., warming, forest change). The high hydromorphological and habitat heterogeneity allow for high variation in species richness across streams (i.e., high β-diversity), and therefore, they contribute to regional biodiversity (i.e., γ-diversity) (Clarke et al., 2008; Finn et al., 2011; Besemer et al., 2013; Jyrkänkallio-Mikkola et al., 2018). However, by inhabiting the smallest, highest elevation streams already, these aquatic species do not have higher elevation refugia reaches to escape to in case environmental and/or biotic conditions deteriorate (e.g., warming, invasion by exotic species). Species loss in these small streams may be difficult to reverse since they lack upstream sources of colonists and colonization from other small streams may be difficult due to high variation in diversity between streams and to limited dispersal capabilities (e.g., macroinvertebrates without flying adults) (Parkyn & Smith, 2011), which will have negative influences on regional diversity. Species extinctions affect all biological-driven ecosystem services such as primary production (supporting service), carbon and nitrogen sequestration (regulating service), and food (provisioning service) (Table 4).

Conclusions

Of the 33 ecosystem services identified by the MEA (2003, 2005), 23 are (fully or partially) provided by small streams; four additional ecosystem services were identified (Table 5). These ecosystems are also key to maintaining aquatic and riparian productivity, as sinks for potentially harmful solutes and in terms of carbon and nitrogen sequestration. Additionally, small streams make a fundamental contribution to regional biodiversity owing to their high variation in species composition and preservation of specialist taxa. Because of their large numbers and broad distribution, small streams also present a wide diversity of environmental and habitat conditions that are favorable for different and diverse organisms. The high number of ecosystem services provided by small streams makes them critical to human wellbeing and biodiversity. Therefore, stronger efforts need to be pursued to protect small streams, and to restore those that are degraded. The protection of small streams (e.g., establishment of micro-reserves) can be extremely cost-efficient considering the gain in biodiversity and other ecosystem services. Nevertheless, it is not enough to protect small streams only on public lands (e.g., protected areas); those within private properties need to be sustainably managed as well. For private owners to engage in the protection of small streams, their importance in the landscape and for human wellbeing, their vulnerability to human activities, and the consequences of environmental changes on their ability to provide ecosystem services need to be conveyed to society.

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Declarations

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