

REVIEW

Current knowledge and potential impacts of climate change on New Zealand's biological heritage

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Abstract: While global climate change is impacting biota across the world, New Zealand's maritime climate is highly variable and relatively mild, so climate change is sometimes seen as a minimal threat to species and ecosystems especially in comparison to the more immediate threat of invasive species. However, climate change will alter rainfall patterns, increase the incidence and severity of extreme events, and gradually increase temperatures which will all modify terrestrial, freshwater, and marine systems. Our comprehensive review of reported climate change impacts in New Zealand indicates that most measured impacts to date are due to indirect impacts (such as exacerbation of invasive species impacts) and most are in the marine realm. Ocean acidification and marine heatwaves are particularly problematic for calcareous organisms and algae respectively. Other notable impacts include thermal squeeze in the alpine zone and impacts of drought on freshwater fish. Very small populations of rare and threatened species can be very vulnerable to extreme events (e.g. fire, floods). While the evidence for climate change impacts is sparse in some regions and for some ecosystems, we encourage ongoing monitoring to identify processes of decline that may need to be mitigated. We identify five key research needs to improve our understanding of the threat of climate change to the biodiversity of Aotearoa New Zealand.

Keywords: biodiversity, extreme events, global change, global warming, invasive species, ocean acidification, sea level rise

Introduction

Climate change is causing increased air and ocean temperatures, sea-level rise, increased atmospheric concentrations of CO₂, changes in precipitation, and reduction in snow and ice cover (McGlone et al. 2010; Lundquist et al. 2011; Stocker et al. 2013; Hendy et al. 2018), causing observable impacts on biodiversity on a global scale (Parmesan & Yohe 2003; Root et al. 2003; Dawson et al. 2011; Rosenzweig et al. 2008). There is a high risk of extinctions of endemic species in biodiversity hotspots across the world (Malcolm et al. 2006) because of direct and indirect impacts of climate change. Furthermore, sub-lethal impacts on species physiology and ecological interactions are causing declines in ecosystem functions (Dawson et al. 2011).

Aotearoa New Zealand is one of the three regions most susceptible to extinction risks as a result of climate change because of a large proportion of endemic species with small population and range sizes (Urban 2015). However, datasets describing modern climate change impacts for New Zealand are rare compared to the available information for northern hemisphere species and ecosystems (Lundquist et al. 2011; Cabrelli et al. 2015). Perhaps because of the scarcity of data, there is uncertainty about the extent and variability of

effects that have been observed in New Zealand (Lundquist et al. 2011; McGlone & Walker 2011; Christie 2014) but McGlone et al. (2010) concluded that there is no evidence of changes in biodiversity over the last hundred years that can be definitively ascribed to global warming as opposed to climate variability. As these reviews are up to ten years old, and given the growing national concern around climate change impacts on New Zealand ecosystems, a new review and synthesis is timely.

In this review, we focus on both measured and predicted effects on New Zealand species and ecosystems associated with climate change. We used Google Scholar to search combinations of the terms climate change, New Zealand, species, biota, marine, terrestrial, freshwater, birds, soil, temperature, sea-level rise, alpine, warming, and ocean acidification (OA). Using Google Scholar allowed us to capture work that is outside standard journal articles, such as MacDiarmid et al. (2012), Christie (2014), and Ministry for Primary Industries (2016). We also looked at texts that cited relevant search results for a more comprehensive scoping of the literature. The emphasis was on effects on New Zealand endemic and native species within New Zealand and its surrounding exclusive economic zone, but we include reference

to effects on species that occur in New Zealand and have been studied elsewhere where appropriate.

Future climate projections for New Zealand are complicated by the highly variable maritime climate and complex topography. Details of changes in temperature, precipitation patterns, wind, storms, and other climate factors are expanded in regional modelling produced by Ministry for the Environment (2016) and Ministry for the Environment and Stats NZ (2020) with some additional context provided by Hopkins et al. (2015). While considering past climates is important for understanding potential impacts of future climate change (McGlone et al. 2010; McGlone & Walker 2011), we confine the scope of this review to current and future climate because interacting factors such as invasive species and habitat fragmentation were not a feature of past climates (Macinnis-Ng et al. 2021).

We found numbers of publications related to climate change impacts on New Zealand's biodiversity have been increasing since 1981 with a general trend towards more research on effects of climate change and its drivers on New Zealand's biological heritage (Fig. 1). This increase in published research indicates a heightened interest in understanding climate change and how it impacts native and endemic species and ecosystems across marine, freshwater, and terrestrial environments.

Coastal and marine environments

Climate change impacts in marine environments include lower ocean productivity, changes in food web interactions, decreasing populations of habitat-forming species, range shifts, and higher incidence of disease (Hoegh-Guldberg & Bruno 2010). Elevated atmospheric CO₂, air and water temperature, available oxygen and nutrients, and ocean acidification all modify the marine environment (Doney et al. 2012). By 2100, New Zealand's marine environment will have decreased surface mixed layer depth, pH, chlorophyll-a concentration, net primary production, and particle export as a result of climatic change (Law et al. 2018). Sea level rise, ocean warming, and ocean acidification are the three most influential processes (Table 1).

Average global sea level rise is 20 cm over the last century (Miller & Douglas 2004), making our coastal cities and habitats particularly vulnerable (Foley & Carlines 2019). Melting glaciers and polar ice sheets and expansion of warming water combine in a two-factor process to cause rising sea levels (Miller & Douglas 2004). Vulnerable coastal habitats include dunes, estuaries, marshlands, beaches, intertidal reefs, mudflats, lagoons, shallow lakes, and offshore islands. Mangrove, seagrass, macrophyte communities, and the associated seabirds, fish, and invertebrates are impacted

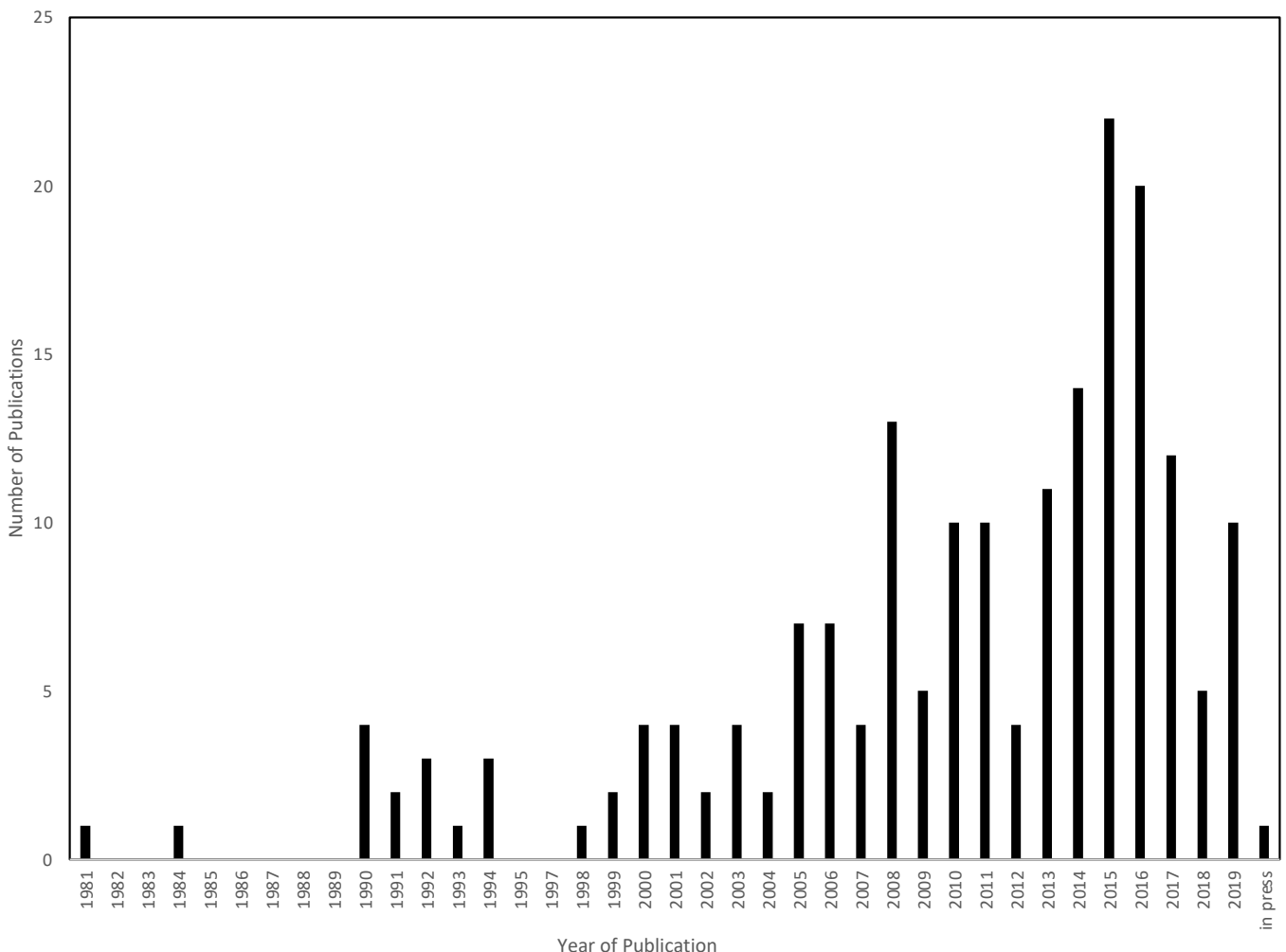


Figure 1. Number of studies relating to New Zealand species and habitats and effects of climate change from 1981 to 2019. Papers included in this figure specifically relate to studies in Aotearoa New Zealand.

Table 1. Examples of climate change impacts in the marine realm of Aotearoa New Zealand.

Climate change process	Ecosystem or species impacted	Type of evidence (field observations, manipulative experiment, modelling etc.)	Mechanism of impact	References
Sea level rise	Mangrove ecosystems	Field observations	Sea-level rise and warming favour mangrove (<i>Avicennia marina</i>) habitat expansion, but ongoing sea-level rise may limit expansion causing coastal squeeze.	Swales et al. (2008), Alongi (2008), Morrisey et al. (2010)
Sea level rise	Whitebait species	Field observations	Whitebait are at risk due sea level rise as the shrinking spring tide zone is essential for spawning.	Burns et al. (1990)
Sea level rise	Shore birds - Shore plover (<i>Thinornis novaeseelandiae</i>), fairy terns (<i>Sternula nereis</i>), Caspian terns (<i>Hydroprogne caspia</i>), black-billed gulls (<i>Chroicocephalus bulleri</i>), and black petrels (<i>Procellaria parkinsoni</i>)	Field observations	Loss of nesting sites due to rising shorelines, and storm surges.	Christie (2014), Whitehead et al. (2019)
Ocean warming	Red moki (<i>Cheilodactylus spectabilis</i>)	Field observations	Stunted growth at warmest edge of distribution, potentially resulting in range reduction.	Neuheimer et al. (2011)
Ocean warming	Sea urchins (<i>Evechinus chloroticus</i>)	Laboratory manipulative experiment	Sea temperatures elevated 3-4 °C caused abnormal development in early growth phases potentially reducing survival and range.	Delorme and Sewell (2013)
Ocean warming	Microphallid (<i>Maritrema novaeseelandensis</i>) parasitising the mudsnail (<i>Zeacumantus subcarinatus</i>)	Field observations, manipulative experiment, simulation modelling	Increased incidence of trematode infection in intertidal communities as water warms.	Poulin and Mouritsen (2006)
Ocean warming	Elephant seal (<i>Mirounga leonina</i>)	Field observations	Macquarie Island population decline attributed to ocean warming but specific drivers are unknown.	Baker et al. (2010)
Ocean warming	Sub-Antarctic diatom (<i>Pseudonitzschia multiseriata</i>)	Manipulative experiment	Enhanced growth with increased warming and iron under conditions predicted by 2100.	Boyd et al. (2015)
Ocean warming	Yellow-eyed penguin (<i>Megadyptes antipodes</i>)	Field observations	Population declines on Otago Peninsula strongly correlated with declining productivity due to changes in rainfall and sea surface temperature.	Peacock et al. (2000)
Ocean warming	Declines of southern (<i>Eudyptes chrysocome</i>) and eastern rockhopper (<i>Eudyptes chrysocome filholi</i>), and erect-crested (<i>Eudyptes sclateri</i>) penguin	Field observations	Decline of populations on Campbell Island and Antipodes Islands tied to warming surface waters.	Cunningham and Moors (1994), Hiscock and Chilvers (2014)
Ocean warming	Little penguins (<i>Eudyptula minor</i>)	Field observations	Breeding success tenuously related to climatic fluctuations, but clear susceptibility to both warming and sea-level rise in Wellington.	Perriman et al. (2000), Rastandeh et al. (2018)
Ocean warming	Australasian gannet (<i>Morus serrator</i>)	Field observations	Population growth associated with higher sea surface temperatures and greater ENSO activity increasing prey availability.	Bunce et al. (2002)
Sea surface temperature anomaly	Gannet (<i>Morus serrator</i>)	Field observations	Sightings in the Hauraki Gulf linked to regional sea surface anomaly.	Srinivasan et al. (2015)
Ocean warming	Sooty shearwater (<i>Ardenna grisea</i>)	Field observations	Population decline concurrent with rising sea temperatures that could affect ocean productivity.	Veit et al. (1997), Shaffer et al. (2006)

Table 1. Continued.

Climate change process	Ecosystem or species impacted	Type of evidence (field observations, manipulative experiment, modelling etc.)	Mechanism of impact	References
ENSO events	Sooty shearwater (<i>Ardenna grisea</i>)	Field observations	Lower abundance occurring prior to an El Niño Southern Oscillation (ENSO) event.	Lyver et al. (1999), Shaffer et al. (2006), Humphries and Möller (2017)
Pacific Decadal and ENSO cycles	Red-billed gulls (<i>Chroicocephalus novaehollandiae scopulinus</i>)	Field observations	Population declines between 1983 and 2003, linked to changes in Pacific decadal oscillation and ENSO.	Mills et al. (2008, 2018)
Storm events	Little penguin (<i>Eudyptula minor</i>)	Field observations and inference	High waves events prevented return to shore and reduced survival in Ōamaru, also evidence of ocean productivity declines causing earlier egg laying.	Agnew et al. (2015)
Marine heat waves	Bull kelp forest (<i>Durvillaea</i> spp.)	Field observations	Local extinction of bull kelp due to marine heat wave across several South Island sites.	Thomsen et al. (2019), Thomsen and South (2019)
Warmer air	Green-lipped mussels (<i>Perna canaliculus</i>)	Reciprocal transplants	Reduced survival, growth and reproduction in warmer air could cause shifts in intertidal assemblage.	N. Ragg unpubl. data in Law et al. (2017)
Warmer air	Mangroves (<i>Avicennia marina</i>) and seagrasses (<i>Zostera muelleri</i>)	Field observations and inference	Southward spread of mangroves due to warmer air encroaches on seagrass meadows.	Burns et al. (1990), Morrisey et al. (2010)
Lower salinity	Sea urchin (<i>Evechinus chloroticus</i>)	Manipulative experiments	Warming from 18°C to 21°C lessened detrimental effects of lowered salinity on embryo survival.	Delorme and Sewell (2014)
Ocean acidification	Green-lipped mussels (<i>Perna canaliculus</i>)	Manipulative experiment	Stunted development and construction of first shell when exposed to high or low pH.	N. Ragg unpubl. data in Law et al. (2017)
Ocean acidification	Juvenile pāua (<i>Haliotis iris</i>)	Manipulative experiment	Decreased growth and shell deposition and shell had higher metabolic energy needs under low pH.	Cunningham et al. (2016), Law et al. (2017)
Ocean acidification	Flat oysters (<i>Ostrea chilensis</i>)	Manipulative experiment	Reduced growth under lowered ocean pH.	Law et al. (2017), Ministry for Primary Industries (2016), Pearce et al. (2016)
Ocean acidification	Pacific and rock oysters (<i>Crassostrea gigas</i> and <i>Saccostrea glomerata</i>)	Manipulative experiment	Both species have significantly lower fertilisation success with elevated pCO ₂ levels.	Gazeau et al. (2013)
Ocean acidification, sea level rise	Cockle (<i>Austrovenus stutchburyi</i>) and pipi (<i>Paphies australis</i>)	Expert assessments	A range of climate change processes will impact on these mahinga kai species.	MacDiarmid et al. (2012)
Ocean acidification	Mudsnails (<i>Zeacumantus subcarinatus</i>)	Manipulative experiment	Reduced survival, growth and shell strength after exposure to lower pH for 90 days.	MacLeod and Poulin (2015, 2016a, 2016b)
Ocean acidification	Trematode infection in shellfish	Manipulative experiment	Mudsnails infected by parasitic trematodes were only minimally affected by lowered pH but uninfected individuals suffered greater mortality.	Law et al. (2017), MacLeod and Poulin (2015, 2016a, 2016b)
Ocean acidification	Paper nautilus (<i>Argonauta nodosa</i>)	Manipulative experiment	Females produce a thin calcium carbonate brood chamber which has reduced mass under high pH.	Wolfe et al. (2012)
Ocean acidification	Sub-Antarctic free-swimming molluscs (<i>Pteropods</i>)	Interpolation from Artic pteropods	Population declines in sub-Antarctic waters are predicted due to acidification.	Comeau et al. (2010)
Ocean acidification	Gastropod (<i>Eatoniella mortoni</i>)	Field observations	Higher abundance at volcanic vents approximating predicted future CO ₂ levels due to more algal biomass as available food.	Connell et al. (2017)

Table 1. Continued.

Climate change process	Ecosystem or species impacted	Type of evidence (field observations, manipulative experiment, modelling etc.)	Mechanism of impact	References
Ocean acidification	Sea urchins (<i>Evechinus chloroticus</i> and <i>Pseudechinus huttoni</i>)	Manipulative experiment	Reduced survival, smaller larvae, significantly reduced skeletal calcification, and damaged larval skeletons at reduced pH.	Clark et al. (2009)
Ocean acidification x ocean warming	Sea urchin (<i>Centrostephanus rodgersii</i>)	Manipulative experiment	Development success declined under lowered pH but increasing temperature likely to allow range expansion by dampening the effect of acidification on development.	Byrne et al. (2013a); Pecorino et al. (2014)
Ocean acidification x ocean warming	Cushion star (<i>Patiriella regularis</i>)	Manipulative experiment	Combined effects of warming and acidification increased mortality, and impeded larval size and development.	Petes et al. (2007), Byrne et al. (2013b)
Ocean acidification	Larvae of cake urchin (<i>Fellaster zelandiae</i>)	Manipulative experiment	Smaller size at the larval stage caused by OA.	Karelitz et al. (2017)
Ocean acidification	Colonial coral (<i>Solenosmilia variabilis</i>)	Manipulative experiment	Skeletal loss and reallocation of energy resources under OA.	Gammon (2016)
Ocean acidification	Kingfish (<i>Seriola lalandi</i>)	Manipulative experiment	Decreased oil globule diameter and potential vulnerability to declining food availability due to OA.	Munday et al. (2016), Law et al. (2017)
Ocean acidification	Common triplefin (<i>Forsterygion lapillum</i>) and other fishes at vents	Field observations	At seafloor CO ₂ seep at White Island and thermal vents, common triplefin had behaviour change and overall fish diversity declined at lower pH.	Nagelkerken et al. (2015)
Ocean acidification	Bacterial enzyme activity	Manipulative experiment	The enzyme leucine aminopeptidase broke down at an increased rate which could affect availability of nutrients and food quality under OA.	Burrell et al. (2017)
Ocean acidification	Coccolithophores (<i>Emiliana huxleyi</i>)	Manipulative experiment	Altered particulate carbon production under decreased pH.	Feng et al. (2016)
Ocean acidification	Cyanobacteria (<i>Synechoccus</i> sp. and <i>Trichodesmium</i> sp.)	Manipulative experiment	Changes in abundance (<i>Synechoccus</i>) and nitrogen fixation rates (<i>Trichodesmium</i>).	Riebesell (2004), Burrell et al. (2017), Law et al. (2017)
Ocean acidification	Coralline algae	Field observations	At natural CO ₂ vents at White Island, loss of coralline algae abundance could have significant impacts on rocky reef function in coastal ecosystems.	Hall-Spencer et al. (2008), Brinkman and Smith (2015)
Ocean acidification	Calcifying coralline algae (<i>Arthrocardia corymbosa</i>)	Manipulative experiment	Reduced growth under reduced and fluctuating pH.	Cornwall et al. (2013, 2014)

due to increased erosion, tidal inundation and decreasing light levels (Table 1) in addition to other human impacts such as sedimentation, eutrophication, and pollution (Lundquist et al. 2011; McGlone & Walker 2011; Spence 2011; MacDiarmid et al. 2012; Rouse et al. 2017; Suyadi et al. 2019).

Ocean warming includes gradual increases in seasonal means and ocean heat waves. New Zealand's surrounding ocean has warmed in the last 36 years with the largest increases in temperature east of Wairarapa (Sutton & Bowen 2019). Warming oceanic temperatures impact fish, invertebrates, seaweeds, mangroves, and marine mammals (see Table 1 for details). Fish physiology may respond as timing of spawning,

egg development rates, and species distribution are all likely to change (McDowall 1992). However, not all species respond negatively to climate change as the sub-Antarctic diatom *Pseudonitzschia multiseries* shows enhanced growth with increased warming and iron under conditions predicted by 2100 (Boyd et al. 2015).

As atmospheric CO₂ concentrations have increased, the carbon balance of oceans has also changed with CO₂ accumulated in surface waters lowering the pH, ocean acidification (OA), and carbonate availability (Orr et al. 2005; Kleypas et al. 2006; Boyd & Law 2011). This results in reductions in survival, calcification, growth, development,

and population sizes of marine biota particularly calcifying taxa (including plankton, corals, and molluscs) (Fabry 2008; Hofmann et al. 2010; Kroeker et al. 2013; Tracey et al. 2013). However, impacts can be species-specific; Ries et al. (2009) studied 18 different marine calcifiers, encompassing biota that produced different forms of calcium carbonate, and found a mixed response to increased $p\text{CO}_2$ (10 showed lower net calcification, seven increased their calcification, and one showed no reaction).

Within New Zealand, the impact of OA is already observable for microbes, macroalgae, lophophorates, sponges, corals, molluscs, echinoderms, and fish (Turley 2006; Lundquist et al. 2011; Law et al. 2017). Of these, molluscs are one of the groups most vulnerable to OA (Kroeker et al. 2013), with major impacts on juveniles of different species (Law et al. 2017). Many molluscs impacted by OA are mahinga kai species such as cockle *Austrovenus stutchburyi* and pipi *Paphies australis* (Table 1), but for species like pāua *Haliotis iris* the mechanisms are complicated and the details of impacts are still emerging (Hurd et al. 2011).

Echinoderm sensitivity to OA is linked to their magnesium calcite endoskeletons and inability for their acid-base balance to accommodate lowered pH (Miles et al. 2007; Smith et al. 2016). While there are several examples of echinoderms being influenced by OA (Table 1), vulnerability to OA is variable between species. For instance, the adult stage of *E. choloroticus* may have some resilience to OA as they experience natural fluctuations of pH due to their own respiration and calcification (Hurd et al. 2011).

Corals of cold and deep waters will also be susceptible to OA (Guinotte et al. 2006; Lundquist et al. 2011; Law et al. 2017). Lower pH will not only reduce the capacity of deep-sea scleractinian and gorgonian corals to produce skeletons, but also reduce how much suitable habitat they create for other marine biota (Tracey et al. 2013). Temperate and subtropical shallow-water corals such as those found in the Kermadec region may also be substantially impacted by OA through decreased calcification and increased carbonate dissolution rates (Law et al. 2017). Not all calcifying corals may be negatively impacted by lower pH; widespread deep-sea species *Solenosmilia variabilis* showed no growth difference under projected lower pH compared to current levels, although a loss of skeletal colouration was ascribed to tissue loss and potentially due to reallocation of energy resources (Gammon 2016). Further, many cold-water corals can withstand some amount of aragonite undersaturation, even though coral distribution is highly dependent on aragonite and calcite saturation states (Tracey et al. 2013; Bostock et al. 2015).

Increased partial pressure of carbon dioxide can induce behavioural and neurosensory responses in fish (Heuer & Grosell 2014; Munday et al. 2016; Nagelkerken et al. 2017); however, New Zealand studies are confined to kingfish *Seriola lalandi*, common triplefin *Forsterygion lapillum*, and thermal vent fish communities (Law et al. 2017) as described in Table 1.

Microbes (bacteria, phytoplankton, cyanobacteria) are prone to impacts from OA (Riebesell 2004; Burrell et al. 2017; Law et al. 2017; Table 1). Lower pH accelerated bacterial extracellular activity of New Zealand species (Burrell et al. 2017) while phytoplankton may benefit from elevated dissolved inorganic carbon with enhanced productivity increasing biomass (Law et al. 2017). However, calcifying phytoplankton may suffer from lowered carbonate ion saturation with decreased capacity for plate production and maintenance (Riebesell 2004; Law et al. 2017). Other studies in New Zealand

waters found that higher CO_2 and acidification did not affect competition in a mixed diatom community, or among benthic diatoms and coralline algae (Tatters et al. 2013; James et al. 2014; Roleda et al. 2015).

For macroalgae, there are records of OA impacts for coralline algae and kelps (Table 1). Much of the research focuses on natural CO_2 vents at White Island where pH, temperature and dissolved oxygen conditions are comparable to projected future ocean conditions (Brinkman & Smith 2015). Lower pH caused deformation and dissolution on crustose coralline algae, although differences in skeletal geochemistry were insignificant (Brinkman & Smith 2015). Coralline species often form the base of non-calcifying macroalgae beds (e.g. kelp). Loss of coralline growth due to competition and reduced growth, which may be exacerbated by higher CO_2 conditions, could have a major effect on rocky reef function in coastal ecosystems (Hepburn et al. 2011). The coralline seaweed *Sporolithon durum* may be resilient against OA, as it already copes with reduced pH at its surface as a result of its own metabolism (Hurd et al. 2011). Kelps may be more resilient to OA as spore germination of giant kelp *Macrocystis pyrifera* is insensitive to lowered pH (Roleda et al. 2012; Leal et al. 2017) and growth, photosynthesis, and carbonic anhydrase activity of *M. pyrifera* were also unaffected (Fernández et al. 2015), although combined environmental stressors may interact, producing a pH impact. Similarly, *Ulva rigida* in the Otago Harbour was insensitive to OA (Rautenberger et al. 2015). Little is known about how New Zealand sponges may react to acidification (Law et al. 2017). Two demosponges, *Tethya bergquistae* and *Crella incrustans*, had minor changes in respiration rates, although warming may be a more critical threat (Law et al. 2017).

Seabirds can be particularly vulnerable to climate change because they are exposed to a range of change processes at the interface of land and sea, particularly for nesting. Processes that impact seabirds include warming oceans, intensification of El Niño Southern Oscillation (ENSO), sea level rise, and more frequent storms in addition to indirect impacts such as climate-induced reductions in ocean productivity. Globally, penguins are sensitive to the effects of climate change (Boersma 2008; Forcada & Trathan 2009), but impacts are often indirect (Trathan et al. 2015). A range of seabirds feature in the literature summary of Table 1, including penguins, shorebirds, and seafaring birds.

Many of the examples of impacted seabirds involve complicated mechanisms of climate impacts. For instance, the sooty shearwater (tītī *Ardenna grisea*) is a migratory bird with breeding grounds in New Zealand and over-wintering grounds in the northern hemisphere. With such a huge geographic range, this species could be influenced by a variety of regional climate events. Decreasing populations have occurred concurrently with changing ocean currents and rising sea temperatures that could affect ocean productivity (Veit et al. 1997; Lyver et al. 1999; Shaffer et al. 2006; Mills et al. 2008). Lower abundance of sooty shearwaters before an ENSO event suggests they are a sensitive indicator of oceanic conditions (Lyver et al. 1999; Shaffer et al. 2006; Humphries & Möller 2017).

Overall, sea-level rise, warming water temperatures, and ocean acidification (Lundquist et al. 2011; Rouse et al. 2017) have been identified as the marine climate change processes that are most problematic for New Zealand and of the taxa reviewed, seabirds are particularly susceptible.

Freshwater environments

Freshwater environments are particularly vulnerable to human-induced climate change because availability and temperature of water are very sensitive to climatic conditions, and habitats are highly fragmented (Woodward et al. 2010). Physical changes in freshwater ecosystems are predicted to be widespread with water availability fluctuating due to increased extreme flood and drought frequency and temperature and sea-level rise (Collins & Tait 2016). Extreme flooding may also alter river morphology which may change habitat quality and availability (Death et al. 2015). Measured impacts are summarised in Table 2, but substantial knowledge gaps remain, particularly when impacts are indirect and have complicated mechanisms (Macinnis-Ng et al. 2021).

New Zealand's freshwater biota is often described as depauperate with a high degree of habitat and trophic generalism owing to life-history evolution in geographic isolation and unpredictable, variable climatic conditions (Winterbourn et al. 1981). For example, Winterbourn et al. (1981) noted that hatching, development, and emergence periods of New Zealand aquatic invertebrates are highly asynchronous, flexible, and non-seasonal, reflecting a bet-hedging strategy suitable for unpredictable hydrological conditions. Likewise, the lack of strong vertebrate predator pressure in permanent ponds and their rapid, flexible development and drought tolerance, enables the many New Zealand pond invertebrates to occupy broad hydrological niches in ponds with vastly different rates of drying and permanence (Wissinger et al. 2009; Galatowitsch & McIntosh 2016; Greig & Galatowitsch 2016). Similarly,

Table 2. Examples of climate change impacts in the freshwater realm of Aotearoa New Zealand.

Climate change process	Ecosystem or species impacted	Type of evidence (field observations, manipulative experiment, modelling etc.)	Mechanism of impact	References
Warming and flooding of freshwater	Native galaxiid fishes	Field observations	Native fish have broader thermal tolerances and ability to take refuge in drought and floods than introduced salmonids.	McIntosh et al. (2010), Richardson et al. (1994)
Warming freshwater	Galaxiid fish (<i>Galaxias paucispondylus</i>)	Field sampling	Temperature sensitive native fish confined to warmer waters and excluded from cooler waters by introduced species.	Boddy and McIntosh (2017)
Warming freshwater	Introduced brown and rainbow trout	Field observations	Reduction of distributions as winter water temperatures warm.	Scott and Poynter (1991)
Warming freshwater	Invertebrate taxa	Field observations	Thermally restricted, cold water tolerant taxa such as ephemeroptera, plecoptera, diptera have poor ability to adapt to warming waters and high elevation species have no options for migration.	Quinn and Hickey (1990), Quinn et al. (1994), Jenkins et al. (2011), Anderson et al. (2016)
Warming freshwater	Shortfin (<i>Anguilla australis</i>) and longfin (<i>Anguilla dieffenbachii</i>) eels	Field observations	Migration of glass eels inhibited by water temperatures above 22°C.	August and Hicks (2008)
Warming freshwater	Freshwater lakes	Field and expert observations	Warming temperatures exacerbate thermal stratification reducing water mixing and causing anoxia.	Hamilton et al. (2013), Robertson et al. (2016)
Warming water and nutrient interactions	Macroinvertebrate and periphyton communities	Mesocosm experiments	Sediment and nutrient inputs interact with warming water to produce detrimental impacts on stream biota. Streams with high sediment loads especially vulnerable to warming water impacts.	Piggott et al. (2015a, 2015b)
Glacial melt	Mayflies (<i>Deleatidium cornutum</i>)	Observations and expert opinion	Species confined to glacial-fed streams will lose habitat as glaciers decline.	Winterbourn et al. (2008)
Sea level rise	Zooplankton	Field and laboratory trials	Salt water inundation of coastal freshwater lakes reduces biodiversity and abundance of zooplankton.	Schallenberg et al. (2003)
Interactions with land use change and freshwater extraction	Rivers and other freshwater bodies	Expert observations	Reduced water quality and reduced flows make freshwater systems more vulnerable to climate change impacts.	Robertson et al. (2016)
Changing flow regimes due to altered rainfall patterns	Shortjaw kōkopu and banded kōkopu (<i>Galaxias postvectis</i> and <i>G. fasciatus</i>)	Field observations	Modified reproductive cues for diadromous species using stream margins as egg deposition sites.	Charteris et al. (2003)
Changing flow regimes due to altered rainfall patterns	Ephemeral waterbodies such as ponds and fens	Expert observations	Ephemeral and pakihi bogs shift towards more permanent systems.	Robertson et al. (2016)

Table 2. Continued.

Climate change process	Ecosystem or species impacted	Type of evidence (field observations, manipulative experiment, modelling etc.)	Mechanism of impact	References
Increased nutrient input due to changed flow regimes	Algal blooms in freshwater lakes	Field and expert observations	Shifts to eutrophic state in shallow lakes, causing algal blooms under increased flow regimes and rising temperatures	Paerl and Paul (2012), Sinha et al. (2012), Wagner and Adrian (2009)
Drought and forest removal	Brown mudfish	Field observations and modelling	Reduced habitat size due to podocarp forest removal makes remaining populations highly vulnerable to drought	White et al. (2016), White et al. (2017)
Altered rainfall patterns	Bird nesting habitat in braided rivers	Field observations	As spring floods increase in frequency, nest failure will be more likely	McGlone and Walker (2011)
Interactions between climate change and other anthropogenic impacts	Macroinvertebrate communities	Field observations	Taxonomic homogenisation of assemblages due to climatic processes combined with interacting factors impacting populations and communities.	Mouton et al. (2020)

some native New Zealand fish appear more flexible in their tolerance of different hydrological conditions than introduced salmonids. For example, some native galaxiids are able to seek refuge from salmonid predation in systems prone to extreme flooding and drying, which are poorly tolerated by salmonids (McIntosh 2000; McIntosh et al. 2010). Salmonids are likewise more vulnerable to warmer waters compared to native species which generally have wider thermal tolerances (McDowall 1992; Richardson et al. 1994).

Habitat generalism may increase the resilience of some native aquatic fauna to novel climates under global warming. For example, effects of increasing temperatures on native fish may be minor as most species have wide north-south distributions and eurythermic adaptations (McDowall 1992). In contrast, more specialised salmonids are expected to show major southwards shifts, primarily due to reproduction failure, resulting in possible extirpation of Northland populations (Scott & Poynter 1991). This process may release habitat for galaxiids that will be free of salmonid competition and predation in warmer waters, but it may have the opposite effect in cooler waters (Boddy & McIntosh 2017). In contrast, many specialised indigenous species are high-altitude cold-tolerant species which may be severely affected by increasing temperature (Jenkins et al. 2011), while low-altitude systems may be strongly impacted by changes in hydrology and sea-level rise (Schallenberg et al. 2003). Similarly, the ability to migrate and disperse will largely affect how species can adapt to changing conditions, and this varies widely between species and systems in New Zealand (McDowall 2006). Meanwhile, many freshwater ecosystems are highly impacted by existing land-use change and water abstraction which will exacerbate future climate changes due to global warming (Robertson et al. 2016; Macinnis-Ng et al. 2021).

Vulnerability along altitudinal gradients and changes in flow regimes

High-elevation species are often thermally restricted and likely to be disproportionately affected by increasing water temperatures (Jenkins et al. 2011). Systems located above the bush line or below glaciers are some of the most heavily disturbed, owing to occasionally heavy rainfall and steep topography leading to extreme flooding and drying, but they are also some of the coldest. Many species inhabiting

these systems specialise in tolerating extreme disturbance and cold temperatures, but are poor at competing with other species which prevent them from establishing in warmer lower elevation systems. Winterbourn et al. (2008) suggested competitive ability may limit *Deleatidium cornutum* mayflies to glacier-fed streams in the South Island, making them susceptible to habitat loss from glacial melt and competition as lower elevation mayfly species advance upstream with increasing temperatures (Winterbourn et al. 2008). Alternatively, upper thermal limits may be directly limited by poor ability to acclimate to warmer waters, as shown in some stoneflies (Quinn et al. 1994), which are notable for being particularly thermally restricted compared to other invertebrate taxa (Quinn & Hickey 1990). Such mechanisms have resulted in a high degree of endemism in alpine aquatic invertebrates including numerous Ephemeroptera, Plecoptera, and Diptera which specialise in cold water tolerance (Anderson et al. 2016). Whilst some taxa may be able to migrate upstream as temperatures rise, there is an ultimate elevation limit to this (Jenkins et al. 2011). Consequently, there are concerns that many high elevation specialist taxa will go locally extinct with global warming, particularly given that we are already seeing significant glacial retreat which is altering fundamental characteristics of many high elevation streams (Winterbourn et al. 2008; Jenkins et al. 2011; Anderson et al. 2016).

Unlike wetland and pond invertebrates, which are widely distributed amongst different systems, there is a disproportionately high level of local endemism in wetland plant species (Kilroy et al. 2006; Tanentzap et al. 2014). Of the area currently occupied by wetlands, 12% will receive decreased rainfall and 51% will experience increased rainfall under climate change (Robertson et al. 2016), with rainfall increases occurring primarily on the west coast and decreases on the east (Mullan et al. 2005). Consequently, west coast wetlands consisting primarily of ephemeral and pakihi bogs are at risk of shifting towards more permanent states (e.g. ephemeral to swamp), aquatic systems (e.g. shallow water to pond or lake), or higher nutrient systems (e.g. fen to swamp) (Robertson et al. 2016). Decreased rainfall will most likely affect north and east coast wetlands (e.g. bogs and Northland gumlands) resulting in peat growth cessation or retreat, decreased wetland extent and change in vegetation composition, including invasion of dryland species, many of which are invasive weeds such

as blackberry *Rubus fruticosus* and gorse *Ulex europaeus* (Robertson et al. 2016).

Increased rainfall and greater flood frequency and intensity can disturb freshwater ecosystems, and increase soil erosion, sedimentation, turbidity, strip benthic habitat and communities, and prevent fish from visually locating prey (Thrush et al. 2004; Ryan & Ryan 2006; Lundquist et al. 2011). A panel considering threats to New Zealand's freshwater fish expected that these types of climate variability could exacerbate species declines (Allibone et al. 2010). Higher occurrence of extreme rainfall events under climate change might also aid flood-mediated movement of alien species (Hamilton et al. 2013) and changes in disturbance patterns may reduce the competitive advantages native species have over invasive plants in ephemeral wetlands (Tanentzap et al. 2014). Lower rainfall and drought pose a huge threat to aquatic life, potential higher loadings of nitrogen and phosphorus in streams, higher incidence of bacterial contamination, fish mortality from strandings and lack of deep-water refuges, and oxygen depletion affecting aerobic organisms. Pollutants entering waterways will also be less diluted in lower flows (Allan & Flecker 1993). Diminished stream flows in eight east coast South Island rivers during the period 1958–2007 are associated with a decline in the number of flood events (McKerchar et al. 2010). Shifts in timing, regularity and intensity of floods could be a significant threat for the reproductive cues of shortjaw kokopu *Galaxias postvectis* and banded kokopu *G. fasciatus* as diadromous species using stream margins as egg deposition sites (Charteris et al. 2003).

Hydrological change due to sea-level rise is also a potential threat for lowland ecosystems, particularly coastal freshwater lakes (Hamilton et al. 2013; Robertson et al. 2016). Saline intrusion resulting from extreme tides is a feature of many coastal lakes and acts as a disturbance on the aquatic community which can cause local extinctions. Research indicates that such saline disturbances could have significant negative effects on diversity and abundance of zooplankton in New Zealand coastal lakes (Schallenberg et al. 2003). Coastal lake zooplankton are resilient to such incursions provided they are only temporary (Duggan & White 2010); however, there are concerns such resilience would be insufficient if incursions increased in frequency or duration following sea-level rise (Hamilton et al. 2013). Coastal lake fish species may be physiologically resilient to saltwater intrusions but the impacts of changing community structure following the loss of zooplankton and introduction of estuarine fish species are unclear (Hamilton et al. 2013). Such a change to more estuarine biota is possible as indicated by some coastal lakes, e.g. Lake Waihola, which has shifted between estuarine and freshwater lake states following sea-level decline over the last 4000 years (Schallenberg et al. 2013). Rising sea levels are expected to cause this lake to eventually transition back to an estuarine state (Schallenberg et al. 2013). In such cases, there are concerns that submerged macrophytes in brackish coastal lakes and lagoons may disappear due to their reliance on periods of low salinity for reproduction (Hamilton et al. 2013).

Migratory and dispersal ability

The ability to migrate or disperse between habitats will likely be a key trait determining species resilience to climate change across fragmented freshwater and terrestrial habitats. Much of New Zealand's invertebrate fauna are highly mobile due to the existence of adult flying stages. Even invertebrates lacking flight are remarkably good at dispersing great distances as noted by the presence of New Zealand mudsnails *Potamopyrgus*

antipodarum in North American streams, which are thought to have hitch-hiked in the guts of migrating geese (Hall et al. 2006). Good dispersal ability has also been noted in temporary pond invertebrates as a strategy to occupy a broad niche across pond permanence gradients (Galatowitsch & McIntosh 2016).

Dispersal ability in fish is possibly more limited due to the inability to hitch-hike or self-disperse over-land. In fish there are large differences in distributional extent between species that are diadromous (those which migrate to the sea either to spawn or develop as larvae) or non-diadromous (McDowall 2006). Diadromous life-histories enable species to recolonise streams following disturbance, whereas non-diadromous species tend to disperse only within river sections and are therefore potentially less resilient to disturbance than diadromous species. Consequently, diadromous species have a much greater longitudinal and latitudinal distribution and therefore occupy a greater range of temperature and hydrological conditions in general (Leathwick et al. 2005; Leathwick et al. 2008) meaning they are potentially less sensitive to global warming (McDowall 1992). Nevertheless, migratory behaviour in diadromous species is influenced by climatic conditions beyond New Zealand; for instance, changing thermal fronts in Tongan spawning areas of eels may have led to a delay in seasonal recruitment of eels by several weeks in the Waikato river over the last 30 years (Jellyman et al. 2009). Meanwhile migration of eels up-river may be inhibited by temperatures exceeding 22°C (August & Hicks 2008). Consequently, changes in temperature may have a greater impact on diadromous fish compared to non-diadromous species which may be affected more by changes in rainfall variability under global warming.

Existing impacts

Freshwater systems have become increasingly impacted by pollution from nutrient addition, sedimentation, urban run-off, and damming which are contributing to freshwater biodiversity crises both in New Zealand (Gluckman 2017) and globally (Dudgeon et al. 2006), particularly in lowland rivers and lakes. Experimental stream mesocosms indicate that the combined effects of warming temperatures and agricultural stressors (sediment and nutrients) detrimentally influence macroinvertebrate and periphyton composition and dynamics in Otago (Piggott et al. 2015a; Piggott et al. 2015b). A more recent study of macroinvertebrate assemblages in 64 rivers found interactions between climate factors and other drivers of environmental change caused taxonomic homogenisation of communities (Moulon et al. 2020). While they found taxonomic and functional diversity could be independent, Moulon et al. (2020) highlighted the need to understand future trajectories of both especially because ecosystem resilience in such cases may have already been compromised thus increasing ecosystem vulnerability to climate change. This is particularly true in systems affected by water abstraction for irrigation, industrial and domestic use, which has been steadily increasing over recent decades to feed agricultural booms and population growth (Gluckman 2017) and is likely to increase as extreme droughts increase in frequency and magnitude with climate change (Vörösmarty et al. 2010). Water abstraction increases the chances that systems will go dry, but also reduces habitat availability (and thus population sizes) when water is present. Although the New Zealand aquatic biota may be generally well adapted to stochastic water availability, this combination of increased environmental stochasticity and reduced population size can rapidly increase the likelihood of population extinction

(Lande 1993) locally and more broadly.

Habitat size is often a governing factor influencing interactions between climate change and other human derived stressors. For example, metapopulation modelling of brown mudfish in forested wetlands indicates that this species can retain large sustainable population sizes, even under the most severe rates of extreme droughts projected by IPCC climate change scenarios (White 2016). However, because this species thrives in tip-up pools formed by the root excavations of windblown podocarps (White et al. 2015), forest clear-felling leads to metapopulation extinction under relatively moderate increases in extreme drought frequency because habitat size is reduced due to the absence of large tip-up pools under deforestation (White 2016). This process amplifies the severity of drying whilst simultaneously reducing population resilience to droughts by reducing population size (White et al. 2016; White et al. 2017). Consequently, mudfish metapopulations can withstand either climate change or clear-felling change in isolation, but not in combination (White 2016).

Similar mechanisms mediated by habitat size may also be important for fish population dynamics in flowing water ecosystems. Habitat size reduction in streams and rivers alter aquatic food-webs and fish populations by reducing average top predator size (usually fish) and decreasing food chain length as a result (McHugh et al. 2015). In South Island rivers reductions in habitat size interact with disturbance regimes to affect top fish size (Jellyman et al. 2014). Fish size declined with river disturbance index (typically floods) and habitat size; fish were smallest where habitats are both small and highly disturbed (Jellyman et al. 2014). These results indicate that reductions in habitat size from water abstraction combined with increased climate variability may result in synergistic negative effects on fish population persistence, and disproportionately affect large-bodied species. Consequently, unmodified natural flow regimes may likewise be important for maintaining sustainable population sizes of aquatic fish and invertebrates in streams and rivers under climate change.

Habitat size also has implications for how lacustrine ecosystems may respond to global warming. Rising temperatures may lead to more continuous periods of thermal stratification, resulting in potential anoxic dead zones in deeper lakes (Hamilton et al. 2013). Extended thermal stratification episodes have been observed previously in Lake Taupō and Lake Pupuke as a result of unusually warm water due to a strong El Niño event (Hamilton et al. 2013). Due to their depth, thermal stratification resulted in poor mixing of bottom waters and thus anoxia for over three years (Hamilton et al. 2013). Such anoxic bottom water episodes also occur in eutrophic Lake Rotorua and Lake Hayes for several weeks each year during hot summer temperatures (Robertson et al. 2016). These episodes may place pressure on salmonid populations where trout become stressed due to anoxia in bottom waters and excessive temperatures near the surface which may exceed 20°C in some cases (Robertson et al. 2016).

Thermal stratification is much weaker in shallow lakes; however, temperature increases could still lead to anoxic periods therein due to eutrophication (Hamilton et al. 2013). Models predict shallow lakes, e.g. Lake Ellesmere/Te Waihora, will experience increased nutrient loading and eutrophication under IPCC temperature increase scenarios leading to 56% increases in the frequency of hypoxia (Trolle et al. 2011). Such predictions assume constant nutrient inputs from human land-use which would need to be reduced in order to mitigate that effect of temperature increase (Trolle et al. 2011). Shallow

lakes are also more prone to major wind disturbances which can suspend lake sediment and cause ecosystem state transitions from one dominated by macrophytes towards a turbid eutrophic state dominated by cyanobacteria (Schallenberg & Sorrell 2009). Cyanobacteria *Cylindrospermopsis raciborskii* blooms have been ascribed to climate change (Wagner & Adrian 2009; Paerl & Paul 2012; Sinha et al. 2012). Schallenberg and Sorrell (2009) showed that the probability of ecosystem state transitions in New Zealand lakes decreases with habitat depth and increases with the percentage of the catchment in pasture which implicates an effect of nutrients. Consequently, shallow lakes that are currently macrophyte dominated and non-eutrophic may become increasingly likely to shift to a eutrophic state as temperatures and disturbance frequencies increase with global warming.

Shifting interactions between introduced, invasive and native species under climate change is also a concern. In addition to the expected southward contraction of introduced salmonids (Scott & Poynter 1991), other warm-water pest fish, e.g. *Gambusia affinis* and several invasive Cyprinids could show range expansions with global warming (Ling 2010). *Gambusia* are voracious predators and are known to out-compete native black mudfish *Neochanna diversus* (Ling & Willis 2005) and consume some whitebait species (e.g. *Galaxias maculatus*) (Rowe et al. 2007). Introduced goldfish *Carassius auratus* are also likely to be advantaged by warmer waters (Hamilton et al. 2013), and freshwater parasites might also see heightened reproduction (Ryan & Ryan 2006). Meanwhile, global warming is expected to make conditions more favourable for some invasive invertebrates including the mosquito *Aedes notoscriptus*, which may grow in abundance and distribution given the potential increased availability of the temporary habitats they thrive in (Hunt et al. 2017).

Terrestrial environments

Evidence of impacts of climate change in terrestrial ecosystems is growing (see Table 3 for examples) but many of the mechanisms are indirect through processes of exacerbation of other factors such as invasive species and habitat clearance and fragmentation (Macinnis-Ng et al. 2021). Key vulnerabilities include small, isolated populations and exposed rare ecosystems (Williams et al. 2007). Key unknowns include invertebrate vulnerability, sensitivity of rare plants and understanding how ecosystem processes such as carbon capture and storage, water and nutrient cycle modulation, and pollination services will be influenced by the different climate change factors across the country.

Vertebrate and invertebrate fauna

Rare and threatened terrestrial species (especially birds) are over-represented in the sanctuary system (Innes et al. 2019) of Aotearoa New Zealand. Small populations are carefully monitored and managed to protect these species from invasive predators, but small, isolated populations may be vulnerable to climate change, and particularly to extreme events such as fires which will be more frequent under climate change. Many of the likely impacts are predicted and not yet measured but of the terrestrial vertebrates, there are some clear examples of responses to climate change in birds (Evans et al. 2003; Chauvenet et al. 2013), bats (Pryde et al. 2005), herpetofauna (Bell et al. 2004; Mitchell et al. 2008), with further effects predicted in beetles (Rizvanovic et al. 2019).

Table 3. Examples of climate change impacts in the terrestrial realm of Aotearoa New Zealand.

Climate change process	Ecosystem or species impacted	Type of evidence (field observations, manipulative experiment, modelling etc.)	Mechanism of impact	References
Rising temperatures and heavier rainfall events	Hihi (<i>Notiomystis cincta</i>)	Field observations and modelling	Population dynamics strongly influenced by climate and small sub-populations are vulnerable to extreme events.	Chauvenet et al. (2013), Correia et al. (2015)
Warmer winters	Long-tailed bats (<i>Chalinolobus tuberculatus</i>)	Field studies and modelling	Bat survival declines when winter temperatures are above average.	Pryde et al. (2005), Schaubert et al. (2008)
Warming temperatures	Tuatara (<i>Sphenodon</i> spp.)	Observations and modelling	Male bias due to temperature-dependent sex determination.	Grayson et al. (2014), Mitchell et al. (2008, 2010)
Warming temperatures	Tussock grasses (<i>Chionochloa</i> spp.)	Observations and models	Mast seeding events likely to be more frequent.	Monks et al. (2016)
Warming temperatures	Tussock grassland	Field experiment	Increased soil respiration in tussock grassland.	Graham et al. (2014)
Warming temperatures	Alpine flora	Field experiment	Changed phenology of native plants, increasing competition for pollinator services.	Giejsztowt et al. (2020)
Warming temperatures	Mountain beech (<i>Nothofagus solandri</i> var. <i>cliffortioides</i>)	Field study and modelling	More frequent seed production at high elevations.	Richardson et al. (2005)
Warming temperatures and rainfall shifts	Kūmarahou (<i>Pomaderris kumeraho</i>) and kuta (<i>Eleocharis sphacelata</i>)	Modelling	Changing climate shifts likely distribution of culturally important species, likely reducing access.	Bond et al. (2019)
Drought	Kauri (<i>Agathis australis</i>)	Field study	Natural drought increased leaf litter fall in kauri.	Macinnis-Ng and Schwendenmann (2015)
Drought	Kauri (<i>Agathis australis</i>)	Field study	Natural drought reduced tree water use.	Macinnis-Ng et al. (2013), Macinnis-Ng et al. (2016)
Warming alpine zone	Vulnerable alpine biota	Field observations and modelling	Endemic forest birds threatened by expanding ranges of invasive species.	Walker et al. (2019)
Warming alpine zone	Alpine flora and invertebrates	Modelling	Decline in vascular plant and invertebrate taxa.	White and Sedcole (1991), Halloy and Mark (2003), Winterbourn et al. (2008), Chinn and Chinn (2020)
A range of climate factors including warming temperatures, less rainfall, fire	Invasive flora	Modelling and field studies	Establishment and spread of invasive species favoured by climate change.	Field and Forde (1990), Sheppard and Stanley (2014), Sheppard et al. (2014, 2016), Thuiller et al. (2007), Perry et al. (2014)
Warmer winters	Invasive hymenoptera, wasps (<i>Vespula</i> spp.) and Argentine ants (<i>Linepithema humile</i>)	Modelling and field studies	Range expansion due to milder winters impacting on birds and native invertebrates.	Beggs (2001), Harris and Barker (2007)

Although seabirds dominate avifauna vulnerable to climate change through direct and indirect processes (McGlone & Walker 2011), land-based birds are also at risk. Hihi *Notiomystis cincta* is an example of a species that exists only in managed populations threatened by warming and interruptions to feeding in heavy rainfall. Potential future suitable habitats are outside their historic range (Chauvenet et al. 2013) and while supplementary feeding may provide protection from heavier rainfall and stochastic rain events, it is only likely to delay but not prevent extinction (Correia et al. 2015). Other native birds could be at higher risk of avian malaria via increased range size of vectors (Garamszegi 2011). Five mōhua *Mohoua ochrocephala* died of avian malaria at Orana Wildlife Park in Canterbury from 2003–2005, and both native (Derraik et al. 2008) and non-native (Tompkins & Gleeson 2006) mosquitoes are potential vectors for the disease. Further, introduced species (e.g. house sparrow *Passer domesticus*, blackbird *Turdus merula* and song thrush *Turdus philomelos*) may also

be carriers of the disease (Derraik et al. 2008).

For birds using braided rivers as nesting habitat, higher frequency of spring flooding will likely result in nest failure (McGlone & Walker, 2011) for species like wrybill *Anarhynchus frontalis* (Cruz et al. 2013; Christie 2014). Finally, there is growing evidence with long-term data showing birds are laying their eggs earlier concomitant with warming (Dunn & Winkler, 2010), and welcome swallows *Hirundo neoxena* demonstrate this (Evans et al. 2003).

Population declines of long-tailed bat *Chalinolobus tuberculatus* in the Eglinton Valley have been tied to climate change by Pryde et al. (2005). One model showed survival decreased in warmer winters, possibly due to higher temperatures resulting in higher bat activity consuming vital fat stores, or through interaction with predators and beech seed fall (Pryde et al. 2005; Schaubert et al. 2008).

Tuatara *Sphenodon* spp. have temperature-dependent sex determination where more males hatch when incubation

temperatures are higher, putting tuatara at risk in a warming climate where long generation times and male bias would cause population decline (Mitchell et al. 2008; Grayson et al. 2014). While populations are currently sustainable with about 60% of hatchlings being male (Mitchell et al. 2010), without making adaptations such as deeper nests or nesting in cooler locations, tuatara hatchlings would all be male by 2085 under current climate predictions, and a population viability analysis indicates that if sex ratios of tuatara surpass 85% male, the population of *S. guntheri* on North Brother Island could become extinct (Mitchell et al. 2010; Grayson et al. 2014). Any adaptations that could occur in nesting behaviour or response to temperature would not happen rapidly enough due to slow generation times (Mitchell et al. 2010). Migration of tuatara to cooler climes is not possible as many are on island sanctuaries for protection from invasive predators. Some populations may be at even greater risk with significantly lower reproductive rates; *S. guntheri* females on North Brother Island breed approximately every nine years, whereas *S. punctatus* breed every three to five years (Mitchell et al. 2010).

Declines in Archey's frog *Leiopelma archeyi* populations on the Coromandel Peninsula between 1996 and 2001 have been tied to disease and climatic factors (Bell et al. 2004), consistent with climate impacts on frogs globally (Stuart et al. 2004). Increasing temperature may also have an effect on the egg-laying skink *Oligosoma suteri*, with positive outcomes including increased range and shorter incubation periods, but these advantages may be counteracted by physiological factors and invasive predators (Stenhouse et al. 2018).

Three New Zealand forest beetles are predicted to be impacted by climate change: *Agyrtodes labralis* could see reduced distribution by 2100 as well as loss of half of their unique haplotypes, while *Bracynopus scutellaris* and *Epistranus lawsoni* may expand their ranges with minor differences in genetic diversity (Rizvanovic et al. 2019).

Flora

Range shifts and changes in phenology will be key responses to climate change in the flora (Wardle & Coleman 1992; Whitehead et al. 1992; Leathwick et al. 1996; Cullen et al. 2001; Christie 2014). These impacts include increased frequency of seed mast events for beech and tussock, which will likely increase predator irruptions (McKone et al. 1998; Richardson et al. 2005; Schaubert et al. 2008; Lundquist et al. 2011). Flowering of *Chionochloa* snow tussock during the mast season is driven by the interaction between stored plant resources and synchronisation cues (Monks et al. 2016). As high summer temperatures before *Chionochloa* flowering stimulates masting (McKone et al. 1998), a higher occurrence of mast events is likely under climate change (Monks et al. 2016). Models indicate treelines moving higher in elevation with southwards movement of northern trees (Wardle & Coleman 1992; Leathwick et al. 1996) but Cullen et al. (2001) argue no significant change to treeline has occurred, and that Wardle & Coleman's (1992) results can be attributed instead to low-density populations and their limited recruitment, and response to natural disturbance as opposed to warming. Leathwick et al. (1996) also predicted a large increase in range of tawa *Beilschmiedia tawa* with warming. Mountain beech *Fuscospora cliffortioides* and kāmahi *Pterophylla racemosa* produce excess honeydew in warmer temperatures or during drought, which can encourage damage from enlarged *Platypus* beetle populations, leading to mature tree die-back (Wardle 1984). Warming soils increased soil respiration in

tussock grassland, possibly prompting higher CO₂ emissions (Graham et al. 2014). Beyond ecological impacts, specific cultural impacts due to responses of flora to changing climate could include reduced access to plants used for weaving and medicinal purposes due to shifts in distributions in response to temperatures and rainfall (Bond et al. 2019).

Plants are particularly vulnerable to extreme events including drought and fire. Kauri *Agathis australis* had reduced tree water use (Macinnis-Ng et al. 2016) and a drought deciduous response with increased litterfall during a dry summer, resulting in greater fluxes of carbon and nitrogen (Macinnis-Ng & Schwendenmann 2015), but the ongoing impacts on forest productivity are unclear. Drought is expected to occur more frequently and with greater intensity in New Zealand (Ministry for the Environment 2016), and this is a key stressor for forests and all flora. Increased drought occurrence also has potential implications for restoration plantings as some colonising species commonly used in Auckland, e.g. *Coprosma robusta*, *Myrsine australis*, and *Sophora microphylla* are drought-sensitive (Seward 2016). Plant disease occurrence is expected to increase with drought for New Zealand's economically important plants (Wakelin et al. 2018), and this may hold for native species too (e.g. kauri dieback and myrtle rust). Wind damage may also pose an issue for forests under a changing climate. Modelling showed planted forests were more susceptible to wind damage due to increased plant height without accompanying increased girth (Moore & Watt 2015). Soil ecosystem services in the primary sector are also vulnerable to climate change via incapacity to regulate water and nutrients (Orwin et al. 2015), which could also impact natural systems.

Bishop and Landers (2019) identified native terrestrial ecosystems in Auckland that are likely to be vulnerable to sea-level inundation, noting that 42% of these ecosystems have one or more risk factors that could increase their susceptibility to disadvantaging climate change effects. Vulnerable ecosystems include coastal habitats and forests. Hare et al. (2019) also identified climate change as a conservation issue for pīngao *Ficinia spiralis*, but the mechanisms are unclear. If myrtle rust *Austropuccinia psidii* and kauri dieback *Phytophthora agathidicida* are also exacerbated by climate change, additional ecosystems around Auckland and beyond could be at risk (Bishop & Landers 2019; Bradshaw et al. 2020).

Alpine systems

Glacier retreat over the last century correlated with a yearly temperature increase totalling 0.6°C (Chinn 1996), and future projections indicate decreasing numbers of snow days are reducing alpine habitat extent, potentially making alpine areas highly vulnerable to climate change (McGlone & Walker 2011; Ministry for the Environment 2016). However, evidence for direct impacts on alpine biota are sparse. Treelines in New Zealand have not shifted significantly despite warming occurring (Cullen et al. 2001), and it is possible that little change to critical ice and snow line for species survival has transpired (McGlone & Walker 2011). Bannister et al. (2005) found that it would take recurrent and / or intense frosts concurrent with warming for alpine plants relying on snowpack protection to be detrimentally affected. Further, invasive *Pinus contorta* recruitment was unaffected by climate variability and instead by favourable microsites (Tomiolo et al. 2016).

Populations of alpine invertebrates may decline with temperature increases (McGlone & Walker 2011). More complicated indirect processes include clear evidence for the

spread of pest species increasing, causing thermal squeeze (Walker et al. 2019). Although warming may initially promote improved survival and reproduction of plant species during winter in temperate environs, this may be offset by frost damage, pest invasion, or disruption of plant and pollinator cycles (Kreyling 2010). However, New Zealand tree species could potentially adapt to increased frost (Kreyling 2010). A warming manipulation study showed rising temperatures changed phenology of native plants, increased the overlap period between native and invasive plants, and increased competition for pollinator services (Giejsztowt et al. 2020). When plant densities were high, warming also caused lower seed mass, potentially further disrupting reproduction in native plants (Giejsztowt et al. 2020).

Species-area models have indicated that a 3°C increase in temperature could lead up to a 50% decline in native vascular taxa with further losses due to disappearance of alpine islands (Halloy & Mark 2003) with associated declines in populations of alpine grasshoppers (White & Sedcole 1991) and mayflies (Winterbourn et al. 2008). Climate modelling also shows high elevation invertebrate taxa track the snowline within a 20 m range indicating sensitivity to climate change (Chinn & Chinn 2020) but alpine invertebrate communities are highly variable between years making detection of climatic impacts difficult (Paler et al. 2021). Regarding pest species, rabbits now inhabit Ruapehu at 1800 m (nearly twice as high as their typical elevational limit) which could be due to diminished snow cover (Flux 2001).

Invasive plants

Invasive flora often have adaptive advantages over native species with traits that are beneficial in a rapidly changing climate (Dukes & Mooney 1999). Globally, the overall consequence of higher levels of CO₂ and warming temperatures is greater plant diversity at a regional scale, mainly driven by naturalisation of introduced plant species (Woodward & Kelly 2008). The introduction of new weeds and the proliferation of existing weeds is one of the most problematic and likely outcomes of climate change (McGlone & Walker 2011; Christie 2014). Climate change may have an impact on the geographical distribution of species and increase the spread of invasive plants into novel locations, particularly for species that prefer warmer and drier conditions (Thuiller et al. 2007; Sheppard et al. 2014). Extreme climatic events can contribute to species invasions in a number of ways: (1) facilitating seed dispersal into new areas, (2) lowering the resistance of native assemblages to weeds taking hold, (3) indirect impact via species competition, (4) altering interactions with natural enemies, (5) and promoting disturbances (e.g. fire) that may create habitat for particular weeds to establish (McGlone & Walker 2011; Diez et al. 2012; Lu et al. 2013; Perry et al. 2014).

New Zealand will likely be a future hotspot for the spread of invasive species due to climate change (Sheppard et al. 2016), with naturalised species constituting 53% of all vascular plants, and approximately 25 049 alien species occurring in gardens (Diez et al. 2009). Warming is predicted to encourage further spread of grasses (Field & Forde 1990), conifers (McGlone & Walker 2011), naturalised and ornamental species (Sheppard et al. 2016). Species with adaptations to fire will be favoured as fires become more common and more severe (Perry et al. 2014). In the case of previously introduced species with fire adaptations, there may be a large invasion debt that could manifest as unprecedented spread of existing exotic flora after fire disturbance (Stanley & Bassett 2015). Although

not all weeds will be advantaged by warmer temperatures in New Zealand, the balance may be in favour of exotics (Marini et al. 2009; McGlone & Walker 2011). Northland is at risk from up to 100 weed species, with 17 already in a critical growth phase (Williams 2008). *Paspalum dilatatum*, carpet grass *Axonopus affinis* and knot-root bristle *Setaria geniculata* increased their range from 1978 to 1990 associated with warming, with other species also increasing following a two-to-three year period of warmer winters and summers (Field & Forde 1990). Higher rainfall has been suggested to indirectly lead to increased spread of woody weeds, and higher temperatures are likely to spread subtropical grasses southward (Popay et al. 2002). Yellow bristle grass *Setaria pumila* is also expected to increase its distribution with warming, mainly presenting a problem for dairy farms (Lamoureaux & Bourdôt 2014). McGlone and Walker (2011) assert the potential for increased spread and change of ecosystems by conifers, such as Douglas fir *Pseudotsuga menziesii* due to greater growth capacity than in its natural range (Waring et al. 2008), and lodgepole pine *Pinus contorta* due to its prolific growth, seed production and dispersal (Ledgard 2001). As recently naturalised species, the bangalow palm *Archontophoenix cunninghamiana*, common guava *Psidium guajava* and Queensland umbrella tree *Schefflera actinophylla* are likely to threaten native species through competition and higher invasiveness associated with climate change (Sheppard et al. 2016) and some of these species have drought tolerance (Sheppard 2014), potentially enhancing survival in drier parts of the country. Further, *S. actinophylla* is likely to grow more rapidly under future climate conditions, and especially under higher CO₂ levels (Sheppard & Stanley 2014). Japanese honeysuckle *Lonicera japonica* showed increased growth when exposed to higher CO₂ levels in North America (Sasek & Strain 1991) and could respond similarly in New Zealand. Chinese windmill palm *Trachycarpus fortunei* has been spreading into semi-natural forests globally including from gardens in the North Island, possibly due to warmer winters and longer growing seasons (Walther et al. 2007). Another study models high suitability areas for *T. fortunei* alongside warming and the palm may be a useful climate change indicator (Aguilar et al. 2017). A species distribution model of Mexican daisy *Erigeron karvinskianus* shows increased range expansion southward under present and predicted climate (Hannah et al. 2019). Biocontrol agents could also potentially be affected by a changing climate; the tansy ragwort flea beetle *Longitarsus jacobaeae*, introduced to manage ragwort, may not be able to tolerate changes on a local scale and therefore may have a reduced effect on controlling ragwort; however, the impact is expected to be small nationally (Gerard et al. 2013).

Invasive animals

Globally, exotic animals have spread to areas where prior to warming they were unable to survive (Walther et al. 2009). New Zealand has experienced effects of introduced species including insects, mammals, birds, and fish (Hay 1990; Clout & Lowe 2000; Koehn & McDowall 2004; Watt et al. 2008; McGlone & Walker 2011). Many of these effects are exacerbated by climate change (Macinnis-Ng et al. 2021; described below).

Abundance and range of invertebrates are strongly influenced by climate (Parmesan 2006; McGlone & Walker 2011). Watt et al. (2008) predicted populations of *Vespula* spp. and *Polistes* spp. wasps will grow as they tolerate warmer winter conditions (Clout & Lowe 2000; Beggs 2001; McGlone

& Walker 2011). *Vespa* spp. have significant impacts on ecological interactions as they compete with native birds for food, especially beech honeydew, as well as nectar and insects and they also predate on native invertebrates and attack chicks in the nest (Clout & Lowe 2000; Beggs 2001). The range of big-headed ants *Pheidole megacephala* and Argentine ants *Linepithema humile* are predicted to expand with climate change and are considered a major pest in New Zealand due to their impact on arthropods (Lester 2005; Harris & Barker 2007; McGlone et al. 2010; McGlone & Walker 2011). Argentine ants reduced the foraging success of native ants in North America and could affect New Zealand species in a similar manner (Human & Gordon 1996). *Aedes* spp. mosquitoes may also spread with the creation of more suitable habitat (Clout & Lowe 2000). If established in New Zealand, the Queensland fruit fly *Bactrocera tryoni* and brown marmorated stink bug *Halyomorpha halys* are at high risk of spreading to the south of New Zealand under predicted warming scenarios (Aguilar et al. 2015a; Fraser et al. 2017).

More frequent mast events in beech forest driven by climate warming stimulate population explosions for mammalian predators, which has a severe impact on prey (McGlone & Walker 2011; Tompkins et al. 2013). Spikes in rodent populations feeding on seed increase stoat abundances. Stoats are particularly detrimental to native birds and lizards, often as a result of prey-switching following rodent population decline after seed mast resources are depleted (McGlone & Walker 2011). Tompkins et al. (2013) predict higher average stoat and rat abundance with concomitant increases in mast frequencies. Warm and dry areas are also prime habitat for rabbits which threaten native herbs and shrubs, as well as allowing harmful levels of predator populations of stoats and feral cats (McGlone & Walker 2011). Species distribution modelling indicates the North Island will increase the habitable range of stray domestic cats due to warming (Aguilar et al. 2015b). The breeding season of rodents, possums, goats, and pigs are predicted to be lengthened as the climate warms which may enable them to repopulate more quickly following pest control (Hay 1990).

Other invasive animals that may be affected and impact on New Zealand biota include Indian myna *Acridotheres tristis* and sub-tropical aquarium fish (Clout & Lowe 2000; Koehn & McDowall 2004). As ranges of invasive species expand due to more favourable climatic conditions, populations of more vulnerable native species may go extinct under increased predation pressure. A key vulnerability has been identified in the alpine zone where thermal squeeze is impacting a number of bird species, particularly those that are large, nest in tree hollows and are poor dispersers (including kea *Nestor notabilis* and kākā *N. meridionalis*) as rising temperatures reduce areas of cool refugia from mammalian predators (Walker et al. 2019). Consequently, maintaining and increasing management of invasive species will be even more important as the climate changes.

Conclusions

Invasive pests and weeds, vegetation clearance, waterway pollution and climate change are major threats to ecological integrity and biodiversity conservation in Aotearoa (McGlone et al. 2020). While impacts of the first four factors are clearly visible, climate change is sometimes thought of as a future threat, but our review identifies a range of current impacts for

species and habitats in three major biomes: marine, freshwater, and terrestrial (Fig. 2). Effects of atmospheric and oceanic warming, sea-level rise, increased CO₂, change in rainfall patterns, and loss of snow and ice cover are exacerbated by other human impacts and threaten numerous species around the country and surrounding waters. Many of the identified impacts are indirect, interacting with existing threats to biodiversity, such as invasive predators and invasive plants (Macinnis-Ng et al. 2021). Since mechanisms of impact can be complicated, and climate change occurs against a backdrop of an already variable climate, impacts can be difficult to quantify and attribute to climate processes. There are also likely to be a variety of other unknown impacts which we are not yet looking for. However, increasing numbers of studies are exploring potential climate change impacts (Fig. 1) with the bulk of research using manipulative and modelling approaches to predict responses of species and ecosystems to climatic change with observations of impacts in the field (Tables 1–3) remaining rare. Ocean acidification and spread of invasive plants are two areas which have gained much insight over recent years with several researchers focussing efforts in these areas. Another large-scale threat is sea-level rise, given New Zealand's extensive coastline. Many projected effects are based on minimum-moderate predicted levels of warming and other climatic change to reflect realistic future projections and studies of extreme events are uncommon. Given uncertainties around climate projections, it will be increasingly important to establish and continue research, monitoring, and management of at-risk species and ecosystems in order to mitigate the consequences of climate change on New Zealand's biota. While we have divided our review into marine, freshwater and terrestrial biomes, there are some clear sensitivities where ecosystems intersect. Species and processes that are important for connectivity of biomes in the context of climate change include seabirds, nutrient inputs from land to freshwater and sea level inundation of coastal ecosystems.

The literature on climate change impacts in New Zealand is comparatively sparse, particularly in comparison to other countries like Australia which have a larger scientific community and a longer history of climate change research. Given the relatively small body of work, there are many knowledge gaps regarding future impacts of climate on biodiversity. We identify four key research needs relating to known unknowns (Fig. 3). The first is biocultural relationships with ecosystems, particularly with respect to access and monitoring of Māori food (mahinga kai) and other resources. Examples of climate change impacts on culturally significant biotic resources include Lyver et al. (1999), MacDiarmid et al. (2012) and Bond et al. (2019) but there are likely further vulnerabilities (Carter 2019). Second, impacts of climate on ecosystem processes (particularly carbon uptake and storage of forests, other vegetation, and marine systems) are largely unknown. Much of the research in the marine biome is based on single-species tests of reproduction and survival but the broader ecological impacts are often unclear. For forest systems, carbon storage will be reduced by droughts and fires, but the timeframes and quantities of these carbon reductions are unknown. These ecosystem processes influence ecosystem services such as climate change mitigation so better understanding of these processes is essential for defining the full threat of climate change. Third, the impacts of extreme events in terrestrial, marine, and freshwater systems (particularly floods, storms, droughts and fires for terrestrial and freshwater systems and heatwaves in marine systems) are also important for defining

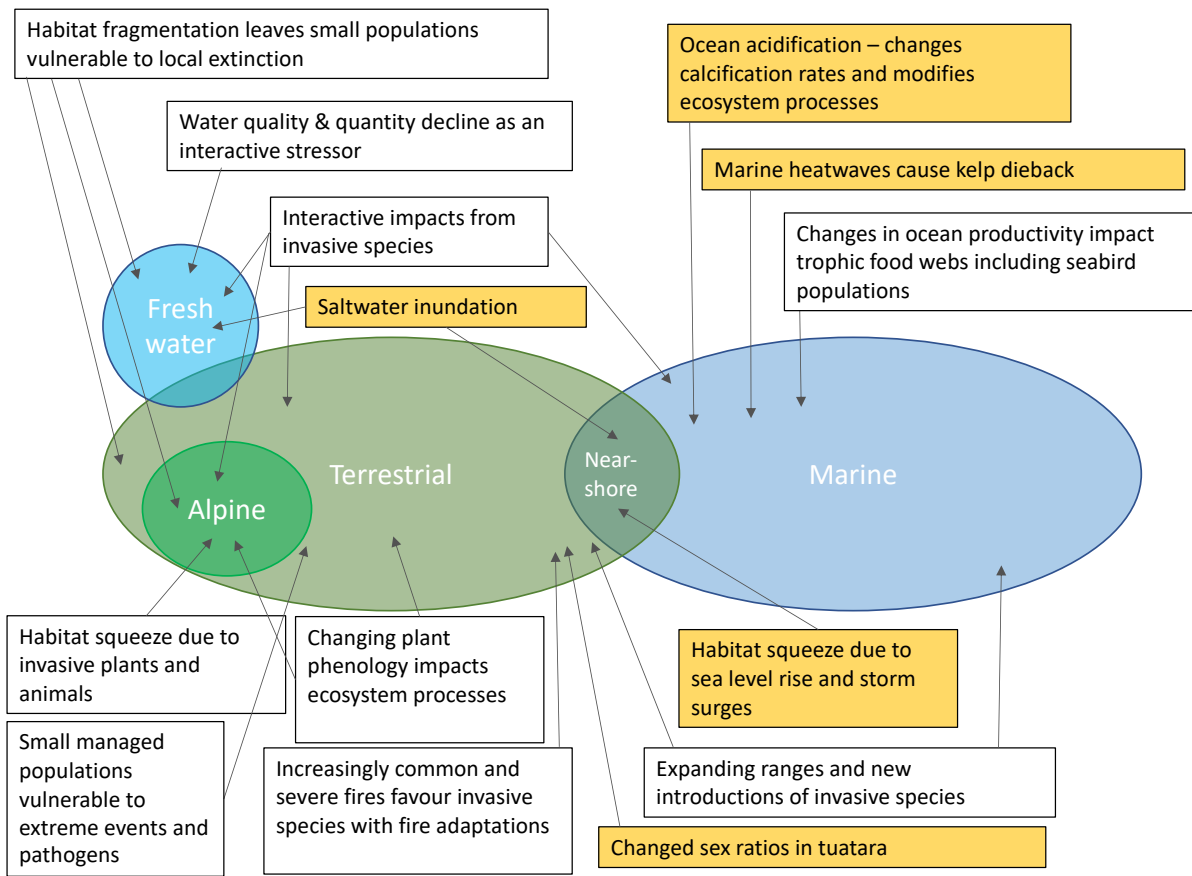


Figure 2: Schematic summary of climate change impacts in Aotearoa New Zealand identified in this review across marine, terrestrial, freshwater, alpine and near-shore ecosystems. Direct impacts are shaded orange while indirect impacts are unshaded.

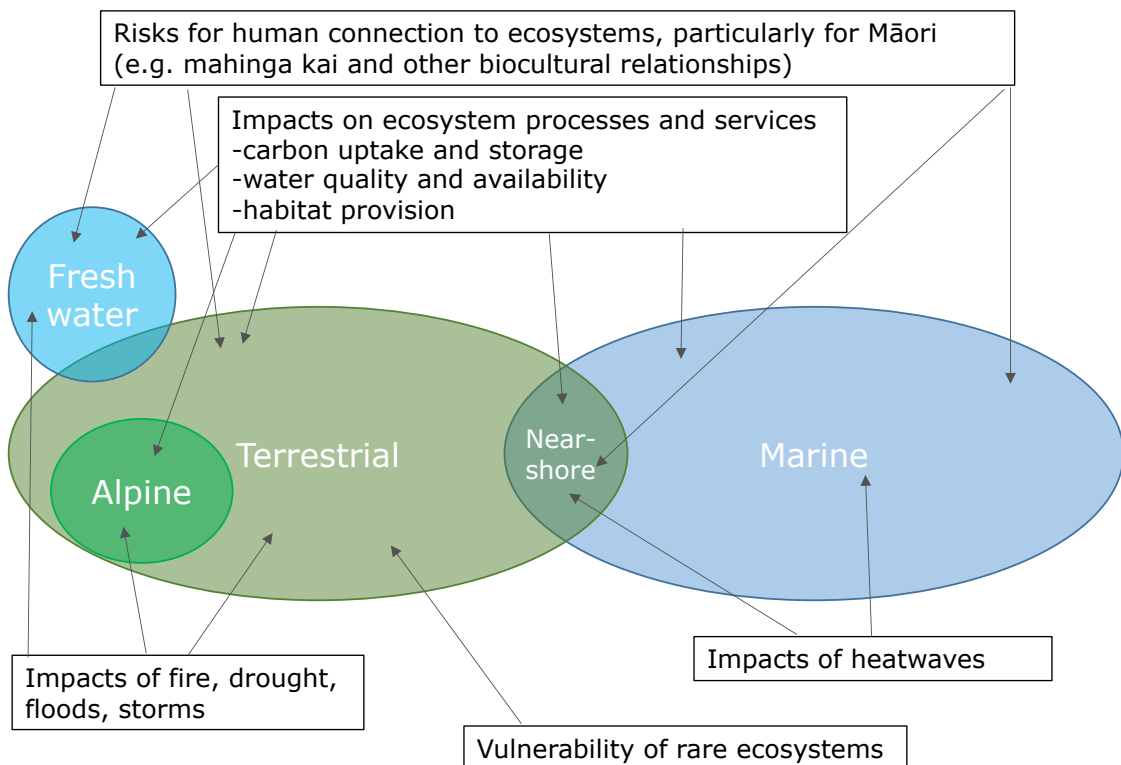


Figure 3: Schematic diagram of key knowledge gaps regarding climate change impacts across ecosystems of Aotearoa New Zealand. This is not an exhaustive list of known unknowns but rather identifies some of the most pressing research needs.

climate change impacts. Extreme events are the most damaging processes for biological systems under future climates. Down-scaled regional climate modelling to characterise severity and frequency of extreme events can be used in process-based or mechanistic models to capture the full impacts of extreme events and their legacy effects. Finally, quantifying vulnerability of rare ecosystems to a range of impacts including extreme events and sea level rise is a vital research need for biodiversity conservation as many of our endemic species are found in rare systems. These key knowledge gaps have been highlighted because they potentially pose the greatest threat and are consistent with the need for holistic understanding of ecological integrity for biodiversity conservation (McGlone et al. 2020). Additional and emerging research needs include management of new and ongoing biosecurity threats in vulnerable systems. We advocate for climate change impacts to be considered in all ecological and environmental management plans because our review shows impacts are likely to be wide-ranging, even if they can be difficult to detect.

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Author contributions

LJK conducted the literature review, constructed Fig. 1, and drafted the introduction, marine, and terrestrial sections. RSAW drafted the freshwater section. CM drafted the conclusions, compiled the tables and constructed Figs. 2 and 3. All authors revised and edited the manuscript.

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