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FOCUS ARTICLE

The role of freshwater bioacoustics in ecological research

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Abstract

Conventional methodologies used to estimate biodiversity in freshwater ecosystems can be nonselective and invasive, sometimes leading to capture and potential injury of vulnerable species. Therefore, interest in noninvasive surveying techniques is growing among freshwater ecologists. Passive acoustic monitoring, the noninvasive recording of environmental sounds, has been shown to effectively survey biota in terrestrial and marine ecosystems. However, knowledge of the sounds produced by freshwater species is relatively scarce. Furthermore, little is known about the representation of different freshwater taxonomic groups and habitat types within the literature. Here we present results of a systematic review of research literature on freshwater bioacoustics and identify promising areas of future research. The review showed that fish are the focal taxonomic group in 44% of published studies and were studied primarily in laboratory aquaria and lotic habitats. By contrast, lentic habitats and other taxonomic groups have received relatively little research interest. It is particularly striking that arthropods are only represented by 26% of studies, despite their significant contributions to freshwater soundscapes. This indicates a mismatch between the representation of taxonomic groups within the freshwater bioacoustic literature and their relative acoustic contribution to natural freshwater soundscapes. In addition, the review indicates an ongoing shift from behavioral studies, often with focus on a single taxonomic group, towards field-based studies using ecoacoustic approaches. On the basis of this review we suggest that future freshwater bioacoustics research should focus on passive acoustic monitoring and arthropod sound, which would likely yield novel insights into freshwater ecosystem function and condition.

This article is categorized under:

Water and Life > Nature of Freshwater Ecosystems

Water and Life > Conservation, Management, and Awareness

Water and Life > Methods

KEYWORDS

auditory ecology, biodiversity, ecoacoustics, ecological assessment

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1 | INTRODUCTION

Biodiversity and ecosystem functions are closely linked, and monitoring biological diversity and abundance is essential for developing an understanding of ecosystem condition and processes (McGrady-Steed, Harris, & Morin, 1997). Many methods used to estimate biodiversity such as quadrats (Stevens, Dise, Mountford, & Gowing, 2004) and camera traps (Silveira, Jacomo, & Diniz-Filho, 2003) can underestimate the diversity of fauna present in a habitat. In particular, the number of individuals sampled, and the number, size and distribution of sampling areas can have a strong influence on values of estimated biodiversity (Gotelli & Colwell, 2011). Furthermore, biodiversity estimates are often extrapolated over large temporal and spatial scales to compensate for the logistical difficulties associated with sampling large areas for long periods of time (Gasc, Pavoine, Lellouch, Grandcolas, & Sueur, 2015).

In freshwater systems conventional methodologies used to estimate biodiversity, such as kick sampling, fyke netting and trapping, are nonselective and invasive, sometimes leading to the capture of vulnerable species. Moreover, these methods can necessitate substantial manual labor as field sites must be visited frequently to deploy and check equipment, and there can be requirements for laboratory processing and species identification. In addition, if used in multiple waterways, traps and nets may present a biosecurity risk to other freshwater ecosystems by spreading disease or invasive species. Passive acoustic monitoring, the noninvasive recording of environmental sounds, has been shown to effectively survey biodiversity in terrestrial (Blumstein et al., 2011; Fristrup & Mennitt, 2012; Llusia, Márquez, & Bowker, 2011; Sugai, Silva, Ribeiro Jr, & Llusia, 2018) and marine (Croll et al., 2002; di Sciara & Gordon, 1997; Montgomery & Radford, 2017; Ramcharitar, Gannon, & Popper, 2006) ecosystems. Despite this, soundscapes (i.e., representations of all the acoustic signals in an environment; Table 1) of freshwater ecosystems remain largely unexplored (Linke et al., 2018).

In a recent review, Linke et al. (2018) identified 2,740 freshwater bioacoustics articles by entering the search terms “freshwater + bioacoustics” into Google Scholar on the 28th of August 2017. Linke et al. noted that the freshwater bioacoustics literature could be categorized into two groups: (a) studies that investigated the physiology and behavioral elements of biological sound production, and (b) studies that investigated anthropogenic and physically generated sound and their effects on aquatic animals. Linke et al. also noted that passive acoustic monitoring is becoming increasingly popular with freshwater ecologists, but knowledge of sounds produced by freshwater species is relatively scarce. Rountree, Bolgan, and Juanes (2018) and Rountree, Juanes, and Bolgan (2018) revealed that only 87 freshwater fish species in North America and Europe have been the subject of bioacoustics studies, comprising at most 5% of freshwater fish diversity of these particularly well-studied freshwater ecoregions. Furthermore, Ladich and Popper (2004) state that the hearing capabilities of only ~100 fish species have been studied, all of which are able to detect sound, highlighting the biological significance of sound (Fay & Popper, 2000). Moreover, both Aiken (1985) and Desjonquères, Rybak, Castella, Llusia, and Sueur (2018) note that most underwater biological sounds in freshwater ecosystems are likely

TABLE 1 List of key terms and their definitions

Term	Definition	Reference
Bioacoustics	“The use of acoustics to study any facets of animals such as auditory capabilities, sound production, communications, foraging behavior, in short, anything having to do with their natural history.”	Au and Hastings (1996)
Soundscape	“The collection of biological, geophysical and anthropogenic sounds that emanate from a landscape and which vary over space and time reflecting important ecosystem processes and human activities.”	Pijanowski, Farina, Gage, Dumyahn, and Krause (2011)
Ecoacoustics	“A theoretical and applied discipline that studies sound along a broad range of spatial and temporal scales in order to tackle biodiversity and other ecological questions.”	Sueur and Farina (2015)
Passive acoustic monitoring	“Passive acoustic monitoring (PAM) is a noninvasive method for surveying wild animals using remote acoustic technologies such as microphone arrays, hydrophones, or other autonomous recording devices.” The term passive allows this method to be distinguished from a more typical recording method in bioacoustics: focal monitoring, where a specific animal is recorded by someone in the field. Another antonym of passive which we are not considering here is active acoustics or sonar which we do not discuss in this paper.	Kalan et al. (2015)

produced by arthropods. Despite this, the sounds arthropods produce individually, and the soundscapes they generate collectively, appear to have received very little research interest to date (Desjonquères et al., 2018; Sueur, Mackie, & Windmill, 2011).

Despite growing interest in the potential of passive acoustic monitoring and the increasing number of studies investigating the soundscapes of freshwater ecosystems, there has been no systematic review of the representation of different freshwater taxonomic groups and habitat types in the literature. This article builds on previous reviews of the freshwater bioacoustic literature (Linke et al., 2018; Rountree, Bolgan, et al., 2018; Rountree, Juanes, et al., 2018) by outlining the results of a systematic review and identifying the representation of taxonomic groups and habitat types studied (Box 1).

2 | TAXONOMIC FOCUS OF FRESHWATER BIOACOUSTIC STUDIES

In total 124 papers met the selection criteria, 72 papers from the 2,756 papers initially listed from our search of the Web of Science database, and 52 papers from an additional survey of the reference literature and our own personal archives. Thirteen papers (11%) reported recordings of underwater soundscapes, and thus did not focus on any particular taxonomic group. Most studies identified by this review, however, reported descriptions of sounds produced by a single taxonomic group, of which “fish” was the most commonly represented (44% of papers; Figure 1). In total, 80 species of fish within 13 orders and 20 families were studied within these papers. Perciformes (perch-like fishes) have been the most well represented order, with 31 species from six families represented by 23 papers, 16 of which were Cichlidae (Table 2). Salmoniformes (salmonids; four species in one family), Cypriniformes (carps, minnows and loaches; eight species in two families) and Acipenseriformes (sturgeons and paddlefishes; four species in one family) were also well represented. The Padanian goby *Padogobius martensii* was the most studied fish species, appearing in three papers (Lugli, Yan, and Fine, 2003; Lugli, Pavan, & Torricelli, 1996; Lugli, Torricelli, et al., 1996; Torricelli et al., 1986). *P. martensii* sound production has been subject to extensive study in the laboratory (Lugli et al., 2003), often with a focus on courtship behavior (Lugli et al., 2003; Torricelli et al., 1986). The round goby *Neogobius melanostomus* (Rollo, Andraso, Janssen, and Higgs, 2007; Rollo & Higgs, 2008), the croaking gourami *Trichopsis vittata* (Ladich, 2007;

BOX 1 Sidebar title: Literature review methodology

The literature was surveyed on May 2nd, 2019 in Web of Science (Web of Science Core Collection) using the following search terms: “*ALL = ((acoust* OR bioacoust* OR ecoacoust*) AND (aquatic OR freshwater OR underwater OR water)) NOT ALL = (ocean OR sea OR sonar OR telemetry) NOT WC = (geo* OR medic* OR physic* OR patholog* OR agricultu* OR engineer* OR meteo* OR chemi* OR math*)*”, yielding 6,899 results. These results were then refined by: document types: (Article) and Web of Science categories: (*Acoustics OR Marine Freshwater Biology OR Fisheries OR Environmental Studies OR Zoology OR Multidisciplinary Sciences OR Environmental Sciences OR Ecology OR Water Resources OR Behavioural Sciences OR Limnology OR Entomology OR Remote Sensing OR Biology Biodiversity Conservation*), yielding 2,756 results. Studies were then selected using the following selection criteria: (a) the paper included an underwater recording, and (b) a recording of a freshwater species or soundscape. We note that a number of arthropod-orientated freshwater bioacoustics research articles were not detected by this review. Indeed, Aiken (1985) includes about 300 references to established or suspected sounds produced by aquatic insects. Although many of these studies do not include an underwater recording, several could meet our inclusion criteria. Similarly, some fish species identified by Rountree, Bolgan, et al. (2018); Rountree, Juanes, et al. (2018)) were missed by our search. Nevertheless, the search terms used do capture the most significant studies in the field of freshwater bioacoustics and provide a representative sample of the literature. To ensure the most representative sample of studies, we additionally surveyed the cited literature of reference reviews in the field of freshwater bioacoustics: Aiken, 1985, Linke et al., 2018, Rountree, Bolgan, et al., 2018; Rountree, Juanes, et al., 2018 and Desjonquères et al., 2020 as well as our own personal literature archives. We used the above criteria to select the articles that we included in the systematic review. This search yielded an additional 52 papers.

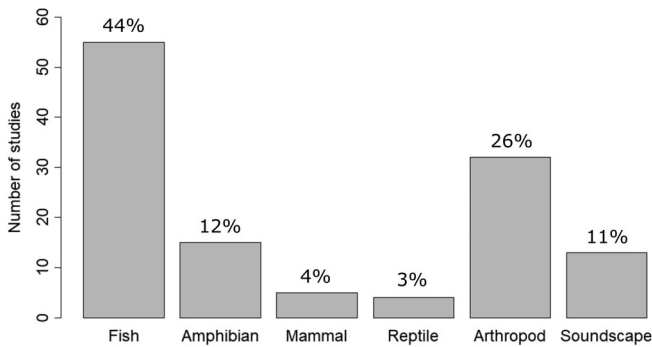


FIGURE 1 Taxonomic group representation within 124 freshwater bioacoustics research articles considered in the systematic review. Percentages have been rounded to the nearest integer

Ladich & Schleinzer, 2015), the burbot *Lota lota* (Cott et al., 2014; Grabowski et al., 2020), and the Arno goby *Padogobius nigricans* (Lugli, Pavan, & Torricelli, 1996; Lugli, Torricelli, et al., 1996; Malavasi et al., 2008) were represented by two studies. Rountree, Bolgan, et al. (2018) and Rountree, Juanes, et al. (2018) also report the most acoustically well-studied orders of temperate freshwater fish, with qualitatively similar results to those from this systematic review. Specifically, Rountree, Bolgan, et al. (2018) and Rountree, Juanes, et al. (2018) reported that 68 species of fish in 12 orders have been studied, including 28 species of Cypriniformes in four families, 18 species of Perciformes in five families, 11 species of Salmoniformes in one family, and 11 species of Acipenseriformes in one family.

The large number of studies orientated towards fish is perhaps in part due to the familiarity that researchers from different disciplines have with fish husbandry. Animal behavior and ecotoxicology laboratories possess the expertise and equipment required to keep fish in captivity (Lynn, Egar, Walker, Sperry, & Ramenofsky, 2007), which can easily be adapted for use in bioacoustics studies. Furthermore, both *P. martensii* and *T. vittata* are straightforward to obtain for research purposes as the former is a common species that occupies very shallow water (<0.5 m; Lugli et al., 2003) in southern Europe, and the latter is a popular aquarium fish frequently traded around the world (Courtenay & Stauffer, 1990).

Freshwater fish species can possess significant economic, ecological and cultural value (Linke et al., 2018). One such species, the Arctic charr *Salvelinus alpinus*, has recently become extinct in multiple locations in the UK and Ireland and could benefit from conservation interventions (Maitland, Winfield, McCarthy, & Igoe, 2007). The species was represented by two studies in this review (Bolgan, O'Brien, Rountree, and Gammell, 2016; Bolgan et al., 2018), with one study using passive acoustic monitoring to successfully identify spawning sounds produced by Arctic charr disturbing gravel in order to assess breeding behavior and aide conservation efforts (Bolgan et al., 2018). Passive acoustic monitoring was also used by Straight et al. (2014, 2015) on a larger scale to detect spawning behavior of the river redhorse *Moxostoma carinatum* and robust redhorse *Moxostoma robustum*. In total, several hundred spawning events were recorded in multiple rivers in north Georgia (United States). The spawning events were identified by characterizing the unique pattern of dominant frequencies, amplitude variation and duration of the spawning event audio signal. These data were then integrated into an automated detection software, which was capable of identifying 80–82% of known spawning events (Straight et al., 2014).

Research papers investigating 33 species of amphibian in nine families (two orders: Anura and Caudata) were identified by this review. Anura was the most represented order, within which Pipidae was the most represented family, with 20 species represented by five studies (Kwong-Brown et al., 2019; Ringeis, Krumscheid, Bishop, De Vries, & Elepfandt, 2017; Tobias, Corke, Korsh, Yin, & Kelley, 2010; Vignal & Kelley, 2007; Yager, 1992). Kwong-Brown et al. (2019) filmed the larynx of 18 *Xenopus* (Pipidae) frogs as they produced sound in order to identify the mechanisms behind sound production underwater. *Xenopus* are well known to researchers as model organisms in fields such as vertebrate embryology and genomics (Hellsten et al., 2010), which may explain their notable presence in the literature. Five papers focused on freshwater mammal bioacoustics covering four species within four families, the most studied of which was the common hippopotamus *Hippopotamus amphibius* (Barklow, 1997, 2004; Maust-Mohl et al., 2018). Other species included the Amazon river dolphin *Inia geoffrensis* and the tucuxi *Sotalia fluviatilis* (Table 2). Four papers reported investigations of underwater reptile sounds, which focussed on three species, the Arrau turtle *Podocnemis expansa* (Ferrara et al., 2012, 2014), the American alligator *Alligator mississippiensis* (Reber et al., 2017) and the Northern snake-necked turtle *Chelodina oblonga* (Giles, Davis, McCauley, & Kuchling, 2009).

Only four papers identified by the search terms of this review investigated freshwater arthropod sounds. Of these only two (Sueur et al., 2011; Wilson, Flinn, West, & Hereford, 2015) included underwater recordings of biological

TABLE 2 Freshwater species categorized by taxonomic group that were included in the 124 freshwater bioacoustics research articles identified by this review

Taxon	Species	Family (order)	Reference
Fish	<i>Oreochromis mossambicus</i>	Cichlidae (Perciformes)	Amorim, Fonseca, and Almada (2003)
Fish	<i>Ameiurus nebulosus</i> , <i>Ictalurus punctatus</i>	Ictaluridae (Siluriformes)	Anderson, Rountree, and Juanes (2008)
Fish	<i>Metriaclima zebra</i>	Cichlidae (Perciformes)	Bertucci, Attia, Beauchaud, and Mathevon (2013)
Fish	<i>Acipenser fulvescens</i>	Acipenseridae (Acipenseriformes)	Bocast, Bruch, and Koenigs (2014)
Fish	<i>Salvelinus alpinus</i>	Salmonidae (Salmoniformes)	Bolgan et al. (2016)
Fish	<i>Salvelinus alpinus</i>	Salmonidae (Salmoniformes)	Bolgan et al. (2018)
Fish	<i>Neolamprologus pulcher</i>	Cichlidae (Perciformes)	Bruintjes and Radford (2013)
Fish	<i>Cottus rhenanus</i> , <i>Cottus perifretum</i>	Cottidae (Scorpaeniformes)	Colleye, Ovidio, Salmon, and Parmentier (2013)
Fish	<i>Lota lota</i>	Lotidae (Gadiformes)	Cott et al. (2014)
Fish	<i>Pollimyrus isidori</i> , <i>Pollimyrus adspersus</i> , <i>Petrocephalus ballayi</i>	Mormyridae (Osteoglossiformes)	Crawford (1997)
Fish	<i>Pollimyrus isidori</i>	Mormyridae (Osteoglossiformes)	Crawford, Jacob, and Bénech (1997)
Fish	<i>Cynotilapia afra</i> , <i>Labeotropheus fuelleborni</i> , <i>Maylandia aurora</i> , <i>Maylandia callainos</i> , <i>Maylandia zebra</i> , <i>Petrotilapia nigra</i>	Cichlidae (Perciformes)	Danley, Husemann, and Chetta (2012)
Fish	<i>Ictalurus furcatus</i>	Ictaluridae (Siluriformes)	Ghahramani, Mohajer, and Fine (2014)
Fish	<i>Economidichthys pygmaeus</i>	Gobiidae (Perciformes)	Gkenas, Malavasi, Georgalas, Leonardos, and Torricelli (2010)
Fish	<i>Cyprinella venusta</i>	Cyprinidae (Cypriniformes)	Holt and Johnston (2015)
Fish	<i>Neogobius melanostomus</i>	Gobiidae (Perciformes)	Rollo, Andraso, Janssen, and Higgs (2007)
Fish	<i>Padogobius nigricans</i>	Gobiidae (Perciformes)	Lugli, Pavan, and Torricelli (1996)
Fish	<i>Padogobius martensii</i>	Gobiidae (Perciformes)	Lugli, Torricelli, Pavan, and Miller (1996)
Fish	<i>Cyprinodon bifasciatus</i>	Cyprinodontidae (Cyprinodontiformes)	Johnson (2000)
Fish	<i>Oryzias latipes</i>	Adrianchthyidae (Beloniformes)	Kang, Qiu, Moroishi, and Oshima (2017)
Fish	<i>Cottus paulus</i>	Cottidae (Scorpaeniformes)	Kierl and Johnston (2010)
Fish	<i>Megalodoras uranoscopus</i> , <i>Agamyxis pectinifrons</i> , <i>Amblydoras affinis</i> , <i>Hemidoras morrisi</i> , <i>Oxydoras niger</i>	Doradidae (Siluriformes)	Knight and Ladich (2014)
Fish	<i>Trichopsis vittata</i>	Osphronemidae (Perciformes)	Ladich (2007)
Fish	<i>Trichopsis vittata</i>	Osphronemidae (Perciformes)	Ladich and Schleinzer (2015)
Fish	<i>Pollimyrus marianne</i>	Mormyridae (Osteoglossiformes)	Lamml and Kramer (2005)
Fish	<i>Marcusenius macrolepidotus</i>	Mormyridae (Osteoglossiformes)	Lamml and Kramer (2007)

(Continues)

TABLE 2 (Continued)

Taxon	Species	Family (order)	Reference
Fish	<i>Pomatoschistus minutus</i>	Gobiidae (Perciformes)	Lugli (2013)
Fish	<i>Padogobius martensii</i> , <i>Gobius nigricans</i>	Gobiidae (Perciformes)	Lugli et al. (2003)
Fish	<i>Ictalurus furcatus</i>	Ictaluridae (Siluriformes)	Mohajer, Ghahramani, and Fine (2015)
Fish	<i>Acipenser oxyrinchus</i>	Acipenseridae (Acipenseriformes)	Sulak, Edwards, Hill, and Randall (2002)
Fish	<i>Neogobius melanostomus</i>	Gobiidae (Perciformes)	Rollo and Higgs (2008)
Fish	<i>Alosa pseudoharengus</i>	Clupeidae (Clupeiformes)	Rountree, Juanes, et al. (2018)
	<i>Catostomus commersonii</i>	Catostomidae (Cypriniformes)	
	<i>Salvelinus fontinalis</i> , <i>Salmo trutta</i> , <i>Oncorhynchus mykiss</i>	Salmonidae (Salmoniformes)	
Fish	<i>Lepomis macrochirus</i>	Centrarchidae (Perciformes)	Scholik and Yan (2002a)
Fish	<i>Pimephales promelas</i>	Cyprinidae (Cypriniformes)	Scholik and Yan (2002b)
Fish	<i>Pseudorasbora parva</i>	Cyprinidae (Cypriniformes)	Scholz and Ladich (2006)
Fish	<i>Metriaclima callainos</i> , <i>Metriaclima lombardoi</i> , <i>Melanochromis auratus</i> , <i>Melanochromis johanni</i> , <i>Melanochromis cyaneorhabdos</i>	Cichlidae (Perciformes)	Smith and van Staaden (2009)
Fish	<i>Etheostoma crossopterum</i> , <i>Etheostoma flabellare</i>	Percidae (Perciformes)	Speares, Holt, and Johnston (2011)
Fish	<i>Moxostoma carinatum</i> , <i>Moxostoma robustum</i>	Catostomidae (Cypriniformes)	Straight, Freeman, and Freeman (2014)
Fish	<i>Moxostoma carinatum</i> , <i>Moxostoma robustum</i>	Catostomidae (Cypriniformes)	Straight, Rhett Jackson, Freeman, and Freeman (2015)
Fish	<i>Padogobius martensii</i>	Gobiidae (Perciformes)	Torricelli, Lugli, and Gandolfi (1986)
Fish	<i>Gasterosteus aculeatus</i> , <i>Phoxinus phoxinus</i>	Gasterosteidae (Gasterosteiformes) Cyprinidae (Cypriniformes)	Voellmy et al. (2014)
Fish	<i>Cottus bairdi</i>	Cottidae (Scorpaeniformes)	Whang and Janssen (1994)
Fish	<i>Tilapia mariae</i>	Cichlidae (Perciformes)	Kottege, Jurdak, Kroon, and Jones (2015)
Fish	<i>Pundamilia nyererei</i> , <i>P. pundamilia</i> , <i>Neochromis onnicaeruleus</i>	Cichlidae (Perciformes)	Verzijden et al. (2010)
Fish	<i>Pygocentrus nattereri</i> , <i>Serrasalmus maculatus</i> , <i>S. cf. sanchezi</i> , <i>S. spp.</i>	Serrasalminae (Characiformes)	Rountree and Juanes (2020)
Fish	<i>Neogobius melanostomus</i>	Gobiidae (Perciformes)	Higgs and Humphrey (2020)
Fish	<i>Phoxinus phoxinus</i>	Cyprinidae (Cypriniformes)	Hanache et al. (2020)
Fish	<i>Lota lota</i>	Lotidae (Gadiformes)	Grabowski, Young, and Cott (2020)
Fish	<i>Cyprinodon bifasciatus</i>	Cyprinodontidae (Cyprinodontiformes)	Johnson (2000)
Fish	<i>Scaphirhynchus albus</i> , <i>S. platyrhynchus</i>	Acipenseridae (Acipenseriformes)	Johnston and Phillips (2003)
Fish	<i>Codoma ornata</i>	Cyprinidae (Cypriniformes)	Johnston and Vives (2003)
Fish	<i>Pomatoschistus marmoratus</i> , <i>P. canestrinii</i> , <i>Knipowitschia panizzae</i> , <i>K. punctatissima</i> , <i>Padogobius nigricans</i> , <i>P. bonelli</i>	Gobiidae (Perciformes)	Malavasi, Collatuzzo, and Torricelli (2008)

(Continues)

TABLE 2 (Continued)

Taxon	Species	Family (order)	Reference
Fish	<i>Serrasalmus elongatus</i> , <i>S. marginatus</i> , <i>S. compressus</i> , <i>S. manueli</i> , <i>S. spilopleura</i> , <i>S. rhombeus</i> , <i>S. eigenmanni</i> , <i>Pygocentrus nattereri</i>	Serrasalminae (Characiformes)	Mélotte, Vigouroux, Michel, and Parmentier (2016)
Fish	<i>Aplodinotus grunniens</i>	Sciaenidae (Perciformes)	Rountree and Juanes (2017)
Fish	<i>Padogobius martensi</i>	Gobiidae (Perciformes)	Torricelli, Lugli, and Pavan (1990)
Amphibian	<i>Telmatobius oxycephalu</i> , <i>Telmatobius hintoni</i> , <i>Telmatobius culeus</i>	Telmatobiidae (Anura)	Brunetti, Muñoz Saravia, Barrionuevo, and Reichle (2017)
Amphibian	<i>Amphiuma means</i>	Amphiumidae (Caudata)	Crovo, Zeyl, and Johnston (2016)
Amphibian	<i>Siren intermedia</i>	Sirenidae (Caudata)	Gehlbach and Walker (1970)
Amphibian	<i>Rana palustris</i>	Ranidae (Anura)	Given (2008)
Amphibian	<i>Ichthyosaura alpestris</i> , <i>Lissotriton vulgaris</i>	Salamandridae (Caudata)	Hubáček, Šugerková, and Gvoždík (2019)
Amphibian	<i>Xenopus pygmaeus</i> , <i>X. ruwensoriensis</i> , <i>X. amieti</i> , <i>X. boumbaensis</i> , <i>X. allofraseri</i> , <i>X. andrei</i> , <i>X. itombwensis</i> , <i>X. wittei</i> , <i>X. vestitus</i> , <i>X. lenduensis</i> , <i>X. largeni</i> , <i>X. gilli</i> , <i>X. poweri</i> , <i>X. laevis</i> , <i>X. victorianus</i> , <i>X. petersii</i> , <i>X. borealis</i> and <i>X. mueller</i>	Pipidae (Anura)	Kwong-Brown et al. (2019)
Amphibian	<i>Ceratophrys ornata</i>	Ceratophryidae (Anura)	Natale et al. (2011)
Amphibian	<i>Rana italica</i>	Ranidae (Anura)	Razzetti, Sacchi, and Platz (2006)
Amphibian	<i>Gephyromantis azzurrae</i>	Mantellidae (Anura)	Reeve et al. (2011)
Amphibian	<i>Xenopus laevis</i>	Pipidae (Anura)	Ringeis et al. (2017)
Amphibian	<i>Pelobates fuscus</i>	Pelobatidae (Anura)	ten Hagen et al. (2016)
Amphibian	<i>Xenopus laevis</i>	Pipidae (Anura)	Tobias et al. (2010)
Amphibian	<i>Xenopus laevis</i>	Pipidae (Anura)	Vignal and Kelley (2007)
Amphibian	<i>Xenopus borealis</i>	Pipidae (Anura)	Yager (1992)
Amphibian	<i>Pelobates fuscus</i>	Pelobatidae (Anura)	Dutilleux and Curé (2020)
Mammal	<i>Hippopotamus amphibius</i>	Hippopotamidae (Cetartiodactyla)	Barklow (2004)
Mammal	<i>Hippopotamus amphibius</i>	Hippopotamidae (Cetartiodactyla)	Barklow (1997)
Mammal	<i>Inia geoffrensis</i> <i>Sotalia fluviatilis</i>	Iniidae (Cetartiodactyla) Delphinidae, (Cetartiodactyla)	Campbell, Alfaro-Shigueto, Godley, and Mangel (2017)
Mammal	<i>Hippopotamus amphibius</i>	Hippopotamidae (Cetartiodactyla)	Maust-Mohl, Soltis, and Reiss (2018)
Mammal	<i>Neophocaena phocaenoides</i>	Phocoenidae (Cetartiodactyla)	Mooney, Li, Ketten, Wang, and Wang (2011)
Reptile	<i>Podocnemis expansa</i>	Podocnemididae (Testudines)	Ferrara, Vogt, and Sousa- Lima (2012)
Reptile	<i>Podocnemis expansa</i>	Podocnemididae (Testudines)	Ferrara, Vogt, Sousa-Lima, Tardio, and Bernardes (2014)
Reptile	<i>Alligator mississippiensis</i>	Alligatoridae (Crocodylia)	Reber et al. (2017)

(Continues)

TABLE 2 (Continued)

Taxon	Species	Family (order)	Reference
Reptile	<i>Chelodina oblonga</i>	Chelidae (Testudines)	Giles et al. (2009)
Arthropod	<i>Micronecta scholtzi</i>	Corixidae (Hemiptera)	Sueur et al. (2011)
Arthropod	<i>Berosus pantherinus</i> , <i>Tropisternus blatchleyi</i> , <i>Tropisternus collaris</i>	Hydrophilidae (Coleoptera)	Wilson et al. (2015)
Arthropod	<i>Micronecta scholtzi</i>	Corixidae (Hemiptera)	Desjonquères et al. (2020)
Arthropod	<i>Euastacus armatus</i>	Parastacidae (Decapoda)	Sandeman and Wilkens (1982)
Arthropod	<i>Palmaeorixa nana</i>	Corixidae (Hemiptera)	Aiken (1982a, 1982b)
Arthropod	<i>Palmaeorixa nana</i>	Corixidae (Hemiptera)	Aiken (1982a, 1982b)
Arthropod	<i>Micronecta batilla</i>	Corixidae (Hemiptera)	Bailey (1983)
Arthropod	<i>Callicorixa praeusta</i> , <i>Sigara striata</i>	Corixidae (Hemiptera)	Finke (1968)
Arthropod	<i>Sigara striata</i>	Corixidae (Hemiptera)	Finke and Prager (1980)
Arthropod	<i>Corixa panzeri</i> , <i>C. dentipes</i> , <i>C. punctata</i>	Corixidae (Hemiptera)	Finke and Prager (1981)
Arthropod	<i>Cenocorixa bifada</i> , <i>C. kuiterti</i> , <i>C. andersoni</i> , <i>C. utahensis</i> , <i>C. dakotensis</i> , <i>C. blaisdelli</i> , <i>C. wileyae</i> , <i>C. expleta</i>	Corixidae (Hemiptera)	Jansson (1973)
Arthropod	<i>Cenocorixa bifada</i> , <i>C. kuiterti</i> , <i>C. andersoni</i> , <i>C. utahensis</i> , <i>C. dakotensis</i> , <i>C. blaisdelli</i> , <i>C. wileyae</i> , <i>C. expleta</i>	Corixidae (Hemiptera)	Jansson (1972)
Arthropod	<i>Cenocorixa bifada</i> , <i>C. andersoni</i> , <i>C. blaisdelli</i> , <i>C. expleta</i>	Corixidae (Hemiptera)	Jansson (1974a, 1974b)
Arthropod	<i>Cenocorixa bifada</i> , <i>C. kuiterti</i> , <i>C. andersoni</i> , <i>C. utahensis</i> , <i>C. dakotensis</i> , <i>C. blaisdelli</i> , <i>C. wileyae</i> , <i>C. expleta</i>	Corixidae (Hemiptera)	Jansson (1974a, 1974b)
Arthropod	<i>Palmaeorixa buenoi</i> , <i>Corisella tarsalis</i> , <i>Trichocorixa macroceps</i> , <i>T. naias</i> , <i>Callicorixa audeni</i> , <i>C. vulnerata</i> , <i>Sigara solensis</i> , <i>S. omani</i> , <i>S. nevadensis</i> , <i>S. compressoidea</i> , <i>S. mackinacensis</i> , <i>S. signata</i>	Corixidae (Hemiptera)	Jansson (1976)
Arthropod	<i>Micronecta griseola</i> , <i>M. minutissima</i> , <i>M. poweri</i>	Micronectidae (Hemiptera)	Jansson (1977a, 1977b)
Arthropod	<i>Micronecta griseola</i> , <i>M. minutissima</i> , <i>M. poweri</i>	Micronectidae (Hemiptera)	Jansson (1977a, 1977b)
Arthropod	<i>Arctocorisa carinata</i>	Corixidae (Hemiptera)	Jansson (1979)
Arthropod	<i>Hydropsyche angustipennis</i> , <i>H. siltalai</i> , <i>H. nevae</i> , <i>H. pellucidula</i>	Hydropsychidae (Trichoptera)	Vuoristo and Jansson (1979)
Arthropod	<i>Micronecta griseola</i> , <i>M. minutissima</i> , <i>M. poweri</i> , <i>M. tasmanica</i> , <i>Tenagobia fuscata</i> , <i>T. incerta</i> , <i>T. spinifera</i>	Micronectidae (Hemiptera)	Jansson (1989)
Arthropod	<i>Hydropsyche fulvipes</i> , <i>H. angustipennis</i> , <i>H. contubernalis</i> , <i>H. pellucidula</i> , <i>H. instabilis</i> , <i>Diplectrona felix</i> , <i>D. modesta</i> , <i>Potamyia flava</i>	Hydropsychidae (Trichoptera)	Johnstone (1964)
Arthropod	<i>Micronecta batilla</i>	Corixidae (Hemiptera)	King (1976)
Arthropod	<i>Micronecta concordia</i> , <i>M. tasmanica</i> , <i>M. robusta</i>	Micronectidae (Hemiptera)	King (1999a, 1999b, 1999c)
Arthropod	<i>Micronecta illiesi</i> , <i>M. annae</i> , <i>M. australiensis</i> , <i>M. concordia</i> , <i>M. tasmanica</i> , <i>M. robusta</i> , <i>M. gracilis</i> , <i>M. major</i> , <i>M. dixonia</i>	Micronectidae (Hemiptera)	King (1999a, 1999b, 1999c)
Arthropod	<i>Micronecta concordia</i>	Micronectidae (Hemiptera)	King (1999a, 1999b, 1999c)
Arthropod	<i>Tropisternus mixtus</i> , <i>T. nimbatus</i> , <i>T. glaber</i>	Hydrophilidae (Coleoptera)	Ryker (1972)

(Continues)

TABLE 2 (Continued)

Taxon	Species	Family (order)	Reference
Arthropod	<i>Hydropsyche pelucidula</i> , <i>H. siltalai</i>	Hydropsychidae (Trichoptera)	Silver (1980)
Arthropod	<i>Corixa dentipes</i> , <i>C. punctata</i>	Corixidae (Hemiptera)	Theiss (1982)
Arthropod	<i>Corixa dentipes</i>	Corixidae (Hemiptera)	Theiss (1983)
Arthropod	<i>Corixa dentipes</i> , <i>C. punctata</i>	Corixidae (Hemiptera)	Theiss, Prager, and Streng (1983)
Arthropod	<i>Hydropsyche pelucidula</i>	Hydropsychidae (Trichoptera)	Silver and Halls (1980)
Arthropod	<i>Buenoa macrotibialis</i>	Notonectidae (Hemiptera)	Wilcox (1975)
Soundscape	N/A	N/A	Desjonquères et al. (2015)
Soundscape	N/A	N/A	Desjonquères et al. (2018)
Soundscape	N/A	N/A	Kuehne, Padgham, and Olden (2013)
Soundscape	N/A	N/A	Lara and Vasconcelos (2018)
Soundscape	N/A	N/A	Marley, Erbe, and Salgado-Kent (2016)
Soundscape	N/A	N/A	Martin and Cott (2016)
Soundscape	N/A	N/A	Amoser and Ladich (2010)
Soundscape	N/A	N/A	Geay et al. (2017)
Soundscape	N/A	N/A	Gottesman et al. (2020)
Soundscape	N/A	N/A	Linke, Decker, Gifford, and Desjonquères (2020)
Soundscape	N/A	N/A	Karaconstantis et al. (2020)
Soundscape	N/A	N/A	Roca, Magnan, and Proulx (2020)
Soundscape	N/A	N/A	Stober (1969)

sound. However, an additional 30 papers were added from surveying the cited literature of reference reviews in the field of freshwater bioacoustics and our own personal literature archives. Trichoptera (caddisflies) were well represented with 11 species in the Hydropsychidae. However, Hemiptera (the true bugs) was found to be the most represented order with 44 species in three families. The Corixidae were the most studied within them, with 28 species represented by 18 papers, followed by Micronectidae with 15 species represented by six papers and Notonectidae represented by one species (Table 2). Sueur et al. (2011) investigated the stridulations of the water boatman *Micronecta scholtzi*, a common lentic arthropod in the Corixidae. Remarkably, when scaled to body length, the amplitude of the sound produced by *M. scholtzi* is higher than any sound produced by marine or terrestrial organisms (Sueur et al., 2011). Wilson et al. (2015) recorded exemplar calls of three water beetle species (Hydrophilidae; Table 2) to identify the acoustic characteristics of each species. An automatic identification system was then constructed using digital signal processing techniques, which was capable of classifying the three beetle species with ~87.5% accuracy (Wilson et al., 2015). Sound production has also been noted in larvae of *Cybister confuses* (Mukerji, 1929) and the great silver diving beetle *Hydrophilus piceus* (Allen, 1956). This research suggests that arthropods produce species-specific sounds that may be catalogued. Knowledge of these sounds could in the future be used with passive acoustic monitoring to identify macroinvertebrates in the natural environment and infer ecosystem condition.

Future bioacoustic research with a focus on freshwater arthropod sound would yield insights into important ecological processes within freshwater ecosystems. Many species of arthropod are ecologically significant, such as the signal crayfish *Pacifastacus leniusculus* and the killer shrimp *Dikerogammarus villosus*, which are highly invasive in freshwater ecosystems around the world (Bubb, Thom, & Lucas, 2004; MacNeil, Boets, & Platvoet, 2012). Several species of crayfish are known to produce sound, including the invasive red swamp crayfish (Favaro, Tirelli, Gamba, & Pessani, 2011) and the endangered white-clawed crayfish (Desjonquères, 2016). Furthermore, mayflies, stoneflies, caddisflies, water beetles

and crayfish exist across broad environmental gradients and are useful indicators of environmental change (Muralidharan, Selvakumar, Sundar, & Raja, 2010). As a result, several biotic indices have been developed to monitor macroinvertebrate communities, such as the Biological Monitoring Working Party score (Muralidharan et al., 2010) and the River Invertebrate Prediction and Classification System (Wright, Furse, & Moss, 1998). Such biotic indices are used by regulators in the UK to provide evidence that habitat quality requirements of the Water Framework Directive (2000) (Directive (2000/60/EC)) are achieved. These indices could therefore be used as a model to inform ecoacoustic bioassessment indices.

3 | FOCAL HABITATS OF FRESHWATER BIOACOUSTIC STUDIES

In total 71 papers (53%) identified by this review were conducted in a laboratory. Such studies benefit from the ability to reduce background noise and make detailed physiological observations while controlling environmental parameters that influence acoustic behavior, such as water temperature (Torricelli et al., 1990). However, interpretations of acoustic behavior from recordings conducted in a laboratory may be influenced by the unnatural absorption and scattering of soundwaves inside small aquaria (Akamatsu, Okumura, Novarini, & Yan, 2002), and the cut-off phenomenon (Urick, 1967), which can cause low frequencies to quickly decay and therefore be undetected by a hydrophone while higher resonant frequencies of the aquarium are amplified.

Rivers were the most studied natural habitat, being the research focus of 32 papers (24%). The majority of research conducted in rivers focused on the topics of “Behaviour” (15 papers) or “Ecoacoustics” (10 papers), while the remaining studies focused on aspects of the physiology of sound production. Lake and pond habitat types, however, were only a research focus of 15 papers each (11%; Figure 2). Notably, the soundscapes of temperate freshwater ponds were not investigated until when Desjonquères et al. (2015) used passive acoustic monitoring to record the soundscapes of three ponds in Chevreuse (France) for 1 min every 15 min over an 84-day period. Each pond was shown to possess unique daily patterns of acoustic activity and composition, indicating that the ponds contained high levels of acoustic diversity. Furthermore, Bolgan et al. (2018) recorded the first underwater soundscape of Arctic charr spawning grounds in Lake Windermere (United Kingdom) using three passive acoustic monitoring stations. They identified three distinct sound groups: fish air passage sounds; macroinvertebrate sounds and gravel sounds (spawning activity). Passive acoustic monitoring studies are often only conducted in rivers and frequently overlook lentic habitats, which are often more species rich (Dehling, Hof, Brändle, & Brandl, 2010). Wysocki, Amoser, and Ladich (2007) demonstrated that environments with flowing water possess higher levels of background noise due to the movement of water and sediment, often present above 1 kHz which has the effect of masking sounds produced by most fish species. In lentic environments however, sounds produced by fish species are only partly masked.

In contrast to exclusively investigating sounds produced by animals, Tonolla, Lorang, Heutschi, Gotschalk, and Tockner (2011) investigated abiotic sounds in rivers. They suspended a hydrophone from an inflatable cataraft to investigate physical characteristics of underwater sound along stretches of five hydro-geomorphologically different river segments in Switzerland, Italy and the United States in order to characterize the spatial distributions of habitat types along a river segment. Each river segment was identifiable by the sound pressure level, sound variability and the spatial organization of the acoustic signal (31.5 Hz to 16 kHz). Abiotic sound sources, such as turbulence or streambed sediment transport along each river segment influenced spatial soundscape diversity. An increased flow rate was shown to produce higher sound pressure level values over most frequency bands. Such data offer a novel quantification of habitat

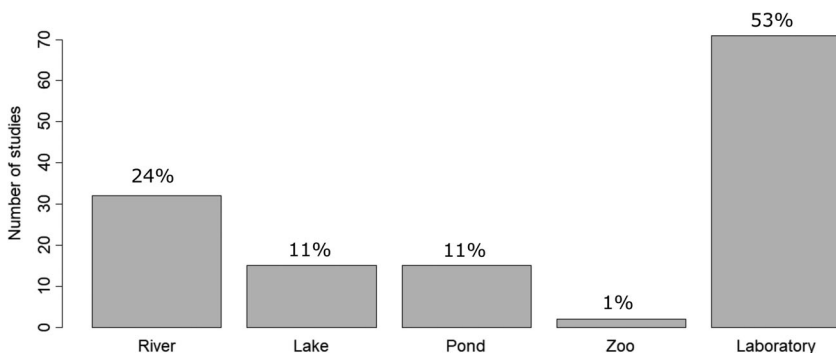


FIGURE 2 Habitat type representation within 124 freshwater bioacoustics research articles. Percentages have been rounded to the nearest integer

heterogeneity along riverine ecosystems. Lumsdon et al. (2018) also provide a comprehensive characterization of riverine soundscapes. They investigated the effect of rapid anthropogenically induced fluctuations in river discharge as a result of dams and hydroelectric plants. Lumsdon et al. (2018) also demonstrated that instances of high river discharge were strongly correlated with an increase in low frequency signals that overlap with the hearing range of common teleosts.

4 | A SHIFT TOWARDS ECOACOUSTICS

Most papers were focused on behavior (48%) while fewer studies addressed ecoacoustic (16%) or physiological (12%) research questions. Several papers focused on a combination of two main topics (behavior and physiology; behavior and ecoacoustics; ecoacoustics and physiology). Interestingly, more papers focused on a combination of behavior and physiology (16%) than on physiology only. Only three studies (Lara & Vasconcelos, 2018; Scholik & Yan, 2002a, 2002b) focused both on physiology and ecoacoustics (2%; Figure 3). Lara and Vasconcelos (2018) characterized the soundscapes of natural (river) and artificial (laboratory aquarium) zebrafish *Danio rerio* environments and found that the soundscapes of artificial environments possessed high noise levels, potentially causing auditory masking. Scholik and Yan (2002a, 2002b) studied the effect of anthropogenic sound (a small boat) on the hearing capabilities of zebrafish and fathead minnow *Pimephales promelas* in a laboratory.

Traditionally, bioacoustics studies have focussed on behavioral and physiological aspects of sound production (Yager, 1992) and have only recently sought to describe biological sound at a soundscape scale and address ecological research questions in the form of ecoacoustics using passive acoustic monitoring (Desjonquères et al., 2018). The results of this systematic review confirm this shift from behavioral studies, often with a focus on a single taxonomic group, towards an approach orientated towards ecoacoustics and conservation biology. Since 2000, the number of ecoacoustics articles has grown dramatically (2001–2005: 1 article, 2006–2010: 2, 2011–2015: 6 and 2016–2020: 16) while the number of behavioral studies remained stable with an average of 14 papers every five years.

One emerging challenge of using passive acoustic monitoring is appropriate analysis of large amounts of data generated. In order to overcome this issue, several acoustic indices have recently been developed that enable inference of biological diversity from the spectral (frequency) and temporal (time) elements of audio files (Sueur, Pavoine, Hamerlynck, & Duvail, 2008; Table 3). Acoustic indices also allow ecologists to analyze audio files in a standardized and automated way (Sueur et al., 2008; Sueur, Farina, Gasc, Pieretti, & Pavoine, 2014), and require little expertise to calculate and interpret (Gasc et al., 2015). However, the majority of acoustic indices have been designed to estimate diversity of avian and terrestrial fauna in temperate woodlands. These include the Spectral (*Hf*), Temporal (*Ht*) and Acoustic (*H*) Entropy indices (Sueur et al., 2008), the Acoustic Complexity Index (*ACI*; Pieretti, Farina, & Morri, 2011), and the Acoustic Richness Index (*AR*; Depraetere et al., 2012). Gasc et al. (2015) highlight the need to consider the dominant vocal taxonomic groups present in an ecosystem before selecting appropriate acoustic indices to analyze passive acoustic monitoring data. Biological sounds produced in the arthropod dominated underwater soundscape of a freshwater

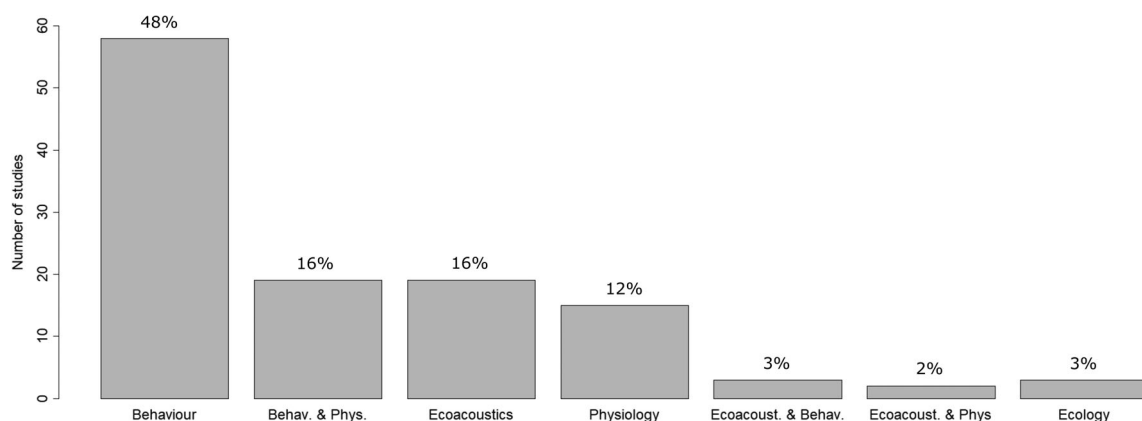


FIGURE 3 Topic of research representation within 124 freshwater bioacoustics research articles. Percentages have been rounded to the nearest integer. Behav., behavior; Ecoacoust., Ecoacoustics; Phys., physiology

TABLE 3 Acoustic indices frequently used by bioacousticians

Acoustic index	Description	Developed for	Reference
Spectral entropy (H_f)	“Measures the evenness of the amplitude envelope over the time units... by dividing the Shannon index by its maximum” (Sueur et al., 2008)	Terrestrial fauna (in a coastal forest, Tanzania)	Sueur et al. (2008)
Temporal entropy (H_t)	“A mean spectrum $s(f)$ is first computed using a Short Time Fourier Transform (STFT) based on a nonoverlapping sliding function window of sample width τ . This mean spectrum $s(f)$ is similarly transformed into a probability mass function $S(f)$ of length N used to compute the spectral entropy H_t ” (Sueur et al., 2008)	Terrestrial fauna (in a coastal forest, Tanzania)	Sueur et al. (2008)
Acoustic entropy (H)	A function of H_t and H_f	Terrestrial fauna (in a coastal forest, Tanzania)	Sueur et al. (2008)
Acoustic richness (AR)	A ranked index based on the temporal entropy and amplitude of a signal	Birds (in a temperate woodland, France)	Depraetere et al. (2012)
Acoustic evenness index (AEI)	“Calculated by dividing the spectrogram into bins (default 10) and taking the proportion of the signals in each bin above a threshold (default -50 dBFS). The AEI is the result of the Gini index applied to these bins” (Villanueva-Rivera, Pijanowski & Villanueva-Rivera, 2018)	Birds and terrestrial biota (in forest, agricultural land and urban areas, Indiana, United States)	Villanueva-Rivera et al. (2018)
Acoustic complexity index (ACI)	“Calculated on the basis of a matrix of the intensities extrapolated from the spectrogram (divided into temporal steps and frequency bins), the ACI calculates the absolute difference between two adjacent values of intensity in a single frequency bin” (Pieretti et al., 2011)	Birds (in temperate woodland, Italy)	Pieretti et al. (2011)
Acoustic diversity index (ADI)	“Calculated by dividing the spectrogram into bins (default 10) and taking the proportion of the signals in each bin above a threshold (default -50 dBFS). The ADI is the result of the Shannon index applied to these bins” (Villanueva-Rivera et al., 2018)	Birds and terrestrial biota (in forest, agricultural land and urban areas, Indiana, United States)	Villanueva-Rivera, Pijanowski, Doucette, and Pekin (2011)
Bioacoustic index (BI)	Calculated as the “area under each curve included all frequency bands associated with the dB value that was greater than the minimum dB value for each curve. The area values are thus a function of both the sound level and the number of frequency bands used by the avifauna” (Boelman, Asner, Hart, & Martin, 2007)	Birds and terrestrial biota (in forest, savanna, woodland and shrubland, Hawaii, United States)	Boelman et al. (2007)
Normalized difference soundscape index ($NDSI$)	Seeks to “estimate the level of anthropogenic disturbance on the soundscape by computing the ratio of human-generated (anthrophony) to biological (biophony) acoustic components found in field collected sound samples” (Kasten, Gage, Fox, & Joo, 2012)	Birds and terrestrial biota (on an island in Twin Lakes, MI, United States)	Kasten et al. (2012)

habitat differ in their acoustic characteristics to those produced by birds in terrestrial soundscapes. Many birds produce complex songs composed of amplitude and frequency modulations, whereas arthropod sounds usually consist of short repeating phrases without frequency modulations (Gasc et al., 2015). Therefore, different indices might be the most efficient for freshwater and terrestrial soundscapes (Karaconstantis, Desjonquères, Gifford, & Linke, 2020).

To evaluate the ability of acoustic indices for estimation of freshwater biodiversity Desjonquères et al. (2015) analyzed pond soundscape data using six acoustic indices. The temporal entropy (H_t) and spectral entropy (H_f) indices

were shown to correlate negatively with aural parameters defined by manually counting the number and diversity of sound types, and therefore failed to accurately estimate biological diversity. Desjonquères et al. (2015) suggest that the inverse relationship produced by the Temporal and Spectral Entropy indices may be due to their increased sensitivity to background noise. This effect was also observed by Depraetere et al. (2012), who noted that background noise, such as wind and rain, was higher in amplitude than signals produced by biota. Therefore, false high values of spectral frequency can be generated during adverse weather conditions. In contrast to the recommendations made by Gasc et al. (2015) for arthropod-dominated soundscapes, Acoustic Richness (*AR*) was shown not to correlate with aurally defined parameters. However, the median amplitude envelope (*M*), Acoustic Complexity Index (*ACI*), and the number of mean frequency peaks (*NP*) indices were shown to correlate positively with aurally defined parameters. In order to improve estimations of biodiversity, values generated by acoustic indices should be compared with values obtained by conventional means of estimating biodiversity. Furthermore, to estimate ecosystem condition biodiversity values should be obtained from a range of habitat types.

Future research seeking to incorporate a bioacoustic element to estimate freshwater biodiversity should consider the limitations associated with the collection and interpretation of data derived from passive acoustic monitoring. For example, not every species present may be capable of producing sound, and those that do may produce a variety of sounds making species identification or quantification challenging (Gasc et al., 2015; Linke et al., 2018). Furthermore, future research should consider the propagation of biological soundwaves underwater, including the effects of scattering, absorption and the cut-off phenomenon. Accurate estimations of taxa abundance are very challenging to obtain because a chain of short repeating calls could be produced by a single individual rather than a population (Gasc et al., 2015). The type of recording equipment used may also present a detection bias by over-representing individuals calling within the frequency range of the recording equipment (Gibb et al., 2019). Despite these limitations, passive acoustic monitoring provides freshwater ecologists with a powerful noninvasive approach to monitoring freshwater ecosystems.

5 | CONCLUSIONS

Passive acoustic monitoring offers ecologists many benefits that conventional survey methods cannot provide, such as the ability to monitor freshwater ecosystems dynamically, remotely and autonomously with no environmental impact (Gasc et al., 2015; Linke et al., 2018). Furthermore, with the deployment of multiple hydrophones, several sites can be monitored simultaneously, and the data generated analyzed automatically by acoustic indices. As freshwater ecologists increasingly look to utilize passive acoustic monitoring to estimate biodiversity, it is important to consider potential research areas that will improve the effectiveness of this technique in freshwater ecosystems. We therefore suggest two main areas for future freshwater bioacoustic research: (a) to improve methods used to analyze acoustic data from freshwater environments, and (b) to explore the relationship between freshwater soundscape composition and ecosystem condition. Ecologists working in this field could benefit from collaborating with physicists to model the propagation of biological sound in shallow water and the effects of absorption, scattering and the cut-off phenomenon. Moreover, some freshwater species such as some fish and arthropods only perceive particle velocity and not pressure (which is what hydrophones measure) (Hawkins, 1981; Stumpner & Von Helversen, 2001). While in a lot of cases, particle velocity and sound pressure are proportional (Merchant et al., 2015), for other cases, it would be interesting to access the particle velocity as a more representative measure of the ambient soundscape of some species.

The results of this review highlight the potential to increase our understanding of freshwater arthropod sounds, especially in lentic habitats. Macroinvertebrates provide an essential role in the foundation of all freshwater food webs, and therefore ecosystem function (Oertli, 1993). Furthermore, invasive freshwater arthropods, such as several North American crayfish species, are known to alter ecosystem structure and functioning, and therefore perhaps the soundscapes of freshwater ecosystems (Jackson et al., 2014). Thus, a freshwater bioacoustics research agenda with a focus on freshwater arthropods, the dominant vocal taxonomic group present in rivers, lakes and ponds would likely yield novel insights into freshwater ecosystem function and condition.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Jack Greenhalgh: Conceptualization; data curation; methodology; visualization; writing-original draft; writing-review and editing. **Martin Genner:** Methodology; supervision; writing-review and editing. **Gareth Jones:** Methodology; supervision; writing-review and editing. **Camille Desjonquères:** Data curation; methodology; supervision; writing-review and editing.

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