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REVIEW

Animals of New Zealand wetlands

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Abstract: New Zealand wetlands provide many ecosystem services, but their extent has declined by more than 90% since human arrival, highlighting the urgent need to identify and protect them. Wetland delineation in New Zealand depends primarily on vegetation, supported by soil type and hydrological indicators. However, this current approach only partially fulfils the legal definition of wetlands in the Resource Management Act 1991, which requires that an area "support a natural ecosystem of plants and animals that are adapted to wet conditions". Although significant progress has been made in characterising wetland vegetation, far less is known about the diversity, distribution, and abundance of New Zealand wetland animals. Here we review the current state of knowledge about animals supported by New Zealand wetlands, describe their adaptations to wet conditions, and discuss implications for wetland delineation and policy enforcement. Overall, we consider that animals adapted to wet conditions are ubiquitous in habitats that otherwise satisfy current wetland delineation protocols. Major animal groups include macrofauna such as birds and fish, and invertebrates such as annelids, flatworms, nematodes, rotifers, insects, crustaceans, and molluscs. Some of these taxa are widespread, abundant, and can survive extended dry periods and other extreme conditions, suggesting that at least some wet-adapted animals are likely to be present in all delineated wetland ecosystems (based on plants, hydrology, and soils), regardless of their dryness, degradation and damage. However, our review identified major gaps in our fundamental knowledge of New Zealand wetland animal communities, especially for intermittent wetlands. Future work should survey key animal groups across a range of wetland classes throughout New Zealand and develop robust methods to detect and monitor these fundamental but currently overlooked animal groups.

Keywords: amphibians; Aotearoa; birds; delineation; environmental policy; fauna; fish; macroinvertebrates; meiofauna

Introduction

The extent and condition of New Zealand wetlands have declined significantly since human arrival (McGlone 2009). More than 90% of historical vegetated freshwater wetland area has been lost (Ausseil et al. 2011; Ministry for the Environment & Statistics New Zealand 2015), and almost 140 hectares of saline wetland vegetation was destroyed between 1996 and 2018 (Denyer & Peters 2020), placing New Zealand at the extreme end of natural wetland loss globally (Mitsch & Gosselink 2000). This freshwater and saline wetland loss and degradation are ongoing through drainage, nutrient inputs, and non-native species impacts (Ausseil et al. 2011; Robertson et al. 2019; Burge et al. 2020; Denyer & Peters 2020; Burge et al. 2023). The remaining natural wetlands, depending on their size and landscape context, can provide the ecosystem functions and processes that contribute to the provision of many ecosystem services, including food, fibre, fresh water, flood and erosion mitigation, habitat for highly endemic biodiversity, and contributions to cultural human health (Millenium Ecosystem Service Assessment 2005; Clarkson et al. 2013; Patterson & Cole 2013; Pivac & Pivac-Hohaia 2023).

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Vegetation is primarily used to delineate wetland ecosystems, supported by the characterisation of soils and hydrology, which together form the Wetland Delineation Protocols for New Zealand (Clarkson 2014; Fraser et al. 2018; Ministry for the Environment 2021; 2022a). Additionally, where it is sought to identify natural inland wetlands as a requirement of the National Policy Statement for Freshwater Management 2020 (NPS-FM), a Pasture Assessment Exclusion Methodology has been developed to exclude areas of wet pasture that are used for grazing (Ministry for the Environment 2022b). The primary focus is on vegetation because the multi-year lifecycle of most plants allows for inference of the duration and frequency of wetness (Tiner 2017). For example, the presence of hydrophytic vegetation (i.e. plants capable of growing in soils that are often or constantly saturated during the growing season) tends to indicate prolonged wet conditions. To support the wetland delineation protocol, 1124 vascular plants (i.e. those with specialised tissues for the transport of water and minerals throughout the plant, including clubmosses, horsetails, ferns, gymnosperms, and angiosperms) in New Zealand have been assigned a "wetland indicator status" that describes their affinity for wetland ecosystems: obligate wetland, facultative wetland, facultative, facultative upland, or obligate upland (Clarkson et al. 2021). This categorisation and overall delineation approach is consistent with the United States wetland delineation system for regulatory purposes (Environmental Laboratory 1987; U.S. Army Corps of Engineers 2008), upon which the New Zealand protocols are based. Although much is known about wetland vegetation, soils, and hydrology, we know far less about the diversity, distribution, and abundance of wetland animals in New Zealand.

This knowledge gap was recently highlighted by a Court of Appeal decision regarding wetland delineation: *Page v Greater Wellington Regional Council* [2024] NZCA 51. The Court accepted an argument that evidence of wet-adapted animals was required in the criminal context for an area to legally be considered "wetland" as defined by the Resource Management Act (1991; RMA), casting doubt over current wetland delineation protocols. This is because the RMA defines wetlands as "permanently or intermittently wet areas, shallow water, and land water margins that support a natural ecosystem of plants and animals that are adapted to wet conditions". This definition of wetlands is broad, encompassing intermittently wet soils through to permanently inundated lakes, rivers, estuaries, and the marine intertidal zone. A wealth of knowledge exists about animals of permanently inundated habitats, where the Court accepted that wet-adapted animals would be present without requiring site-specific data, given the known ubiquity of aquatic invertebrates. The animals of New Zealand rivers, lakes, and coastal marine ecosystems have been well described, including fish (McDowall 2010; Francis 2024), molluscs (Willan & Davey 2020; Winterbourn 2023), crustaceans (Chapman et al. 2011; Cox & Ahyong 2020), insects (Winterbourn et al. 2006), and sponges (Kelly 2022). Therefore, we focus on the key knowledge gap that is most relevant to current policy: the animals supported by wetlands that are not obviously or permanently wet.

Consideration of animals for the purposes of wetland delineation is not currently standard practice in New Zealand or internationally. Rather, animals are typically used to assign relative wetland condition or significance, after the area has been delineated using other indicators (i.e. plants, soils, hydrology) in the Wetland Delineation Protocols for New Zealand (Clarkson et al. 2004; Venables & Boon 2016; Clarkson & Sorrell 2018; Howe et al. 2023). The state of Queensland, Australia, use the presence of animals from an accepted a list of wet-adapted animals (Department of Environment, Science and Innovation, Queensland 2013) to confirm wetland extent where it is otherwise unclear, but a wetland can be confirmed by vegetation, hydrology, or soils at any stage prior to assessment for animals (Department of Environment and Science 2023). Moreover, relying on animals as a necessary indicator for wetland delineation purposes is an unusual approach because many wet-adapted animal species are difficult to detect, being cryptic, nocturnal, transient, sub-terranean, or minute, or require specialised experts to identify them.

Any requirement to provide evidence of animals adapted to wet conditions being supported by the wetland in question risks adding considerable costs to the already complex and expensive process of delineating wetlands. These increased costs and uncertainty around the exact nature of evidence required to satisfy the criminal standard of proof could result in agencies being reluctant to pursue enforcement action and wetland extent continuing to be lost. We also currently lack explicit direction on the specific morphological, physiological, or behavioural traits for some taxa that meet the legal definition of "adapted to wet conditions" as used in the RMA and for criminal proceedings. For example, some morphological traits are clear evidence of wet adaptation, such as the presence of gills on fish. However, the traits of lesser-known taxa such as soil invertebrates (e.g. cyst and cocoon forms) are less well documented. This is especially true for behavioural adaptations, where the behaviours of macrofauna such as birds and fish are readily observed. In contrast, relatively little is known about the behavioural adaptations of taxa such as invertebrates and meiofauna (small invertebrates able to pass through a 500 μm mesh sieve but retained by a 45 μm sieve), which are easily overlooked and still being discovered and described. Therefore, to restore confidence in the regulatory process for agencies undertaking enforcement action, there is an urgent need to collate current knowledge of animals considered "adapted to wet conditions" in New Zealand, especially for wetlands subject to questions around delineation. In this article we aim to achieve two goals: (1) describe the key morphological, physiological, and behavioural traits that make animals "adapted to wet conditions", and (2) collate existing information on the animal taxa that are adapted to wet conditions and supported by wetlands in New Zealand.

What makes an animal "adapted to wet conditions"?

We take "adapted to wet conditions" to mean an organism having some morphological, physiological, and/or behavioural adaptation, at some stage in their life cycle, that makes them dependant on, or capable of existing for prolonged periods in, wet conditions. Species that have such adaptations may also be capable of inhabiting and utilising non-aquatic habitats (e.g. birds, earthworms, adult stages of aquatic insects, emersed mudfish and cyst-forms of meiofauna), but we consider that does not preclude them from being wet-adapted animals. The RMA definition does not specify whether the wet-adapted plants and animals should be native or non-native, and thus we consider both in this paper.

It is worth noting that our proposed definition excludes some animal species that are considered to be indicators of wetlands, but which lack a specific morphological, physiological, or behavioural adaptation to wet conditions, such that they do not help to satisfy the definition of wetlands under the Resource Management Act 1991. One example of this is the native moth *Houdinia flexilissima* (more popularly known as Fred the Thread), which completes its entire life cycle within wetlands (i.e. is an obligate wetland taxa) and has specialised to develop within the obligate endemic wetland plant *Sporadanthus ferrugineus* (bamboo rush). Although *H. flexilissima* only occurs in wetlands, its larvae live entirely within *S. ferrugineus* stems and the adult moth is a terrestrial organism (Hoare et al. 2006). Therefore, we cannot justify this animal as being directly "adapted to wet conditions", despite it being a wetland obligate taxa. Other examples include the Australasian harrier (*Circus approximans*), a common native bird of prey also known as swamp harrier (an indication of its typical habitat), and the fernbird (*Poodytes punctatus*), a skulking endemic bird frequently associated with the dense, low vegetation that characterises many wetlands. Fernbirds are also often considered to be indicators of wetland ecological integrity due to their sensitivity to non-native mammalian predators (Anderson & Ogden 2003; Clarkson et al. 2004). However, both Australasian harriers and fernbirds lack obvious and specific adaptations to wet conditions. In other words, some species might be excellent diagnostic taxa of wetlands, but are not specifically adapted to them, whereas others possess clear adaptations to wet conditions, but are not confined to them (e.g. New Zealand kingfisher, *Todiramphus sanctus vagans*). These inconsistencies reflect the tension between our current ecological knowledge of wetland animals and the legal definition.

Ecologically speaking, it would be preferable that any animal whose life cycle requires an obligate or facultative wetland plant would be indicative of the presence of a wetland for delineation purposes (in the same way that the plant is). However, many such species may not possess a morphological, physiological, or behavioural adaptation to wet conditions, such as specialist herbivores on above-ground plant material (e.g. Fred the Thread). These species may be considered indirectly adapted to wet conditions, in that they are dependent on wetland habitats and their interactions with other wetland species for foraging, sheltering, roosting, and breeding. For the purposes of this article, however, we take a conservative approach that we consider clearly meets the legal definition of the RMA (i.e. animals with obvious adaptations to wet conditions such as gills, webbed feet, or cutaneous respiration). Nonetheless, we find the exclusion of these and other species to be unsatisfying from an ecological perspective, highlighting an issue with applying the RMA definition of wetlands for delineation and policy implementation.

How might an animal be "supported" by a wetland?

For the term "support" in the RMA definition, we consider that an area will support animals where it provides habitat for wet-adapted animals, regardless of the time of year, length of time an area is wet or saturated, or duration of species occupancy. We define habitat as the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism (Hall et al. 1997). Habitat is species-specific and relates species presence in an area to a wide range of physical and biological characteristics, including more than just vegetation composition and structure. Moreover, habitat provision may be ephemeral, either due to the lifecycle of the organism or the seasonal nature of resources. We therefore consider "support" for wet-adapted species to include both permanent and temporary occupancy of habitat that can itself be permanent or temporary.

In some circumstances, the habitat characteristics that support occupancy can be readily identified, such as food resources (e.g. aquatic invertebrates for dragonfly larvae), sheltering or resting areas (e.g. open water for waterfowl), breeding or nesting areas (e.g. aquatic macrophytes for fish spawning), or other intrinsic properties (e.g. moisture allowing cutaneous respiration of oligochaetes). For other animals that are less readily observed (e.g. meiofauna), we consider that occupancy of an ecosystem is evidence of "support" for the species via habitat.

Wet-adapted animals of New Zealand

We postulate that all New Zealand wetlands that satisfy the current wetland delineation protocols, based on vegetation and supported by soil type and hydrological indicators, will inevitably support wet-adapted animals. In support of this view, here we systematically review current knowledge on the diversity of animals that are adapted to wet conditions and supported by wetlands in New Zealand, such that they contribute to satisfying the definition of wetlands in the RMA (Fig. 1). For each group of organisms, from macrofauna to microscopic meiofauna, we describe the morphological, physiological, and behavioural adaptations that make them "adapted to wet conditions", and where known, describe their occurrence in wetland classes that differ in the presence of water (i.e. permanently wet, intermittently wet, and wet soils).

Birds

New Zealand birds possess a range of morphological, physiological, and behavioural adaptations to wet conditions (Table 1; an extended version of this table is provided in Appendix S1 of the Supplementary Material) (Robertson et al. 1983; O'Donnell 2000; Williams 2004; O'Donnell et al. 2015). Wet-adapted birds generally comprise shorebirds (waders, terns, gulls), cormorants, waterfowl (ducks, swans, geese), grebes, herons, rails (crakes, coots, swamphens), and kingfishers. Other New Zealand bird taxa such as swallows, pipits, pigeons, honeyeaters, and cuckoos that may frequently be seen in freshwater habitats lack the morphological, physiological, and behavioural adaptations to wet conditions seen in the above taxa and are therefore not considered to be "adapted to wet conditions".

The most obvious morphological adaptations of wetland birds include modified legs and feet for standing in water and on soft substrate, and a range of bill shapes for feeding in various wet conditions (Table S1). Webbed feet, lobed toes, and streamlined body shapes (e.g. ducks, gulls, terns, grebes, and coots) support efficient swimming and diving (e.g. Johansson & Norberg 2000), while long legs and toes (e.g. rails, waders, and herons) allow birds to wade in water and exploit aquatic foods unavailable to other species (Zeffer et al. 2003). Wet-adapted birds also possess an array of bill morphologies, including long bills for probing aquatic substrates (e.g. eastern bar-tailed godwit, *Limosa lapponica baueri*), dagger-like bills for stabbing aquatic prey (e.g. Australasian bittern, *Botaurus poiciloptilus*, and white heron, *Ardea modesta*), and modifications for filtering aquatic prey (e.g. lamellae along the upper mandible of Australasian shoveler, *Spatula rhynchotis*) (Heather & Robertson 2015). Many waders also use distal rhynchokinesis, which allows the tip of their upper

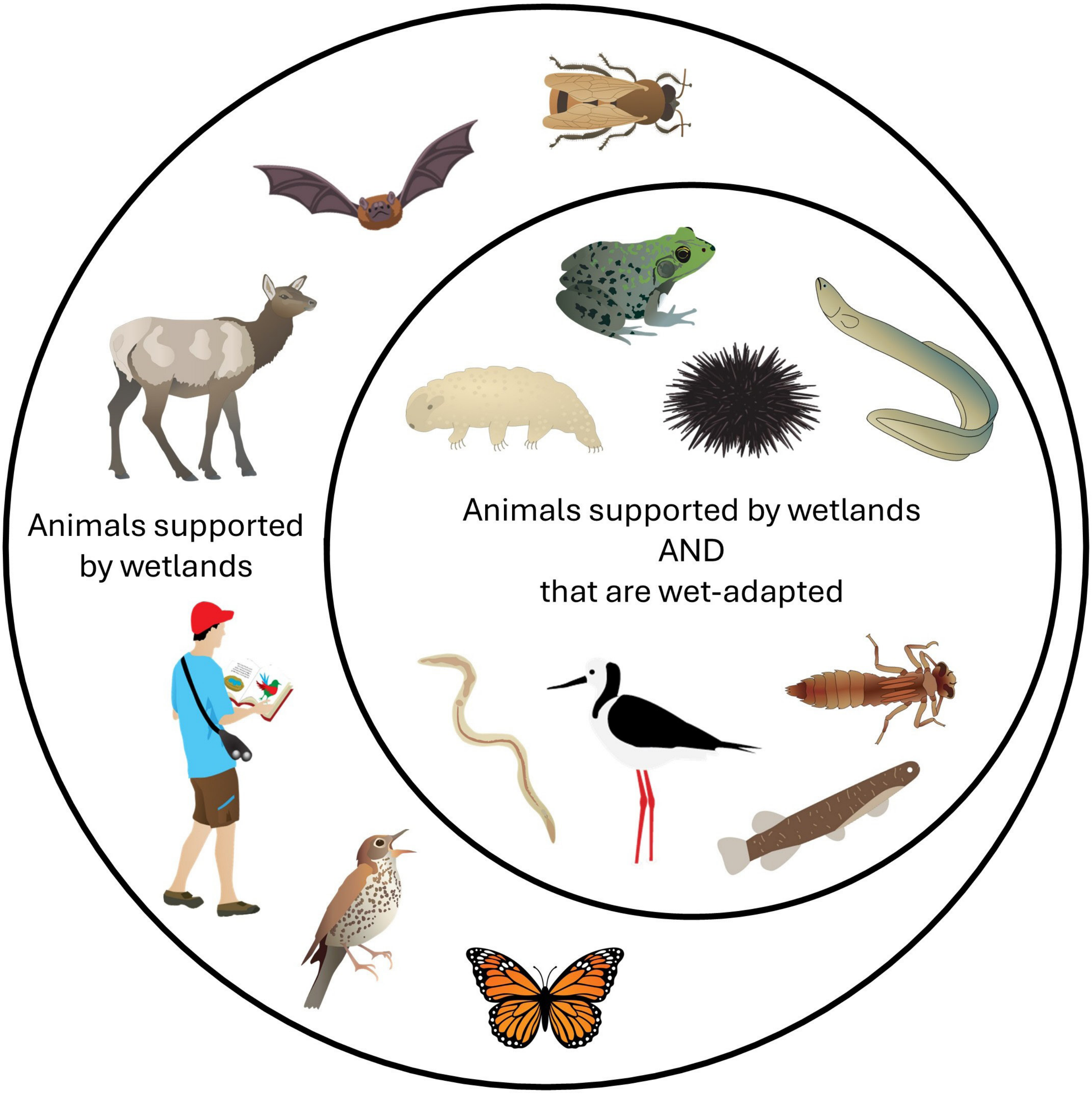

Figure 1. Diagram demonstrating the conceptual framework that underpins the literature review. The inner circle shows wet-adapted species that are supported by freshwater and saline wetlands, thereby meeting the definition of the Resource Management Act (RMA 1991) in New Zealand. Symbols modified from Nicolette Faville, Tracey Saxby, Jane Hawkey, Dieter Tracey, Annie Carew, Kim Kraeer, Lucy Van Essen-Fishman, and Diana Kleine; freely available from the IAN Image Library (ian.umces.edu/imagelibrary/).

Table 1. Examples of adaptations to wet conditions in New Zealand bird species, and the types of support that they are provided by wetland habitat. An extended version of this table with information on species' provenance, threat status, wetland dependence, and occurrence in different wetland water regimes is provided as Appendix S1.

			Type of support provided by wetland habitat		
Common name	**Scientific name**	**Examples of adaptation to wet conditions**	**Breeding**	**Aquatic food sources**	**Shelter/ roosting**
North Island brown kiwi	*Apteryx mantelli*	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Rowi	*Apteryx rowi*	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Haast tokoeka	*Apteryx australis* "Haast"	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Northern Fiordland tokoeka	*Apteryx australis* "northern Fiordland"	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Southern Fiordland tokoeka	*Apteryx australis* "southern Fiordland"	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Stewart Island brown kiwi	*Apteryx australis australis*	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Little spotted kiwi	*Apteryx owenii*	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Great spotted kiwi	*Apteryx maxima*	Long legs, toes, neck, and bill, valve at bill tip	No	Yes	No
Mute swan	*Cygnus olor*	Webbed feet, long neck	Yes	Yes	Yes
Black swan	*Cygnus atratus*	Webbed feet, long neck	Yes	Yes	Yes
Cape Barren goose	*Cereopsis novaehollandiae*	Webbed feet, long neck	Yes	Yes	Yes
Greylag goose	*Anser anser*	Webbed feet, long neck	Yes	Yes	Yes
Canada goose	*Branta canadensis*	Webbed feet, long neck	Yes	Yes	Yes
Paradise shelduck	*Tadorna variegata*	Webbed feet	Yes	Yes	Yes
Australian wood duck	*Chenonetta jubata*	Webbed feet	Yes	Yes	Yes
Whio	*Hymenolaimus malacorhynchos*	Webbed feet, bill-tip skin flap	Yes	Yes	Yes
Grey teal	*Anas gracilis*	Webbed feet	Yes	Yes	Yes
Brown teal	*Anas chlorotis*	Webbed feet	Yes	Yes	Yes
Mallard	*Anas platyrhynchos*	Webbed feet	Yes	Yes	Yes
Grey duck	*Anas superciliosa*	Webbed feet	Yes	Yes	Yes
Australasian shoveler	Spatula rhynchotis	Webbed feet, lamellae on mandible	Yes	Yes	Yes
New Zealand scaup	*Aythya novaeseelandiae*	Webbed feet	Yes	Yes	Yes
Australasian crested grebe	*Podiceps cristatus australis*	Caudal lobed toes	Yes	Yes	Yes
New Zealand dabchick	*Poliocephalus rufopectus*	Caudal lobed toes	Yes	Yes	Yes
Hoary-headed grebe	*Poliocephalus poliocephalus*	Caudal lobed toes	Yes	Yes	Yes
Australasian little grebe	*Tachybaptus novaehollandiae novaehollandiae*	Caudal lobed toes	Yes	Yes	Yes
Banded rail	*Hypotaenidia philippensis assimilis*	Long legs and toes	Yes	Yes	Yes
North Island weka	*Gallirallus australis greyi*	Long legs and toes	Yes	Yes	Yes
Western weka	*Gallirallus australis australis*	Long legs and toes	Yes	Yes	Yes
Buff weka	*Gallirallus australis hectori*	Long legs and toes	Yes	Yes	Yes
Stewart Island weka	*Gallirallus australis scotti*	Long legs and toes	Yes	Yes	Yes
Spotless crake	*Zapornia tabuensis tabuensis*	Long legs and toes	Yes	Yes	Yes
Marsh crake	*Zapornia pusilla affinis*	Long legs and toes	Yes	Yes	Yes
Pukeko	*Porphyrio melanotus melanotus*	Long legs and toes	Yes	Yes	Yes
South Island takahe	*Porphyrio hochstetteri*	Long legs and toes	Yes	Yes	Yes
Australian coot	*Fulica atra australis*	Lobed toes	Yes	Yes	Yes
Variable oystercatcher	*Haematopus unicolor*	Long legs, toes, and bill	Yes	Yes	Yes
South Island pied oystercatcher	*Haematopus finschi*	Long legs, toes, and bill	Yes	Yes	Yes

Table 1. Continued.

Common name	Scientific name	Examples of adaptation to wet conditions	Type of support provided by wetland habitat		
			Breeding	**Aquatic food sources**	**Shelter/ roosting**
Pied stilt	*Himantopus himantopus leucocephalus*	Long legs, toes, neck, and bill	Yes	Yes	Yes
Black stilt	*Himantopus novaezelandiae*	Long legs, toes, neck, and bill	Yes	Yes	Yes
Pacific golden plover	*Pluvialis fulva*	Long legs and toes	No	Yes	Yes
Northern New Zealand dotterel	*Anarhynchus obscurus aquilonius*	Long legs and toes	Yes	Yes	Yes
Southern New Zealand dotterel	*Anarhynchus obscurus obscurus*	Long legs and toes	Yes	Yes	Yes
Banded dotterel	*Anarhynchus bicinctus bicinctus*	Long legs and toes	Yes	Yes	Yes
Wrybill	*Anarhynchus frontalis*	Long legs, toes, and bill	Yes	Yes	Yes
Black-fronted dotterel	*Charadrius melanops*	Long legs and toes	No	Yes	No
Shore plover	*Thinornis novaeseelandiae*	Long legs and toes	No	Yes	Yes
Spur-winged plover	*Vanellus miles novaehollandiae*	Long legs and toes	Yes	Yes	Yes
Asiatic whimbrel	*Numenius phaeopus variegatus*	Long legs, toes, and bill	No	Yes	Yes
Eastern bar-tailed godwit	*Limosa lapponica baueri*	Long legs, toes, and bill	No	Yes	Yes
Red knot	*Calidris canutus rogersi*	Long legs and toes	No	Yes	Yes
Sharp-tailed sandpiper	*Calidris acuminata*	Long legs, toes, and bill	No	Yes	Yes
Red-necked stint	*Calidris ruficollis*	Long legs and toes	No	Yes	Yes
Red-billed gull	*Larus novaehollandiae scopulinus*	Webbed feet	No	Yes	Yes
Black-billed gull	*Larus bulleri*	Webbed feet	No	Yes	Yes
Southern black-backed gull	*Larus dominicanus dominicanus*	Webbed feet	Yes	Yes	Yes
Eastern little tern	*Sternula albifrons sinensis*	Webbed feet	No	Yes	No
New Zealand fairy tern	*Sternula nereis davisae*	Webbed feet	No	Yes	No
Australian tern	*Gelochelidon macrotarsa*	Webbed feet	Yes	Yes	Yes
Caspian tern	*Hydroprogne caspia*	Webbed feet	No	Yes	No
White-winged black tern	*Chlidonias leucopterus*	Webbed feet	No	Yes	Yes
Black-fronted tern	*Chlidonias albostriatus*	Webbed feet	No	Yes	No
White-fronted tern	*Sterna striata striata*	Webbed feet	No	Yes	Yes
Arctic tern	*Sterna paradisaea*	Webbed feet	No	Yes	No
Little shag	*Phalacrocorax melanoleucos brevirostris*	Caudal webbed feet and long neck	Yes	Yes	Yes
Black shag	*Phalacrocorax carbo novaehollandiae*	Caudal webbed feet and long neck	Yes	Yes	Yes
Pied shag	*Phalacrocorax varius varius*	Caudal webbed feet and long neck	Yes	Yes	Yes
Little black shag	*Phalacrocorax sulcirostris*	Caudal webbed feet and long neck	Yes	Yes	Yes
Eastern cattle egret	*Ardea ibis coromanda*	Long legs, toes, neck, and bill	No	Yes	Yes
White heron	*Ardea modesta*	Long legs, toes, neck, and bill	Yes	Yes	Yes
White-faced heron	*Egretta novaehollandiae*	Long legs, toes, neck, and bill	No	Yes	Yes
Nankeen night heron	*Nycticorax caledonicus australasiae*	Long legs, toes, and bill	No	Yes	Yes
Australasian bittern	*Botaurus poiciloptilus*	Long legs, toes, neck, and bill	Yes	Yes	Yes
Glossy ibis	*Plegadis falcinellus*	Long legs, toes, neck, and bill	Yes	Yes	Yes
Royal spoonbill	*Platalea regia*	Long legs, toes, neck, and bill	Yes	Yes	Yes
New Zealand kingfisher	*Todiramphus sanctus vagans*	Nictitating eye membrane	Yes	Yes	Yes

mandible to flex upwards independently of the rest of the bill, helping them to capture prey buried in substrate or suspended in water (Estrella & Masero 2007). Kiwi (*Apteryx* spp.) possess sealable valves at their bill tip that may allow them to feed in wet soils (Reid et al. 1982). Diving birds such as grebes, shags, and some waterfowl also exhibit a range of adaptations for diving, such as buoyancy control, cranial modifications to enhance vision, and traits that reduce drag and enable pursuit of underwater prey (e.g. elongated body, caudally positioned hind limbs, and powerful pelvic and leg musculature) (Fish 2016; Segesdi & Pecsics 2022; Pecsics & Csörgő 2023). Most wet-adapted birds also have an oil-producing uropygial gland near their tails and use this oil to coat their feathers when they preen, which helps maintain their feather structure and waterproofing. This gland is largest in water birds (Vincze et al. 2013; but see Montalti & Salibián 2000), which is thought to relate to their increased need for feather maintenance to maintain waterproofing (e.g. Møller & Laursen 2019). Some birds also possess a nictitating membrane that protects their eyes while diving underwater (e.g. New Zealand kingfisher), among other functions.

Physiological adaptations are less well known but include some diving birds having greater volumes of blood to increase oxygen storage (Butler & Jones 1997), and the ability of the eye lens to change shape through the iris and ciliary muscles, allowing them to see prey underwater (Glasser & Howland 1996; Katzir & Howland 2003). Another example is that many waders have dense clusters of sensitive nerve endings at the end of their bills (known as Herbst corpuscles), which help them to detect prey in substrate or water by sensing changes in pressure waves bouncing back from solid objects (i.e. their prey) (Piersma et al. 1998). The eggs of some wet-adapted birds (e.g. rails) have also been shown to withstand inundation for longer periods than those of terrestrial species (Stermin & David 2020).

New Zealand birds display a range of behavioural adaptations to wet conditions. For example, many wet-adapted birds exhibit a high degree of plasticity in response to changeable conditions (e.g. flooding and drought), such as adjusting the timing of their breeding based on water levels (Zhang et al. 2018), increasing nest elevation and height following flooding (Benvenuti et al. 2018), and producing precocious young able to escape disturbances. Other interesting behavioural adaptations include birds stirring wet substrate to dislodge prey (Recher et al. 1983) and the subtle head movements of herons that help them to compensate for light refraction and calculate the position of prey in water (Katzir & Intrator 1987). Wet-adapted birds also tend to be more mobile than many other species because they must move among networks of water bodies to respond to changing water levels, vegetation cover, and food supplies throughout the year (Haig et al. 1998; Williams 2024). These movements are still not well understood for most New Zealand species (Schlesselmann et al. 2024).

Based on the adaptations described above, we identified 76 New Zealand bird taxa as being both "adapted to wet conditions" and "supported" by freshwater wetlands (Table S1). Of these, 29 bird taxa are obligate (i.e. depend entirely on wetlands for at least one life history stage) and 47 are facultative (i.e. also feed, breed, or shelter in wetlands but are not dependent on them) users of wetlands. Sixty-eight taxa are supported by intermittent wetlands, and 52 taxa by wet soils, usually when they are saturated (Table S1). In making this list, we only considered extant taxa that breed on the New Zealand mainland (North Island, South Island, Stewart Island) or that are classified as "migrant" in the New Zealand Threat Classification System (Robertson et al. 2021).

Fish

Fish are aquatic vertebrates that require aquatic habitat to complete their life cycle (Ishimatsu et al. 2018). The presence of gills (respiratory organs that allow fish to breathe underwater) is their key adaptation to wet conditions, and some taxa can also take up oxygen through their skin when emersed (out of water) but in moist conditions (Meredith 1985). Other morphological adaptations of fish include their streamlined body and fins for efficient swimming and the presence of a swim bladder, an internal gas-filled organ that helps most bony fish control their buoyancy (Facey et al. 2022). All New Zealand freshwater fishes are quite obviously adapted to wet conditions, and some also possess behavioural adaptations that help them persist during dry periods, such as burrowing into wet soils (Ling 2001).

New Zealand has 55 recognised taxa of native freshwater fish, including *Galaxias* and *Neochanna* (Family Galaxiidae), *Retropinna* smelt (Retropinnidae), *Gobiomorphus* bullies (Eleotridae), torrentfish (*Cheimarrichthys fosteri*), lamprey (*Geotria australis*), and *Anguilla* eels (Anguillidae), along with 21 non-native species, some of which are considered invasive (Dunn et al. 2018; Collier & Grainger 2015). Some taxa complete their entire life cycle in freshwater environments (non-diadromous), whereas others migrate between marine and freshwater ecosystems (diadromous). The habitats of these taxa range across a hydrological continuum from lakes through slow-flowing wetlands to fast-flowing, steep streams and rivers (O'Brien & Dunn 2007; Dunn et al. 2020).

The five New Zealand *Neochanna* mudfishes are considered wetland specialists but also occupy seasonally intermittent lake margins and waterways with little or no flow and may tolerate emersion in appropriate conditions for up to several months during drier periods (Ling 2001; O'Brien & Dunn 2007). The non-diadromous *Galaxias* species occur in streams, wetlands, and lakes (Department of Conservation 2004; Dunn et al. 2020; Dunn & O'Brien 2022; Gerbeaux et al. 2022). Habitats occupied within wetlands by these taxa are typically perennial, although some may encounter seasonal fluctuations in water level and flow (Dunn 2011). Diadromous fish species, such as eels and whitebait (*Galaxias* spp. and *Retropinna* smelt), utilise both marine and freshwater habitats at different life stages. Because diadromous taxa require different habitats to complete their life cycle, they also require the presence of suitable passage between those habitats. Fish passage opportunities do not need to be continuously available to be potentially important, and species such as longfin and shortfin eel (*Anguilla dieffenbachii* and *A. australis*, respectively) utilise ephemeral wetlands and flow channels to access more permanent water features.

A recent analysis investigated the non-diadromous *Galaxias* and *Neochanna* fish taxa supported by wetlands in New Zealand by assessing the intersection between mapped known fish habitat areas and mapped wetlands and hydric soils (Dunn 2024). Mapped known fish habitat areas were based on an updated version of the database described by Dunn and O'Brien (2022) (updated 19 January 2024). Mapped wetlands were based on the layer by Belliss et al. (2017), who updated the Wetlands of National Importance (WONI) national wetlands layer (Leathwick et al. 2010) from 2015/16 Sentinel-2A satellite imagery. The scope of WONI was intended to include just palustrine and inland saline wetlands, but some riverine, estuarine, lacustrine, and ephemeral wetlands were included. Hydric soils were identified using the Fundamental Soil Layers (https://lris.scinfo.org.nz/layer/112060-fsl-new-zealand-soil-classification-v11/) and following Fraser et al. (2018).

This study found that the distributions of all 28 taxa examined intersected with either mapped wetlands (Table 2) or hydric soils (Appendix S2) and that 89% of taxa intersected with both the mapped wetlands and hydric soils layers. However, these findings require cautious interpretation due to data limitations. First, the mapped wetlands layer may be incomplete and therefore underestimate taxon occurrences in wetlands deemed too small to map (WONI used a 0.5 hectare minimum polygon size). Second, the areas identified as habitat fragments for freshwater fish may require further refinement through additional sampling (Dunn & O'Brien 2022). Third, data were likely captured over a range of time periods, and older fish records may be from wetlands that were drained prior to the mapping exercise. Finally, the Fundamental Soil Layers dataset was used because of its national coverage, but it lacks the high resolution of datasets with incomplete coverage (i.e. S-Map) which may mean that precise habitat associations of species are not well captured. Additionally, the Fundamental Soil Layers dataset does not include Chatham Island, meaning that *N. rekohua* was not assessed. Potential mapping errors and low resolution could be indirectly assessed in future by comparing the observed fish habitat intersection with wetlands and hydric soils against their null intersection with other ecosystem layers or soil types. Future analyses should also be undertaken for specific taxa where higher resolution data exists, and for other species that utilise wetlands, such as diadromous fish, non-native fish, and fish supported by inundated saltmarsh (e.g. stingrays, flounder). In general, improving the extent and accuracy of maps of ecosystems, soils, and fish habitat will broaden our understanding of freshwater fish habitat preferences and occurrence in wetlands. Despite the caveats given above, these analyses indicate that almost all non-diadromous *Galaxias* and *Neochanna* occur in habitats that intersect with mapped wetlands and hydric soils (Dunn 2024).

We conclude that permanent water features in wetlands are highly likely to support fish, at least on occasion, if there is enough habitat to support non-diadromous species, or if there is access between the freshwater body and the marine environment (fish passage) to enable colonisation by diadromous species. Intermittent water features in wetlands are likely to support fish when they are connected to more permanent water features that contain fish or are inhabited by taxa with emersion tolerance during dry conditions (e.g. *Neochanna* mudfishes). Such temporary areas of aquatic habitat are often utilised for feeding (e.g. eels foraging for macroinvertebrates that emerge from floodplain soils during high water levels), breeding (e.g. diadromous *Galaxias* spawn their eggs in temporarily submerged marginal and riparian habitats), or shelter (e.g. smaller fish moving into shallower water to avoid predation). Therefore, although fish are primarily associated with permanently inundated areas, a wide variety of wetlands will support freshwater fish species. We conclude that the presence of fish in an area otherwise identified as wetland (by vegetation, hydrology, or soils) clearly satisfies the RMA wetland definition as an area supporting wet-adapted

Table 2. Coincidence of known habitat fragments of 28 non-diadromous *Galaxias* and *Neochanna* taxa with mapped wetlands. Reprinted with permission from Dunn (2024).

Taxon	Total known habitat fragments (*n*)	Intersecting wetlands (*n*)	Intersecting wetlands (%)
Galaxias anomalus	88	7	7.95
Galaxias cobitinis	5	0	0.00
Galaxias affinis *cobitinis* "Waitaki"	17	7	41.18
Galaxias depressiceps	55	19	34.55
Galaxias divergens	90	10	11.11
Galaxias affinis *divergens* "northern"	217	13	5.99
Galaxias "dune lakes"	3	0	0.00
Galaxias eldoni	39	15	38.46
Galaxias gollumoides	230	33	14.35
Galaxias gracilis	9	6	66.67
Galaxias macronasus	32	11	34.38
Galaxias "Nevis"	31	5	16.13
Galaxias "northern"	113	0	0.00
Galaxias paucispondylus	156	22	14.10
Galaxias affinis *paucispondylus* "Manuherikia"	1	1	100.00
Galaxias affinis *paucispondylus* "Southland"	11	1	9.09
Galaxias "Pomahaka"	90	6	6.67
Galaxias prognathus	30	5	16.67
Galaxias affinis *prognathus* "Waitaki"	40	7	17.50
Galaxias pullus	44	11	25.00
Galaxias "southern"	102	5	4.90
Galaxias "species D"	202	12	5.94
Galaxias "Teviot"	10	4	40.00
Galaxias vulgaris	455	73	16.04
Neochanna apoda	140	77	55.00
Neochanna burrowsius	144	21	14.58
Neochanna diversus	102	50	49.02
Neochanna heleios	20	14	70.00

animals, but that more work is needed to better understand the distribution of fish taxa across wetland classes and habitat types in general.

Amphibians and reptiles

Frogs are vertebrates that typically have a fully aquatic larval stage before metamorphosing to an often-terrestrial adult stage. Terrestrial adults remain physiologically adapted to wet environments however, with their permeable skin allowing the cutaneous gas and water exchange that is crucial for respiration and osmoregulation. Adaptations also exist to reduce water loss and dehydration in terrestrial environments, such as the secretion of waterproofing substances or formation of cocoons, while still allowing for rapid water absorption when it is available (Cree 1988; Feder 1992; Toledo & Jared 1993).

Six species of frog are extant in New Zealand, and all are adapted to wet conditions. Three non-native species have been introduced from Australia: green and golden bell frog (*Ranoidea aurea*), southern bell frog (*Ranoidea raniformis*), and brown tree frog (*Litoria ewingii*). All three follow the typical life cycle where the eggs and larval stages are strictly dependent on an aquatic environment (Cree 1984; Burns et al. 2018) and are therefore supported by wetland habitats. The native Hochstetter's frog (*Leiopelma hochstetteri*) lays its eggs in shallow ponds and has free-living tadpoles, although they do not swim far from the place of hatching, or even feed, before metamorphosing into adult frogs. This species has been recorded from wetland habitats like forest seepages but is generally encountered alongside small, eroded forest streams (Najera-Hillman 2009). The other two native frog species (Archey's frog, *Leiopelma archeyi*, and Hamilton's frog, *Leiopelma hamiltoni*) undergo development within the egg, hatching at metamorphosis and occupying terrestrial habitats for the duration of their life cycle. They do, however, remain dependent on moist environments to absorb water across the skin and maintain water balance (Cree 1988), but do not typically occur in wetland habitats (although we do not rule out their use), instead preferring moist areas of forest, such as leaf litter, wet vegetation, and boulder fields (Bell & Bell 1994; Hotham et al. 2023). In general, the distribution of New Zealand frog species in wetlands is not well-quantified, but where they do occur, all species would satisfy the RMA wetland definition of wet-adapted animals.

The non-native European alpine newt (*Ichthyosaura alpestris*) is the only other amphibian species that has established a wild breeding population in New Zealand (Bell 2016), after being illegally imported from Italy (Arntzen et al. 2016). It relies on wet habitat for breeding, as the tadpole stage has gills and requires water to breathe. Since their first detection in 2013, alpine newts have been subject to an eradication programme, which was completed successfully in 2024 (Ministry for Primary Industries 2024).

Finally, New Zealand has over 135 reptile taxa (Hitchmough et al. 2021), several of which are supported by wetlands. For example, Northland green gecko (*Naultinus grayii*) and barking gecko (*Naultinus punctatus*) frequently occur in gumlands and swamps, and Alborn skink (*Oligosoma albornense*) is found in a single pakihi wetland near Reefton. Few of these taxa possess known morphological, physiological, or behavioural adaptations to wet conditions (J. Monks, University of Otago, pers. comm.). However, the egg-laying skink (*Oligosoma suteri*) is known for its ability to dive underwater for up to 20 minutes in rocky coastal pools (Hare & Miller 2009), which may be considered wetlands under the RMA. Besides the egg-laying skink and some occasionally encountered marine taxa (e.g. yellow-bellied sea snake, *Hydrophis platurus*), New Zealand's only other wet-adapted reptile is the non-native red-eared slider turtle (*Trachemys scripta elegans*), which has naturalised in some northern regions.

Macroinvertebrates

Macroinvertebrates are invertebrates that are large enough to be caught and retained on a 0.5 mm sieve. This diverse group is dominated by wet-adapted arthropods, molluscs, and several groups of worm-like organisms. Due to the exceptional diversity of these taxa (including many undescribed species), we do not attempt to provide a comprehensive list of taxa that satisfy the RMA wetland definition here (i.e. an animal adapted to wet conditions and supported by the wetland). Rather, we describe some of their key adaptations to wet conditions, focussing on those adaptations that are phylogenetically conserved at high taxonomic levels (e.g. phyla/orders/families), and review the literature on their occurrence in New Zealand wetlands.

Macroinvertebrate adaptations to wet conditions

The aquatic insects associated with freshwater environments have received considerable research attention, including substantial development of methods and tools for using macroinvertebrates as bioindicators (Stark & Maxted 2007). Many aquatic insects are characterised by an immature aquatic stage (larvae or nymph) that requires water for feeding and respiration, while adults spend their (often short) lives flying and resting on substrates above the water. A few taxa have a wet-adapted adult stage, such as Dytiscidae diving beetles and *Sigara* water boatman, with adaptions such as modified legs for swimming or running on the water surface, or exoskeleton hairs that trap air to use while they swim. Some of the more well-known insects with phylogenetically conserved wet-adapted traits include the larval stage of many mayflies, caddisflies, stoneflies, dragonflies, and Dipteran flies such as chironomid midges, blackflies, and mosquitoes.

Many spiders and mites possess adaptations to wet conditions and are supported by wetlands. A recent review identified aquatic habitat associations in species from at least 21 spider families (Crews et al. 2020). Key adaptations include a cuticle and dense hairs that repel water and trap air, increased hydrophobic protein in silk, and tracheae that extend into the prosoma and legs (Crews at al. 2020). Hydrachnidia, also known as water mites, are among the most diverse, abundant, and widespread groups of freshwater arthropods (Di Sabatino et al. 2008). They often possess swimming hairs on their legs, an adaptation for locomotion through water (Kriska 2023). Water mites have complex life cycles (Di Sabatino et al. 2000), including two separate pupae-like resting stages that may allow them to persist during dry periods as part of an invertebrate seedbank, (i.e. all aquatic invertebrate life stages that remain viable in dry sediments) (Stubbington et al. 2019).

Crustaceans (subphyla Crustacea) are a diverse group of arthropods that range in size from large macroinvertebrates (e.g. freshwater crayfish | kōura, *Paranephrops* spp.) to microscopic meiofauna (e.g. ostracods and copepods). Most crustaceans are aquatic, or live near wet environments, with most taxa possessing gills or respiring directly across the integument, both of which require water (Watling & Thiel 2013). Many crustaceans also have flattened or laterally compressed bodies, and limbs modified for efficient swimming (e.g. paddle crabs). Long antennae are also common, an adaptation to help detect chemical signals, vibrations, and touch in water. Some taxa can produce resting eggs that are tolerant of desiccation and extreme temperatures, an adaptation to periodic dryness in between stages that involve dependence on aquatic conditions (e.g. Thiéry 1997). Wet-adapted crustaceans that are likely to occur in wetlands include crabs, crayfish, amphipods, copepods, isopods, shrimp, ostracods, and cladocerans.

Molluscs (phylum Mollusca) are another diverse group of animals that is dominated in freshwater environments by the gastropods (e.g. slugs and snails) and filter-feeding bivalves (e.g. clams and freshwater mussels). Most gastropods are aquatic and adapted to wet conditions through their need to respire across moist skin or using gills. However, some taxa (e.g. Lymnaeidae, Physidae, Planorbidae) possess lung-like structures that allow them to breathe atmospheric oxygen, assisting their ability to survive in oxygen-poor water (Ponder et al. 2019). Almost all bivalves are aquatic and have gills with the dual functions of respiration and filter-feeding. Molluscs also possess other, more specialised, adaptations to wet conditions, including shell shapes that reduce drag in water, multiple ways to attach to substrates, and the operculum, a hard plate that seals the shell opening of some gastropods, preventing desiccation (Ponder et al. 2019).

Several phyla of segmented and unsegmented worms (Annelida, Platyhelminthes, Nematomorpha) occur in wetlands. All are adapted to wet conditions through their cutaneous respiration systems, which require a moist body surface, and their hydrostatic skeleton, which supports body structure and movement through changes in fluid pressure. Other common adaptations to wet conditions include modifications for filter feeding, attachment to substrate, and sensory structures for wet environments. Members of the Crassiclitellata order of earthworms are some of the more conspicuous wet-adapted animals that are supported by wetlands. Earthworms evolved from aquatic freshwater ancestors to become adapted to life in moist terrestrial habitats, and they cannot survive in dry soils (Sims & Gerard 1985). Their cutaneous respiratory system requires a moist body surface, and their excretory system also requires sufficient water to function correctly (Lee 1985). The earthworm cocoon stage has also adapted to tolerate permanent saturation (Lowe & Butt 2005). Moving over the land surface is more efficient than moving through the soil but is often not possible because the land surface is usually too dry. Rainfall provides a wet surface that earthworms can utilise for movement, and their behaviour of surfacing after rainfall is considered an adaptation for dispersal and not an avoidance of drowning (Wetzel et al. 2016). Leeches (subclass Hirudinea) are common in wet areas with low flow, particularly in farmland and urban catchments. Alongside cutaneous respiration (for most taxa), they have suckers that allow them to attach firmly to surfaces or hosts (Feng et al. 2015). Flatworms (phylum Platyhelminthes) also respire across the body surface, making them vulnerable to water loss, and restricting them to environments where dehydration is unlikely, such as open water, amongst leaf litter, between grains of soil, or in host species (Walker & Anderson 2001). Horsehair worms (phylum Nematomorpha) are common in wet environments, such as streams, puddles, and even man-made structures such as water troughs. Adult worms are free-living, but larvae are endoparasites of terrestrial arthropods. They are famous for affecting the behaviour of their hosts, causing the host to seek water and drown, whereupon the adult worm emerges for the aquatic breeding stage (Ponton et al. 2011).

Macroinvertebrate communities of New Zealand wetlands

There have been few systematic studies of the macroinvertebrate communities of New Zealand wetlands. In the most comprehensive physical survey to date, Suren et al. (2010b) examined sweep net samples (300 μm mesh) from the water column of 82 South Island wetlands. They found a diverse community of invertebrates that was dominated by meiofauna (see next section), despite the relatively large mesh size. Sampled sites comprised a range of wetland classes (i.e. swamp, bog, fen, shallow water) but did not include wetlands that experience intermittent saturation or inundation (e.g. ephemeral wetland, seepage, marsh, pakihi, and gumland), highlighting the lack of empirical studies of animals in wetlands that are not permanently inundated. In a similar study, sweep net samples (also 300 μm mesh) from 40 minimally disturbed wetlands throughout New Zealand found 133 invertebrate taxa (Suren & Sorrell 2010). The diverse community was dominated by chironomid midges (20% of all individuals and found at 80% of sites), copepods (12% of individuals; 88% of sites), aquatic mites (8% of individuals; also the most widespread taxa, found at 90% of sites), and nematodes (7% of individuals; 88% of sites). Except for midges, aquatic insects comprised only a small proportion of individuals, with the next most common insects being the damselfly *Xanthocnemis zealandicus* (3% of individuals) and *Oxyethira* caddisflies (2%). Another survey of 29 lowland perennial wetlands found similar invertebrate communities, with samples dominated by midges (19% of individuals), copepods (11%), oligochaetes (11%), the snail *Potamopyrgus antipodarum* (10%), nematodes (7%), and *X. zealandicus* (6%) (Suren et al. 2010a). This survey also found that invertebrate community composition was unrelated to measures of wetland ecological condition (Suren et al. 2010a). A similar study of temporal variation of invertebrate communities in a single West Coast wetland recorded 64 invertebrate taxa, most of which were wet-adapted (Suren & Lambert 2010). A survey of 14 freshwater wetlands in the Ashburton Lakes complex found that macroinvertebrate community composition was dominated by small crustaceans such as cladocerans and ostracods, and differed among temporary, semi-permanent, and permanent ponds (Ekelund 2017). Samples from 14 freshwater wetlands from the lower North Island were also dominated by crustaceans, and this study found that macroinvertebrate diversity and community composition varied more strongly with nutrient levels than with wetland condition (Ekelund 2017). A study of constructed wetland pools near the Waiau River mouth in Southland found that crustaceans (especially *Daphnia* and ostracods) were observed soon after post-drought rewetting and dominated the community (Stuart et al. 2020). Recently, an analysis of environmental DNA (eDNA) water samples from 16 New Zealand wetlands identified 248 animal taxa (Bird et al. 2024a). Community composition varied strongly among wetlands, but was dominated overall by Annelida, Arthropoda, Chordata, and Cnidaria. Other macroinvertebrate surveys have been conducted in wetlands to collect community baseline data (Clarkson et al. 2008) or assess wetland management outcomes (e.g. willow removal, restoration, comparing remnant with pristine wetlands) (Watts et al. 2008; Watts et al. 2012), although these have largely focussed on non-wet-adapted taxa, especially beetles (but see Wech et al. 2017). Taken together, these studies highlight that aquatic invertebrate communities in wetlands are dominated by non-insect taxa such as worms, aquatic mites, small crustaceans, and nematodes. However, there remains little information on the invertebrate communities of wetland soils, which could be sampled and compared across the full range of wetland classes, including the drier parts of wetlands.

Most of the 21 spider families identified as being associated with aquatic habitats (Crews et al. 2020) occur in New Zealand. Some are found in intertidal habitat, such as the splash-zone spiders (Anyphaenidae, with eight described *Amaurobioides* species in New Zealand; Sirvid et al. 2020), and some members of Agelenidae (seven described *Oramia* species in New Zealand), Desidae (including 30 species of *Cambridgea* and twelve species of *Huara*), Dictynidae (nine species), and Theridiidae (including katipō, *Latrodectus katipo*). Other families contain wet-adapted species that occur in inland freshwater and saline wetlands. Notable taxa include the *Dolomedes* water spiders (Pisauridae; five described species in New Zealand) that are typically observed by the presence of their prominent nursery webs on emergent vegetation (Yu et al. 2024). They are covered all over in short, hydrophobic hairs that allow them to use surface tension to stand or run on water. They can also submerge to hunt and hide, encasing themselves in a thin film of air trapped by their hairs. Other New Zealand taxa with known adaptations to wet conditions include the four described species of *Tetragnatha* (Tetragnathidae), some of which may walk on water and even attach their webs to water (Gould et al. 2022).

Over 150 species of water mite are known from New Zealand, with several new species recorded from recent sampling of streams throughout the country (Smit & Pešić 2020). However, most sampling has been from permanent water bodies, with little attention paid to water mites in intermittent wetlands. A study of five Waikato streams found that the abundance and diversity of water mites was low or even absent in streams draining from pastures and non-native pine forest (Boulton et al. 1997), suggesting that these taxa might not be ubiquitous across the full range of wetland types and conditions. Moreover, in Germany, water mites were only detected in bogs that had been rewetted for more than 25 years, which was how long it took to develop the habitat complexity required to support their multifaceted life cycle (Więcek et al. 2013). Taken together, these studies suggest that water mites may be better suited as bioindicators of restoration, rather than for delineation (Goldschmidt 2016; Stubbington et al. 2019).

New Zealand has more than 236 described species of freshwater crustaceans, including 41 Branchiopoda (water fleas and tadpole shrimps), 68 Maxillopoda (mostly copepods), 37 Ostracoda (seed shrimps), and 90 Malacostraca (mostly amphipods and isopods) (Webber et al. 2010; Gordon 2013). In a study of 40 minimally disturbed lowland wetlands, 21 crustacean taxa were identified, making up more than 20% of total individuals sampled, and were present at over 88% of sites (Suren & Sorrell 2010). Cladocerans, copepods, and ostracods are frequently detected and abundant in most studies to date (Suren & Sorrell 2010; Suren et al. 2010b; Taura & Duggan 2020), although these have largely analysed water samples from permanently inundated wetlands. An interesting taxon known from intermittent wetlands is the rare and evolutionarily ancient tadpole shrimp (*Lepidurus*). These crustaceans have a cyst phase that can survive desiccation for months or years and that can disperse to new waterbodies by wind or attached to other animals (Thiéry 1997).

New Zealand freshwater molluscs are represented by over 100 species, dominated by snails in the family Tateidae, with at least 68 described species (Spencer et al. 2009; Gordon 2013; Winterbourn 2023). Little systematic research has been published on their distributions in wetlands, but a wide range of native and non-native snails (e.g. *Potamopyrgus* mud snails), filter-feeding bivalves (e.g. fingernail clams, *Sphaerium* and *Pisidium* spp.), and freshwater mussels (e.g. kākahi, *Echyridella menziesi*) have been recorded from a range of wetland classes (Suren & Sorrell 2010; Winterbourn 2023). A survey of 40 wetlands identified at least seven mollusc genera, although their distributions were reported as patchy, with snails noticeably absent in low pH wetlands (e.g. acidic fens), where acidic conditions may affect their ability to obtain enough free calcium for shell maintenance (Suren et al. 2008; Suren & Sorrell 2010).

New Zealand has over 200 earthworm species (Buckley et al. 2015; Kim et al. 2017), including a range of non-native earthworms that are adapted to intermittent wet conditions. However, observations to date are largely incidental reports or based on eDNA, and we lack systematic survey data across a range of wetland classes throughout the country. Yet, recent evidence indicates that earthworms are widespread and common in New Zealand wetlands. For example, research aimed at developing eDNA protocols for biodiversity monitoring in New Zealand wetlands detected Annelida DNA in 93% (215 of 230) of water samples from Opuatia wetland in Waikato (a mosaic of swamps, marshes, and fens) (Bird et al. 2024a). A related study detected Annelida DNA at 23 of 26 sampling sites across a range of wetlands throughout New Zealand (Bird et al. 2024b). The native *Hologynus bipapillatus* lives in anaerobic wet soils, is common in swamps (Lee 1959), and has been observed in acidic peat bogs with a high water table, such as Kopuatai Peat Dome (S. Bartlam, pers. obs.). Densities of up to 250–350 individuals per square metre have been reported at Moanatuatua Scientific Reserve, a North Island peat bog (Luxton 1982), where the non-native Lumbricid earthworm *Allolobophoridella eiseni* (Levinsen, 1884) has also been recorded (S. Bartlam, pers. obs.). Several non-native earthworms are adapted to intermittent inundated conditions that are commonly found in wetlands. For example, *Octolasion tyrtaeum*, *Amynthas corticis*, and *Lumbricus rubellus* were found in a Waikato intermittent marsh (Bartlam 2017), and *Allolobophora chlorotica*, *Octolasion cyaneum*, and *Aporrectodea caliginosa* have all been found in Bay of Plenty, Hawke's Bay, and Waikato intermittent wetlands (S. Bartlam, pers. obs.). A study of sheep and dairy farms in the Waitaki Basin found that the density and biomass of three non-native earthworm species (*A. caliginosa*, *L. rubellus*, and *Aporrectodea longa*) increased in irrigated compared to non-irrigated sheep and dairy pastures (Manono & Moller 2015), indicating the adaptation of these species to wet soils.

New Zealand has eleven species of leech (Govedich 2001), all of which are adapted to wet conditions. Many occur in wetland habitats, such as Glossiphoniidae, which are common in slow-flowing, weedy streams and ponds, particularly in farmland. New Zealand has over 78 freshwater species of Platyhelminthes (flatworms), mostly consisting of flukes (42 species) and tapeworms (17 species) of freshwater primary (e.g. fish) or intermediate hosts (e.g. aquatic snails) (Gordon 2013). However, their general diversity, distribution, and ecology remains poorly known, including as regards taxa found in wetlands. Finally, New Zealand has six known species of freshwater horsehair worm that infect a range of hosts (Yadav et al. 2018; Doherty et al. 2022), but relatively little is known about their distribution, including their occurrence in wetlands.

Meiofauna

Meiofauna comprise a highly diverse group of very small invertebrates that overlaps taxonomically with macroinvertebrates and includes taxa such as copepods, rotifers, nematodes, tardigrades, and mites. Many meiofauna require wet conditions, but often at a microhabitat scale (e.g. wet films or waterlogged soil rather than open water), rendering them potentially overlooked as wet-adapted species. These taxa possess a range of morphological, physiological, and behavioural adaptations to wet conditions that include feeding and locomotion structures, obligate lifecycles in wet areas, and excretory systems that require wet conditions to function. Many taxa also possess adaptations against desiccation and other stressors that allow them to persist in areas that are only intermittently wet. These persistence adaptations are important because these animals may still be detectable during dry conditions or after habitat modification (e.g. drainage or infilling), although this hypothesis requires testing in the field. In the following paragraphs, we highlight key groups of wet-adapted meiofauna that are likely to be ubiquitous in New Zealand wetlands, including those that are periodically dry.

Meiofauna adaptations to wet conditions

Rotifers (phylum Rotifera) are a widespread but often overlooked member of the meiofauna. They occur in various aquatic habitats, from temporary puddles to permanent water, and are characterised by their feeding apparatus, a ciliated structure called a corona. This structure contains many hundreds of small hairs (cilia) that are used to create water currents that move food particles and allow them to filter feed in wet conditions (Wallace et al. 2006). Rotifers also have a life cycle stage that produces resting eggs, which comprise an encysted embryo that can remain dormant for many years (Gilbert 2016). This adaptation permits persistence in intermittent wetlands (Walsh et al. 2014), including in extreme conditions from the Chihuahuan Desert (Wallace et al. 2005) to Antarctica (Wada et al. 2023).

Nematodes (phylum Nematoda) are the most abundant multicellular animal on earth (Bardgett & van der Putten 2014). There are both parasitic and free-living forms, with the latter occurring widely in soils and freshwater environments, among other habitats. All nematodes are essentially aquatic animals that require water to live and move, inhabiting the wet films around particles when they occur in soils (Neher 2010). They possess a hydrostatic skeleton that supports the nematode body via fluid pressure, such that low water content may severely limit their motility and survival (Grant & Villani 2003; Neher 2010). However, some nematodes are highly tolerant of starvation, desiccation, and other extreme environments, including the atmospheric breakup of spacecraft (Szewczyk et al. 2005). They can also enter a state of suspended metabolism called cryptobiosis, with a previously undescribed species recently being reanimated after 46 000 years in the Siberian permafrost (Shatilovich et al. 2023). Nematodes have also been shown to be resilient to wetland modification. For example, several soil-inhabiting species had higher density in drained compared to natural fens in Poland, including up to 117 years after drainage (Wasilewska 2006).

Tardigrades (phylum Tardigrada, also known as water bears) are eight-legged segmented animals that can be found almost anywhere there is liquid water, including on soil, leaf litter, freshwater sediments, lichens, and mosses (Nelson 2002). Most species are in the meiofauna size category, although some qualify as macroinvertebrates. Like rotifers and nematodes, all tardigrades are aquatic, requiring a film of water around the body to be active. However, they can survive desiccation through cryptobiosis, where they suspend their metabolism and wait for favourable conditions to return (Nelson 2002). Indeed, tardigrades are famous for being extraordinarily resilient to environmental extremes, including several years of dehydration (Guidetti & Jönsson 2002), extreme temperatures (including decades at −20 °C; Tsujimoto et al. 2016), pressures (from the vacuum of space to the bottom of the Marianas Trench; Seki & Toyoshima 1998; Jönsson et al. 2008), and radiation (Horikawa et al. 2009).

Meiofauna communities of New Zealand wetlands

Despite their widespread distributions, meiofauna have been historically under-represented in studies of aquatic invertebrates from New Zealand wetlands, mostly because these smaller animals pass through the mesh of the sampling equipment routinely used to collect macroinvertebrates. However, the few wetland studies that have sampled for meiofauna found that these animals make a substantial contribution to overall wetland biodiversity (Suren et al. 2010b).

Over 450 rotifer species have been recorded in New Zealand (Shiel & Green 1996; Shiel et al. 2009), but very few studies have examined rotifer diversity in wetlands. However, 78 rotifer species were recorded from water samples from 31 North Island lakes, at an average of 21 species per lake, reflecting the high prevalence and diversity of rotifers in wet environments (Duggan et al. 2002). More recently, eighteen rotifer taxa, including a previously unrecorded species, were identified from 38 water samples collected from 21 sites in a Taupō wetland complex (Taura & Duggan 2020). The occurrence and detectability of rotifers in intermittent wetlands during dry periods has yet to be investigated in New Zealand, including the potential for detection of the resting egg stage from soil eDNA. However, international studies strongly suggest that rotifers are likely to be present in these environments (Walsh et al. 2014), while a recent study from Opuatia wetland detected Rotifera in 93% of 230 samples (Bird et al. 2024a).

Nematodes are a diverse and understudied group in New Zealand, with over 650 taxa recorded and more undescribed (Yeates et al. 2012). Despite a lack of systematic sampling, it is likely that nematodes are ubiquitous and abundant in New Zealand wetlands. For example, they were detected in water samples from 90% of 82 surveyed South Island wetlands and made up almost 6% of the total invertebrates (Suren et al. 2010b). Nematodes are not restricted to wet conditions; a global analysis of 6825 soil samples found an average of 2671 nematodes (and up to 20 000) per 100 g of dried soil (van den Hoogen et al. 2020). This study did not explicitly include wetland soil samples, although samples from flooded grasslands ($n = 7$) did have the lowest nematode abundance (183 per 100 g dry soil).

Over 90 species of tardigrade have been recorded from New Zealand (Horning et al. 2010), including several species that occur within glacier ice (Zawierucha et al. 2023). However, very little is known about New Zealand tardigrade distributions, especially in wetlands, where they have been recorded in low abundance but are usually not identified to lower taxonomic levels (Suren & Sorrell 2010; Suren et al. 2010b).

The delineation and animals of challenging wetlands

New Zealand wetlands are diverse ecosystems with multiple classes of habitat defined by their substrate, water regime, nutrient status, and pH (Johnson & Gerbeaux 2004). Open water wetlands (e.g. swamps) are perhaps the best known, and the existence of wet-adapted animals in them is beyond doubt. However, many wetland types are characterised by intermittent wetness and dryness, including ephemeral wetlands (Fig. 2a), marshes, seepages (Figs. 2b & 2c), pakihi, gumlands, saltmarsh, and wetlands that have been drained or infilled (Figure 2d). These intermittent wetland classes can be more challenging to delineate than permanent wetlands, are less obviously perceived as wetlands by non-experts, have received relatively little research attention, are vulnerable to habitat modification, and in consequence are frequently subject to unlawful development requiring enforcement action. The hydrological and ecological differences among wetland classes likely have important implications for what, where, and when animals can be detected in each wetland, although comparative studies are largely missing from the literature.

One consideration is that intermittent wetlands may only support wet-adapted animals during the winter season or after persistent wet weather. However, given the ubiquity of meiofauna and the tolerance of some taxa to periodic drought (e.g. water mite cysts, rotifer resting eggs, mudfish emersion tolerance), we consider that some wet-adapted animals are likely to still be present during dry conditions. This notwithstanding, outside of wetter periods, these wetlands may be difficult to sample, and it may prove challenging to gain conclusive evidence as to animal composition. It is therefore important that any sampling protocol developed to detect wet-adapted animals should be likely to succeed in intermittently wet areas, and that the timing of sampling is carefully considered where possible. We suggest that future

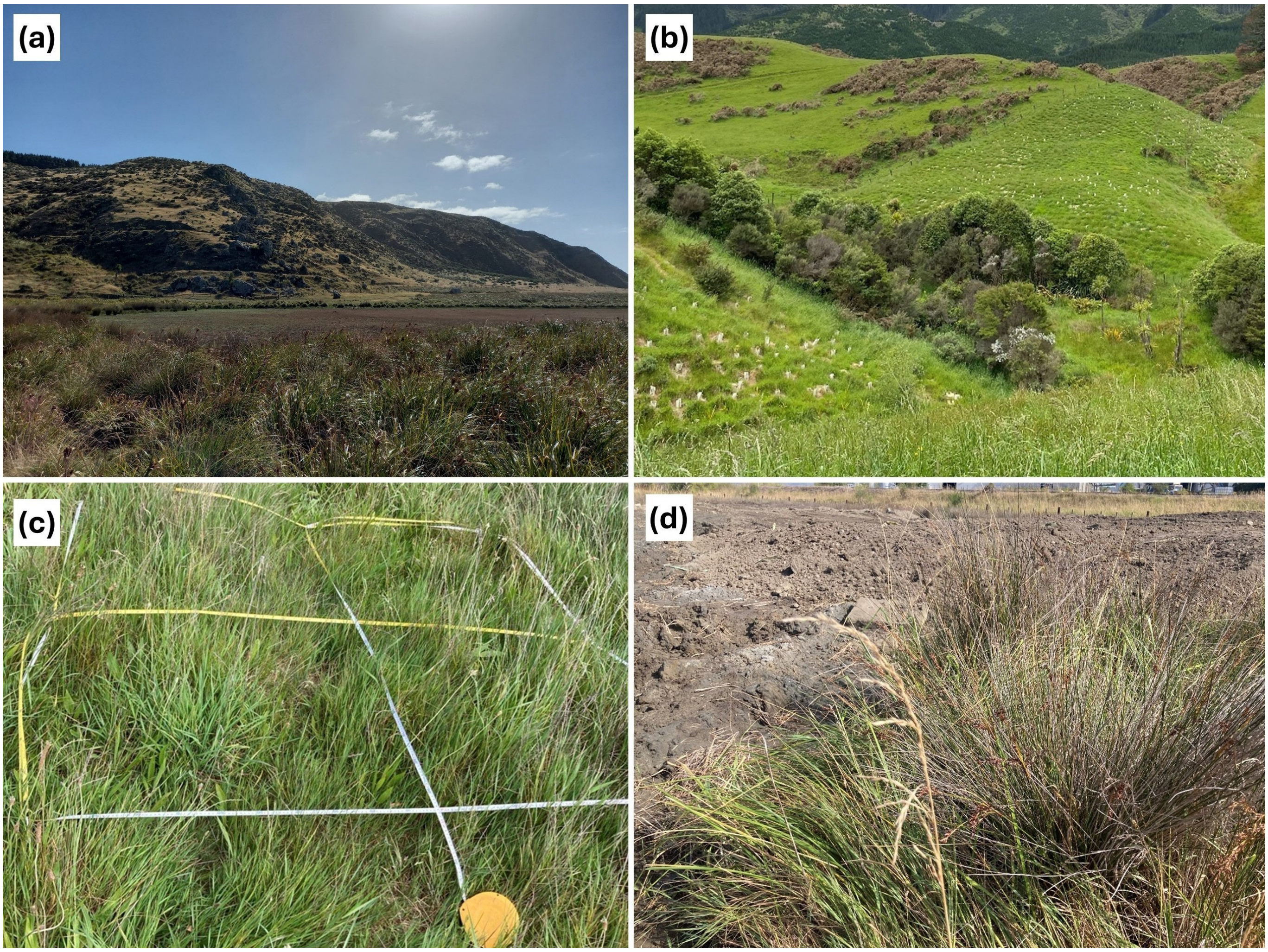

Figure 2. (a) Ephemeral wetland on a coastal terrace in the Wellington Region. This site is intermittently wet, with turf plant species occupying dry mineral soils throughout the summer. (b) Hill country seepage wetland in the Wellington Region where surface water fluctuates from 55 cm below the soil surface (2019) to surface level (2024). Vegetation is dominated by non-native grass and herbs, such as *Holcus lanatus*, *Erythranthe guttata*, and *Lotus pedunculatus*. (c) Marsh wetland near Lincoln in the Canterbury Region that is dominated by the facultative wetland grass *Agrostis stolonifera* (70% cover) and does not meet the pasture exclusion protocol. (d) Infilled saltmarsh wetland in the Hawke's Bay Region, where habitat destruction could make it challenging to confirm the presence of wet-adapted animals. This site was formerly a sea rush (*Juncus kraussii*) and glasswort (*Salicornia quinqueflora*) dominated saltmarsh. Photo credits: (a), (b): Helen White. (c): Paula Godfrey. (d): Annabel Beattie.

research should focus on characterising the wet-adapted invertebrate communities of these challenging wetlands to further strengthen the evidence base for the ubiquitous presence of wet-adapted animals. Furthermore, it would also be useful to assess animal occurrence in drained or infilled wetlands across both temporal and degradation severity gradients to clarify the limits to detection of wet-adapted animals after wetland modification.

Implications for wetland delineation and policy enforcement

The need to satisfy the Court beyond reasonable doubt in criminal cases that wet-adapted animals are supported by the putative wetland may affect council decisions to undertake enforcement action for unauthorised wetland damage or clearance. This is a different standard of proof than that which applies in non-criminal proceedings. If the same requirements were applied outside of the criminal context, the costs associated with wetland mapping, investigation, and monitoring for plan development and resource consenting would increase for applicants, submitters, and councils. Requiring field evidence of animals for wetland delineation is challenging because many wet-adapted animal species are difficult to detect, due to being small, cryptic, nocturnal, transient, or subterranean, and require expert identification. Regional-scale wetland mapping, as required of councils under the NPS-FM, also cannot detect the presence of most wet-adapted animals, as this mapping technique usually involves interpretation of remotely sensed information (e.g. vegetation cover, wetness indices) (Bartlam & Burge 2024; Martin et al. 2024).

On the balance of the information reviewed in this paper, there is strong support for the proposition that wet-adapted animals, particularly meiofauna, are ubiquitous and will therefore inevitably be present in all wetlands that satisfy the definition of wetlands in the RMA 1991 (and current wetland delineation protocols, including soils and hydrology) (Ministry for the Environment 2024). This is the same line of reasoning that was accepted by the Court of Appeal (*Page v Greater Wellington Regional Council* [2024] NZCA 51) for permanently inundated wetland areas and aquatic invertebrates. It is therefore arguable that in light of the evidence presented in this review (which was not before the Court, as it post-dates the decision), field evidence should not be required to demonstrate the presence of wet-adapted animals, which are ubiquitous even in wetlands that are not permanently inundated. However, we equally acknowledge that our reasoning and the information in this review has not been the subject of a Court of Appeal judgement, and therefore the exact evidence required to satisfy the criminal standard of proof is a question yet to be fully tested in a legal setting. Despite this, we contend that the current wetland delineation protocols will accurately identify wetlands that satisfy the RMA definition, and that the evidence in this review provides a solid basis for any future policy guidance around New Zealand wetlands.

At the other end of the evidentiary scale, the Court could require site-specific physical evidence for any enforcement of regulations involving wetlands. In such an event, it is unclear what would satisfy the Court as evidence of the presence of animals adapted to wet conditions and supported by wetlands, but we propose the following forms of evidence in order of robustness: a physical sample (preserved specimen), third party verification (e.g. specialist species identification or laboratory results of eDNA samples), geo-tagged and time-stamped photographs, time-stamped audio recordings, and/or data on a wetland monitoring datasheet provided by a suitably qualified specialist. Furthermore, the tension between the RMA definition and the broader ecological perspective of wetlands could be resolved if animals that are indirectly adapted to wet conditions (i.e. Fred the Thread, Australasian harrier, fernbird) were accepted as evidence within the RMA definition. Ultimately, the requisite burden of proof will be pertinent to the design of any protocols to assess the presence of wetland animals.

Despite our comfort with the proposition that all wetlands are almost certain to support wet-adapted animals, in the case that a council wished to further strengthen the evidential basis for a prosecution, we recommend that they only sample for animals if in a criminal setting and after wetland delineation protocols have been applied and a wetland is considered to exist (Ministry for the Environment 2022a). Where councils choose to undertake animal sampling for disputes, enforcement, or prosecutions, we consider that the most widespread and cost-effective taxa to sample using current methods are nematodes and earthworms. In the absence of clear national guidance on sampling these taxa for enforcement purposes, we offer some interim sampling guidelines (Manaaki Whenua – Landcare Research datastore: https://doi.org/10.7931/q23y-d559). Different methods should be used where councils choose to undertake animal sampling for other purposes, such as characterising biodiversity or quantifying ecological integrity (e.g. Bird et al. 2024a).

Overall, we posit that animals adapted to wet conditions are ubiquitous across all New Zealand wetlands where the current wetland delineation protocols have been satisfied, including intermittent wetlands, wetlands with wet but not inundated soils, and degraded wetlands. If it is accepted that wet-adapted animals are ubiquitous in delineated wetlands, sampling for animals would not be required for wetland delineation or enforcement. In other words, application of the current wetland delineation protocols and reference to the ubiquity of wet-adapted soil invertebrates should satisfy the RMA requirement that a wetland supports animals adapted to wet conditions.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Examples of adaptations to wet conditions in New Zealand bird species, and the types of support that they are provided by wetland habitat.

Appendix S2. Coincidence of 28 non-diadromous *Galaxias* and *Neochanna* taxa with mapped hydric soils. Reprinted with permission from Dunn (2024).

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