Climate-change impacts exacerbate conservation threats in island systems: New Zealand as a case study

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Rapid advances in eradicating invasive species from islands are improving conservation outcomes in these biodiversity hotspots. However, recent conservation gains could be reversed not only by future invasions from non-native species but also by future extinctions of native taxa, both of which may be facilitated by – or exacerbated by interactions among drivers of – global environmental change. We highlight relevant knowledge gaps that must be filled to reduce uncertainty about the ecological effects of future climate change. We use Aotearoa New Zealand as a case study of island ecosystems to demonstrate that in addition to sea-level rise, most ecologically meaningful impacts of climate change on biodiversity responses are indirect and due to exacerbation of existing threats, including the impact of invasive species as well as the loss and fragmentation of habitat. We identify key topics where progress is needed to future-proof conservation management for island ecosystems susceptible to the direct and indirect effects of climate change.

Although islands cover only ~5% of the global land area, they support ~20% of terrestrial plant and vertebrate species (Courchamp *et al*. 2014). Insular species are particularly vulnerable to extinction; one-third of critically endangered species and nearly two-thirds of recent extinctions consisted of species endemic to islands (Tershy *et al*. 2015), and these declines may have impacts on Indigenous peoples (Lyver *et al*. 2019). Several interacting factors contribute to this vulnerability, including invasions by non-native species and habitat loss (Simberloff *et al*. 2013). Island ecosystems are particularly susceptible to multiple climate-change factors, including rising sea level and loss of suitable climatic conditions (Courchamp *et al*. 2014), but conservation and restoration efforts rarely account for such interacting drivers of change (Parmesan *et al*. 2013). Understanding the effects of climate change on island ecosystems necessitates knowing how climate interacts with other ecologically influential processes (eg habitat loss, land transformation, invasive species).

Here, we use the example of New Zealand to highlight interactions between changing climate and other threats to biodiversity, and stress the need to collect and maintain long-term datasets to improve strategies to mitigate climate-change effects. Lessons learned from New Zealand are relevant to islands (and potentially continental systems) elsewhere (Simberloff 2019), particularly with respect to the indirect and interactive effects of climate-change impacts. Although we focus on land-based ecosystems, we note that warming seas and ocean acidification are affecting marine systems in New Zealand's territorial waters, as well as elsewhere. Finally, we emphasize the need to work with Indigenous communities to improve the effectiveness of mitigation and adaptation approaches.

New Zealand (also known by the Indigenous name Aotearoa) consists of three main islands, along with hundreds of smaller islands in rivers, lakes, and harbors, as well

In a nutshell:

- Island systems, such as New Zealand, are hotspots of endemic species vulnerable to extinction
- Although there are few cases of clearly documented climate-change impacts in modern New Zealand, it is unclear if this is due to a paucity of data, the complexity of responses, or a lack of measurable effects
- Interactions between climate change and other threatening processes, such as biological invasions and habitat fragmentation, will drive reductions in biodiversity
- In addition to direct threats, conservation efforts in New Zealand and other islands must address indirect threats posed by climate change to ensure long-term species protection

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as offshore. Like many archipelagos, New Zealand's terrestrial biota is highly endemic at the species level: for instance, 80% of vascular plants, 86% of mollusks, 81% of arthropods, 60% of vertebrates, 36% of mosses and liverworts, and 30% of lichens are native to the country (Lee and Lee 2015). Of the avifauna, at least 59 species have gone extinct since the onset of human settlement beginning in the mid-13th century, and a further 71 species (of 277) are at high risk of future extinction (Robertson *et al.* 2013). Similarly, 41% (22 of 54 native species) of New Zealand's freshwater fish are classified as threatened (Dunn *et al.* 2018). Although over one-third of the land area of New Zealand is managed as public conservation land, this protection is concentrated in mountain landscapes, and many environments are poorly represented (eg flat lowlands, wetlands), which limits opportunities to safeguard a full complement of biodiversity through public conservation management (Cieraad *et al.* 2015). Moreover, over half (45 of 72) of the naturally rare ecosystems in New Zealand are under threat of functional extinction due to multiple causes, including biological invasions and land-use change (Holdaway *et al.* 2012).

The maritime climate of New Zealand is mild but highly variable. Like many islands, there are strong environmental gradients and a high degree of uncertainty in projected climate change. In addition to the oceanic influence, topographic features drive strong gradients, particularly for precipitation; for example, annual precipitation increases from <2000 mm to >12,000 mm over a distance of <25 km in the western South Island (Whitehouse 1985). Regional projections of future climates suggest that dry parts of the country will become drier and wet parts will become wetter (Reisinger *et al.* 2014). Ex-tropical cyclone intensity is expected to increase, causing severe winds, waves, and rainfall. Coastal zones are particularly vulnerable to rising seas, storm surges, and inundation, as well as higher water temperatures and acidity levels (Rouse *et al.* 2017), and the frequency and severity of extreme events (eg floods, droughts, heat waves, fire conditions) are projected to increase in inland regions.

Climate change has been an important driver of New Zealand's unique evolutionary and ecological history (McGlone *et al.* 2010). Glacial and interglacial cycles during the Quaternary Period have driven the contraction of species distributions during unfavorable times and their expansion as conditions improved (Wood *et al.* 2017), but the palaeoecological record indicates that few species went extinct during these events (Martin and Steadman 1999); this suggests that most species were resilient to past climate change. The wave of extinctions following human settlement in the 13th century occurred during a period of stable climate. Current climate change in New Zealand can be highly variable and difficult to detect (McGlone *et al.* 2010; Lundquist *et al.* 2011). More importantly, the context of contemporary climate change differs from that of the past; habitat loss and fragmentation, land-use change, and extinctions restrict the ability of species to adjust their ranges or survive altered disturbance regimes caused by increasing fire and tropical storm activity. Similarly, invasive species exert additional pressure on restricted populations (Walker *et al.* 2019). Overall, the response of ecosystems to past climates provides important but incomplete insights into how ecosystems will respond to future "no-analog" global changes (Williams *et al.* 2013).

Changing climatic conditions influence biota in multiple ways, depending on a given species' physiological tolerances, as well as through habitat shifts, migration, or even extinction (Dawson *et al.* 2011). Approaches for measuring climate-change impacts are generally either empirical and observational (eg paleoecological records) or mechanistic (eg ecophysiological models; Dawson *et al.* 2011). Globally, few studies have linked species' extinction to anthropogenically induced climate change per se; however, climate change is thought to exacerbate extinction risk by altering such factors as species interactions, food availability, and predator distributions, among others (Cahill *et al.* 2013). Loss of ecological interactions can also erode ecosystem functions prior to species extinction (Valiente-Banuet *et al.* 2015). Long-term datasets with broad geographic coverage provide compelling evidence of biotic responses to climate, including shifts in flowering phenology, ranges of butterflies, and bird migrations (Dawson *et al.* 2011). Such geographical range shifts are often not possible for terrestrial species on island ecosystems because of barriers imposed by habitat fragmentation, or restricted elevation ranges for endemic alpine taxa (Halloy and Mark 2003).

◼ Conservation management

Management of non-native invasive species dominates conservation efforts in New Zealand (eg Russell *et al.* 2015; Simberloff 2019). Invasive mammals, birds, invertebrates, and fish prey on native species and disrupt ecological processes and species interactions. Large-scale eradication of biological invaders is widely viewed as a cost-effective long-term measure for protecting threatened biodiversity (Tershy *et al.* 2015). However, it is unclear if the conservation gains from predator management or removal will persist without attempts to address other interacting processes, including climate change. For example, the "predator-free" New Zealand initiative aims to rid the mainland of introduced rats, mustelids, and possums (Russell *et al.* 2015), but this goal is not yet technically achievable and does not address impacts of other invasive species, such as mice, cats, hedgehogs, and pigs, which are not included in national eradication efforts. Achieving large-scale eradication, managing for reinvasion, and preventing effects from cascading through food webs (Russell *et al.* 2015) present major challenges and knowledge gaps, but if successful will provide novel opportunities for improved conservation management that is generalizable to other systems, provided suitable habitat is available.

Panel 1. Mast seeding in New Zealand: understanding its drivers and potential impacts of climate change

The ecology and evolution of mast seeding has been relatively well studied in New Zealand (Kelly and Sork 2002; Schauber *et al.* 2002), perhaps because of the large numbers of mast seeding species in both forest and alpine environments (Figure 1) and the profound trophic effects of masting. The irruptions of introduced rodents and introduced mustelids as a product of the influx of seeds (King 1983) increase the intensity of predation on native fauna (ie prey switching occurs) after the seed resource is depleted and the rodent population crashes (Innes *et al.* 2010). As such, impacts of climate change on mast seeding are likely to have implications for vulnerable native taxa and conservation strategies for their protection (Hegg *et al.* 2012). Mechanistic modeling suggests that mast seeding is driven by the interaction between temperature as the floral induction cue and stored resources in plants (Monks *et al.* 2016); given that both of these factors are climate-sensitive, it is expected that climate change will impact patterns of mast seeding (Schauber *et al.* 2002; Monks *et al.* 2016). Responses of different masting species to climate change are likely to be spatially variable (Allen *et al.* 2014) and taxon-specific. The effects of climate change on mast seeding species are complex and while a large degree of uncertainty remains, it is one of the better-understood processes that may be influenced by a changing climate in New Zealand.

Figure 1. *Chionochloa* sp snow tussock seeding, Pisa Range, Central Otago, New Zealand.

In addition to the impacts of animal invaders, exotic plant species can displace native species, reduce native biodiversity, and potentially decrease the provision of habitat and food for native animals. These impacts are happening in the context of overlying effects of climate change (Sheppard *et al.* 2016). For instance, highly flammable woody weeds can amplify the effects of more frequent and severe wildfire (Perry *et al.* 2014), potentially exacerbated by interactions with invasive mammals (Perry *et al.* 2015; Taylor-Davis *et al.* 2019). Fire can alter successional trajectories and favor the more fire-adapted non-native taxa over native taxa (Perry *et al.* 2014).

Specific conservation threats in New Zealand are further complicated by agricultural and recreational activities. For example, non-native freshwater sports fish, such as brown trout (*Salmo trutta*), are major predators of native galaxiid fishes, driving declines in these vulnerable species (McIntosh *et al.* 2010). Moreover, recent rapid changes in land use are driving widespread extraction of surface and ground water for irrigation and intensive farming, reducing the quality and quantity of water in rivers and lakes (Scarsbrook *et al.* 2016), which in turn can favor non-native fish that may perform better in a warmer world (Lee *et al.* 2017). The current acceleration of intensive land use in New Zealand is placing additional strain on environmental limits and greenhouse-gas emissions, which also contributes to changes in freshwater quality and biodiversity (Yletyinen *et al.* 2019). Island biota are therefore vulnerable to a large number of interacting environmental stressors, many of which are exacerbated by climate change (Leclerc *et al.* 2018). Threatening processes may be enhanced or concentrated on islands because populations and ranges tend to be smaller. Island ecosystems therefore pose a distinct challenge for conservation, but also offer opportunities to disentangle the direct effects from the indirect effects of climate change on ecological communities, and to refine conservation management to more proactively address future threats.

■ Defining knowledge gaps of direct impacts of climate change on New Zealand's biota

Few studies have detected direct impacts of recent climate change on New Zealand's biodiversity (eg Lundquist *et al.* 2011), but whether this is due to insufficient research effort, system complexity, or a lack of impacts is unknown (Reisinger *et al.* 2014). There is some evidence of ecological effects of climate change (Panel 1; WebPanels 1 and 2), but poor data coverage or study duration differentially limits understanding across taxa and ecosystems. For example, ~10% of studies evaluated in a recent review of predicted climate-change impacts on New Zealand biodiversity reported actual impacts (Lundquist *et al.* 2011). Similarly, McGlone *et al.* (2010) identified ten examples of measured recent climate-change impacts, five of which consisted of research on seabirds. Climate-change impacts are often indirect (operating through an intermediate factor), interactive (where climate-change effects depend on the effects of another factor), or synergistic (producing a combined effect greater than the sum of separate effects), and in all three cases, changing climate exacerbates other stressors such as habitat fragmentation. Attributing indirect effects to climate change is more complicated than identifying direct effects. In any case, both the Fourth and Fifth Assessment reports of the Intergovernmental Panel on Climate Change (Reisinger *et al.* 2014) identified data deficiency as a major problem in quantifying the impacts of climate change on New Zealand's biota, which results in the potential for numerous "unknown unknowns".
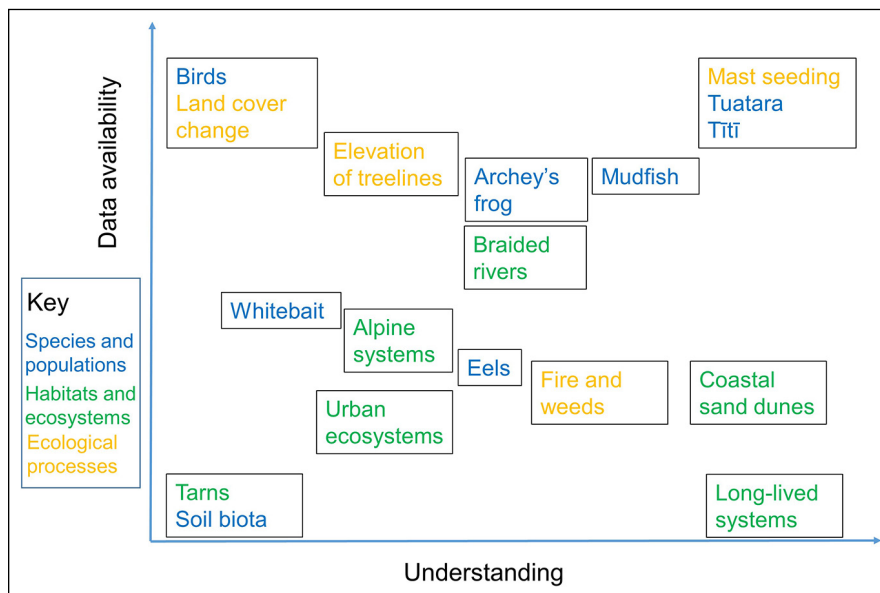
Figure 2. A schematic diagram of a data availability–understanding matrix showing species and populations (blue), habitats and ecosystems (green), and ecological processes (orange) that are vulnerable to climate change in New Zealand. This matrix emerged from a group discussion drawing on a wide spectrum of expertise in ecology, conservation, and Mātauranga Māori (Indigenous knowledge in New Zealand). Items in the same box have similar data availability and understanding. Data availability is self-explanatory, whereas understanding generally requires knowledge, insights, or wisdom. The farther to the right in the space, the better the understanding, and the higher up, the more extensive available datasets are (as a comparative measure only). Increased data availability is not necessarily correlated with improved understanding, because the data format or sampling regime might not be designed to answer questions about climate change. For instance, despite the wealth of information about land-cover change (where it is happening and what it is changing to), there is very little understanding about how this ecological process is influenced by or interacts with climate-change processes. Highlighted taxa include whitebait (*Galaxias* spp), brown mudfish (*Neochanna apoda*), eels (*Anguilla* spp), Archey's frog (*Leiopelma archeyi*), tuatara (*Sphenodon punctatus*), and tītī (*Ardenna grisea*).

Despite incomplete data, several clear examples of biotic responses to changing climatic conditions have been identified, including an increase in male offspring for tuatara (*Sphenodon punctatus*) as temperatures rise (Mitchell *et al.* 2006), and an increased frequency of mast seeding events (Panel 1; Richardson *et al.* 2005). However, the many uncertainties far outnumber examples of well-established impacts. Surveying every taxon and ecosystem across the terrestrial, freshwater, and marine realms is unrealistic. Here, we highlight and discuss the outcome of an expert-guided workshop approach to identifying the species or populations, habitats or ecosystems, and ecological processes most likely to be impacted by climate change. We used our collective knowledge and experience across a range of taxa and ecosystems to position each taxon, ecosystem, and process in a space defined by data availability and understanding (epistemic certainty). The resulting matrix (Figure 2) identifies taxa, ecosystems, and processes that are relatively well or poorly understood, and the relative amount of information available for accurate assessments of climate-change impacts.

Our understanding of the impacts of climate change on mast seeding (Panel 1), tuatara, and culturally important taxa, such as tītī (sooty shearwater, *Ardenna grisea*), is reasonably advanced because data are available for these species and ecological processes. In contrast, we know little about, for instance, soil biota and tarns (Figure 3). Taxa, ecosystems, and processes noted in the bottom left-hand corner of the matrix might be prioritized because they are both poorly understood and have minimal data available. Positioning on this matrix should not be confused with the potential severity of the threat of climate change, as it simply identifies several of the "known unknowns".

■ Indirect impacts of climate change on New Zealand's biota

With the exception of direct loss of island ecosystems to sea-level rise, most impacts of climate change are expected to be indirect: that is, manifested through modification of ecological processes or interactions with other drivers of global change (Tylianakis *et al.* 2008). A well-understood interactive impact of climate change with another stressor is of drought and land-use change driving declines in populations of brown mudfish (*Neochanna apoda*; WebPanel 1). In general, the processes by which climate change affects ecosystems are likely to be complicated, multifaceted (Figure 4), and difficult to detect because of varying life-history strategies (WebPanel 2) and the "noisiness" of short-term datasets. Furthermore, major threats to biodiversity, such as increasing fire risk and non-native-species invasions, are likely to be exacerbated by climate change (WebTable 1). Although the processes exacerbating the direct effects of climate change are intuitive, there are few documented examples of the measurement of indirect impacts. However, predictions of the indirect impacts of climate change – particularly impacts mediated by invasive species – are possible.

Humans have introduced a suite of plants, animals, and microorganisms to New Zealand's ecosystems, many of which have had negative impacts on the native biota (Russell *et al.* 2015). We acknowledge that these introduced pests remain a pressing threat to the biodiversity of New Zealand, but climate change should also be incorporated into management plans for rare and threatened plants and animals, or considered when predicting invasion processes. Many of the characteristics of invasive species that make them problematic (eg greater reproduction or dispersal) may also make

them more resilient to climate change than native species (Sheppard *et al*. 2016). Other mechanisms of threat exacerbation include changes in the interaction of different stressors (eg drought stress and pathogens), increased isolation of already fragmented habitats and populations, and disappearance of suitable conditions and habitats along with a reduction in connectivity.

The success of invasive species following introduction to a new environment can be attributed to broad physiological tolerance (Higgins and Richardson 2014); release from competitors, pathogens, or predators (Mitchell and Power 2003); high levels of phenotypic plasticity (Davidson *et al*. 2011); and rapid evolution (Maron *et al*. 2004). If invasive species can successfully colonize and become established in a new range because of greater tolerance or adaptation to sudden environmental changes, then they may also be more resilient to climate change. There is growing evidence of rapid evolutionary changes for invasive species in their introduced range, reflected in altered morphological (Maron *et al*. 2004) and phenological (Willis *et al*. 2010) patterns, and increased dispersal (Phillips *et al*. 2006). Co-invasions among multiple non-native species can also improve the success or performance of biological invaders. Alternatively, climate change may benefit some invasive species by helping them overcome climatic thresholds; for example, species distribution models validated by field trials show that increases in minimum temperatures (and fewer frosts) will facilitate the spread of subtropical woody weeds in New Zealand (Sheppard *et al*. 2016). In such instances, the future risk of invasion and the management responses required will shift.

A likely yet poorly understood driver of climate-driven indirect effects on island biota is distributional change of existing invasive species causing greater overlap between non-native and native species' ranges. For example, little is known about the influence of Australian brown tree frogs (*Litoria ewingii*; Figure 4a) on New Zealand pond ecosystems; however, these frogs are currently invading South Island alpine tarns (Figure 3), which are themselves poorly studied and vulnerable to climate change (Wissinger *et al*. 2016). In contrast, some effects of climate-driven habitat shifts are predictable, based on knowledge of well-studied invaders like trout (Figure 4b). For example, native alpine galaxiid fish are restricted by warm summer temperatures at one extreme of their temperature range, and by introduced predatory trout at the other extreme (Boddy and McIntosh 2017). As such, rising alpine stream temperatures will shift the distribution of suitable alpine habitat for both galaxiids and their predators, creating complex shifts in the spatial distribution of usable habitat for galaxiids.

Figure 3. Tarns (alpine ponds) in the Kelly Range in the western part of Arthur's Pass National Park, New Zealand. Tarns were (a) full during January 2017, and (b) dry or partially dry in July 2017 following an extremely dry autumn.

In island ecosystems, where variable climates are often the norm, extreme climate events are likely to interact with land-use change to deleteriously affect vulnerable populations. In the case of brown mudfish metapopulations, human-driven land-use change appears to act synergistically with climate change to undermine the processes that confer metapopulation persistence in the face of climate-driven environmental stochasticity. As such, even large mudfish populations are therefore likely to be vulnerable when human disturbances occur alongside increased frequencies of extreme events under climate warming (see WebPanel 1).

The interactive effects of climate change will not always be negative, however. Because natural disturbances are often a critical driver of biodiversity, increases in the frequency of extreme events may in some cases have transient positive effects. In the case of the brown mudfish, a tornado that knocked down a swath of trees in a forest (Figure 4c) greatly increased suitable mudfish habitat, thereby enhancing metapopulation persistence in the face of drought (White *et al*. 2016). Similarly, small increases in stream temperature restrict the habitat of non-native trout, releasing native alpine galaxiids from predation and increasing the amount of suitable galaxiid habitat (Boddy and McIntosh 2017). However, because the thermal ranges of these fish may be relatively small, larger increases in stream temperature (eg 5°C) can negatively affect both introduced and native species (Boddy and McIntosh 2017).

Two high-profile examples of conservation threats in New Zealand that may be exacerbated by climate change exist. First, the destruction of restored areas in the Port Hills of

Figure 4. Likely drivers of indirect effects of climate change on island ecosystems, including: (a) range expansion of invaders, such as the upslope movement of the Australian southern brown tree frog (*Litoria ewingii*) into tarns above treeline; (b) alteration in the range of current invaders, such as trout driven by altering temperatures or environmental extremes such as drought-induced stream drying; and (c) alterations in both natural and human-driven disturbance regimes, such as tornadoes and logging, that have positive and negative effects, respectively, on the habitat quality of brown mudfish living in South Westland tree tip-up pools (formed when a tree falls) and their subsequent ability to survive drought.

Christchurch (South Island) by fire is likely to lead to accelerating invasion by fire-adapted weeds (eg gorse, *Ulex europaeus*). The reproductive cycle of this weed is stimulated by heat, whereas such adaptations are rare among native plants (Perry *et al*. 2014). Pyrogenic weeds are likely to further exaggerate climate-change-induced increases in fire frequency because of their greater flammability compared to native plants. Second, rising sea temperatures threaten the food supply of yellow-eyed penguin (hoiho, *Megadyptes antipodes*). When sea-surface temperatures warm, adult survival declines, most likely due to complex food-web responses; such events are expected to occur more frequently across the country in the future.

▪ Mātauranga Māori as an example of Indigenous knowledge

For many of the world's Indigenous peoples, the natural environment is intrinsic to life (Bond *et al*. 2019; Lyver *et al*. 2019). In New Zealand, Māori have developed customary practices to sustainably manage their resources, and evidence suggests that past climates shaped Māori land-use and horticultural practices (Anderson 2016). Māori-sourced Indigenous knowledge (IK), referred to as Mātauranga Māori, has an increasingly vital role in environmental management and kaitiakitanga (guardianship), including protection of taonga (treasured) species from the threats of invasive species and climate change (Bond *et al*. 2019).

Long-term written datasets are rare in New Zealand, in part because of relatively recent European colonization and the comparatively sparse scientific population. However, Mātauranga Māori holds a wealth of information on climatic conditions that can enhance our understanding of long-term climate variability and the interaction between climate events and ecosystems. For instance, the Māori calendar, maramataka, has been developed over centuries of observations (Hikuroa 2017) and hāpu (subtribes) have their own location-specific maramataka to provide guidance for the timing of gathering mahinga kai (traditional food sources), including fish and other seafood, planting crops, and harvesting food. Because this calendar is based on knowledge that has accrued over generations, some changes in timing and distributions due to environmental change may be captured in the oral histories of these complex frameworks. For instance, oral records of access to and use of mahinga kai provide evidence of a changing climate, whereby chick size and adult abundance of sooty shearwater were both negatively impacted by the El Niño Southern Oscillation (ENSO; Humphries and Möller 2017). Collectors of mahinga kai were the first to identify these patterns, and because ENSO is intensifying, sooty shearwaters will require careful management in a changing climate to maintain this traditional food source. Similarly, Bond *et al*. (2019) modeled access to two culturally important plant species used for medicinal and weaving purposes. Species distribution models indicate that through changes in distribution, access to these species may decrease in some parts of the country under future climate projections. Co-developed projects can use the best of all knowledge systems to achieve effective conservation under climate change. For example, Geary (2010) used IK interviews, empirical data, and population modeling to predict sustainable harvest sizes for tītī, and demonstrated that population numbers will likely fluctuate to a greater degree in the future and that careful monitoring is required to ensure the continued survival of small populations.

▪ Conclusions

We draw on examples from New Zealand to illustrate that many island ecosystems are potentially more vulnerable to indirect than direct effects of climate change. Improving knowledge of these indirect processes and drivers is an opportunity to refine and improve long-term conservation management; as such, climate-change research should be incorporated in all conservation research and management

plans to ensure that current conservation gains persist over the longer term (Nelson *et al.* 2019). Many current threats, such as biological invasions, may be exacerbated under climate change, requiring a better understanding of both data availability and knowledge to identify "known unknowns" regarding conservation vulnerabilities (Figure 2). Few species or ecosystems have been studied comprehensively, creating potential deficiencies in either data or knowledge. However, there are opportunities to overcome some of these potential limitations. For example, data deficiencies can be addressed by uncovering databases or information lost or stored in unusual places, or through support of geographically distributed datasets like the Terrestrial Ecosystem Research Network in Australia. Such datasets have a range of applications, including identifying ecological responses to drivers of ecosystem change and understanding complex ecosystem processes that occur over extended timeframes (Lindenmayer *et al.* 2012). Knowledge gaps and important insights into complex processes can also be addressed, at least in part, through greater inclusion of Indigenous peoples into co-development of knowledge and conservation practice. Respectful partnerships and inclusion of Mātauranga Māori has additional benefits for conserving or renewing culture and peoples' connection to the environment in New Zealand (Lyver *et al.* 2019). Island ecosystems are distinct from mainland systems because they are isolated, influenced by oceanic climates, have high rates of endemism and extinction, and are frequently threatened by invasive species (Whittaker *et al.* 2017). Indirect and interactive effects of climate change must be incorporated alongside direct effects to anticipate and mitigate the impacts of climate change on island ecosystems.

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