

Current Changes in Alpine Ecosystems of Pacific Islands

Abby G Frazier, East-West Center, Honolulu, HI, United States; University of Hawaii at Manoa, Honolulu, HI, United States

Laura Brewington, East-West Center, Honolulu, HI, United States

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Abstract

Alpine ecosystems in the Pacific Islands are isolated and unique, characterized by high levels of endemism. Only Hawai'i and New Zealand have elevations high enough to contain substantial alpine climates, and about 11% of the land area of both island groups is located above treeline. Both of these volcanically active archipelagos are characterized by complex topography, with peaks over 3700 m. These alpine ecosystems have significant cultural, social, and economic value; however, they are threatened by invasion of exotic species, climate change, and human impacts. Nonnative ungulates reduce native shrubland and grassland cover, and threaten populations of endangered birds. Exotic plants alter water yields and increase fire risk, and increased recreational visitation to these remote areas facilitates the introduction of exotic plant seeds, pests, and pathogens. Both New Zealand and Hawai'i have experienced strong warming at higher elevations, and future projections indicate that these robust warming trends will continue. Glacial retreat has been noted in the Southern Alps, with 34% ice volume lost since 1977, and New Zealand may lose 88% of its ice volume by 2100. Snowfall on Hawai'i's mountain peaks is projected to almost entirely disappear by 2100. Changes are occurring rapidly, and additional monitoring and research are needed to conserve these uniquely sensitive, remote regions.

Introduction

Alpine ecosystems occur above the altitudinal limit of forests, known as the treeline. Complex mountainous topography leads to climates that change rapidly with elevation over short distances, resulting in steep gradients in vegetation and hydrology. Alpine ecosystems are often characterized as biodiversity "hotspots" and by high levels of endemism due to the isolation of species at high elevations (Beniston, 2003). On oceanic islands, geographic isolation has further contributed to the endemism found in these rare, unique alpine environments, and they are subject to markedly different oceanic-influenced climates than continental areas (Harter et al., 2015). Treelines here are also found at lower elevations than mainland treelines and are likely controlled by regional climatic factors (Irl et al., 2016).

Many studies have suggested that alpine ecosystems are among the most sensitive to climatic changes (e.g., Diaz et al., 2003), and growing evidence indicates that high mountain environments are warming faster than lower elevation areas (Pepin et al., 2015). This enhanced warming with elevation can accelerate the rate of change in mountain ecosystems, requiring species to respond by acclimating, adapting, moving, or facing extinction (Corlett and Westcott, 2013). For many alpine species, warming is expected to cause substantial range losses (Dullinger et al., 2012), and evidence indicates that many plant species will not be able to keep up with rapid changes in climate expected in the 21st century (Corlett and Westcott, 2013). For islands, the threat of climate change is even greater as native species are often poor competitors against introduced species, have limited potential to migrate because of the surrounding ocean, and for species at the highest elevations, migrating further upward is not possible (Harter et al., 2015). Climate change impacts on high islands can therefore result in a disproportionately high potential for global biodiversity loss.

Changes in high elevation ecosystems and the resources they provide can also be driven by numerous other factors, including overgrazing by livestock, invasion by nonnative species, land use change, and environmental stress from human activities (Beniston, 2003). Islands in particular are more vulnerable to anthropogenic impacts due to their limited land areas (Kier et al., 2009). Alpine ecosystems are susceptible to landslides, soil erosion, and loss of biodiversity and endemic species. Changes to these ecosystems impact the landscape, hydrological regimes, and water resources, with downstream impacts to the lowland areas and a wide range of socioeconomic consequences (Diaz et al., 2003).

In the Pacific Ocean, islands range in size from small low-lying coral atolls at sea level to large islands with volcanic peaks at 4200 m. Alpine ecosystems in the Pacific Islands are primarily concentrated in Hawai'i, New Zealand (Aotearoa), and Papua New Guinea. It should be noted, however, that Tahiti in French Polynesia (maximum elevation 2241 m) and Vanuatu (1879 m) contain some subalpine shrublands with low scrubby and herbaceous vegetation above the cloud forest on the highest peaks (Leuschner, 1996; Meyer et al., 2010). The Solomon Islands (2335 m) are forested to the summits with some local *Sphagnum* moss alpine bogs (Leuschner, 1996). Australia also contains approximately 11,500 km² of alpine and subalpine habitat concentrated mainly in the southeast of the continent and the island of Tasmania (Williams et al., 2008). For more information on alpine ecosystems of Australia, please refer to McDougall and Walsh (2007), Slatyer (2010), and Kirkpatrick (1983). This article focuses on characterizing current changes in alpine environments of Hawai'i and New Zealand. The section "High Elevation Ecosystems in Pacific Islands" describes the vegetation and climate of these ecosystems, while the "Current Changes" section describes current changes in these regions, followed by a "Concluding Remarks" section.

High Elevation Ecosystems in Pacific Islands

Geologic Setting

New Zealand's approximately 260,000 km² of land area today represents only 5% of a much larger, submerged continent known as Zealandia. New Zealand (Fig. 1) is a mountainous country located between 34° and 47°S latitude and 166° to 179°E longitude. Around 11% of the total land area is above the treeline (Halloy and Mark, 2003). The highest point above sea level is Aoraki/Mount Cook (3754 m) located in the Southern Alps on the South Island, and another 222 named peaks have elevations >2300 m (Campbell et al., 2012). Alpine areas on the North Island are limited to a few peaks above treeline, and only the active stratovolcano Mount Ruapehu (2752 m) supports glaciers (Chinn, 2001). The Southern Alps were created by the collision of the Pacific and Australian plates, starting about 5 million years ago, and were extensively glaciated around 20,000 years ago during the Last Glacial Maximum. The Alpine Fault spans the length of the Southern Alps from north to south and regularly produces large earthquakes, which, along with erosion and tectonic activity, have shaped the unique mountain topography found today (Campbell et al., 2012). Active volcanic areas are confined to six areas: five in the North Island and one offshore to the northeast. From a geophysical standpoint, New Zealand possesses characteristics of both islands and continents, so it is not surprising that its remarkable biodiversity occurred as a result of both dispersal from nearby land masses and evolution from ancestors of Zealandia (Wallis and Trewick, 2009).

The Hawaiian archipelago lies in the center of the Pacific plate between 18° and 23°N latitude and 160° and 154°W longitude and was formed by volcanic activity as the plate slowly moved over a hotspot (Macdonald et al., 1983). The islands extend over 2400 km from Hawai'i Island in the southeast to Kure Atoll in the northwest, ranging in age from 0.5 to 28 million years. Hawai'i is nearly 4000 km from the nearest continent, and is one of the most isolated major archipelagos in the world. Eight main islands (Fig. 2) have a land area of 16,637 km² (Juvik and Juvik, 1998), of which Hawai'i Island is the largest and contains three of the four highest peaks: Mauna Kea (4205 m), Mauna Loa (4169 m), and Hualālai (2521 m). Mauna Loa and Hualālai are active shield volcanoes; Mauna Kea is a dormant shield volcano (Juvik and Juvik, 1998). To the west of Hawai'i Island is the island of Maui, whose tallest peak, Haleakalā (3055 m), is also an active shield volcano (Juvik and Juvik, 1998). These four peaks are home to all of Hawai'i's alpine and subalpine vegetation, and similar to New Zealand, Hawai'i's tropical alpine and subalpine regions comprise ~11% of the land area.

Climatology

The climates of Pacific Island highlands are subject to strong influences from the surrounding ocean, and precipitation patterns are predominantly driven by orographic processes. Interdecadal and decadal climate variability are driven by large-scale modes of variability, including the El Niño-Southern Oscillation (ENSO) (Frazier et al., 2018; Sturman and Wanner, 2001). New Zealand experiences westerly winds in the mid-latitudes, while Hawai'i is subject to northeast trade winds in the tropics, and the perpendicular orientation of the mountains to the prevailing moisture-laden winds results in extremely wet windward areas (over 10,000 mm year⁻¹ on both the western slopes in New Zealand and the eastern slopes in Hawai'i; Giambelluca et al., 2013; Hendrikx et al., 2012). Extreme gradients characterize both archipelagos, with a stark contrast in the rain shadow of the dry leeward areas where precipitation can be as little as 500 mm year⁻¹ in New Zealand and ~200 mm year⁻¹ in Hawai'i (Giambelluca et al., 2013; Tait et al., 2006). Mean annual temperatures range from -6.9 to 8.2°C and from 3.6 to 10°C in alpine areas of New Zealand and Hawai'i, respectively (LENZ, 2010; Giambelluca et al., 2014). In New Zealand, cold fronts originating along the eastern side of the mountain range can cause sudden drops in temperature and increases in humidity, with damaging winds (Sturman and Wanner, 2001). Wind speeds exceeding 160 km h⁻¹ have been recorded at the higher elevations in New Zealand. New Zealand experiences extensive seasonal snow cover (Hendrikx et al., 2012), while in Hawai'i, snow occasionally falls on the highest mountains, although no direct measurements of snow are currently recorded (Zhang et al., 2017). In Hawai'i, high elevation areas have some of the lowest evapotranspiration and rainfall rates, the lowest cloud frequency and relative humidity, and the highest solar radiation (Giambelluca et al., 2014). These climate patterns are largely driven by the presence of an atmospheric inversion layer around 2150 m, known as the Trade Wind Inversion (TWI), which caps cloud growth and produces extremely dry, sunny conditions above

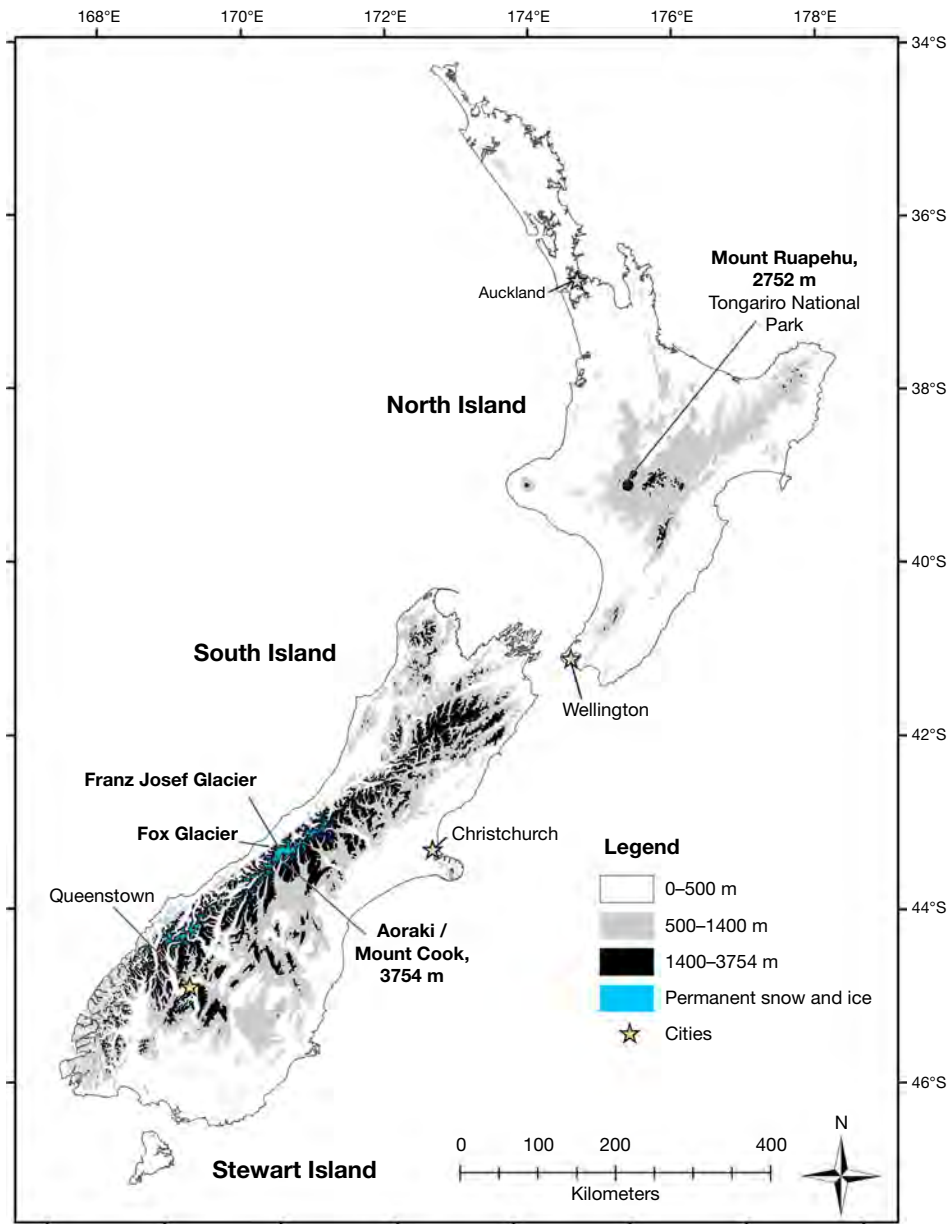


Fig. 1 Elevation zone map of New Zealand showing land above the approximate treeline elevation. Some individual summits and glaciers discussed in the text are labeled.

(Longman et al., 2015a). This sharp change in moisture availability, combined with extreme El Niño-induced drought events, is thought to drive the position of the treeline (Crausbay et al., 2014).

Ecological Zones and Plant Communities

Treelines in New Zealand occur within similar thermal ranges as in other sites worldwide (although at lower elevations; Cieraad et al., 2014). The high altitude tree limit in New Zealand's alpine regions is dominated by two species of evergreen *Nothofagus* trees ranging from ~1000 m in the southern part of the Southern Alps to ~1400 m on the North Island (Wardle, 2008). Above the treeline, the vegetation of the high mountains (Fig. 3) consists of a lower alpine zone dominated by shrubs and tall tussock grasslands and a high alpine zone dominated by dwarfed plant communities and grasslands (Mark et al., 2000). There are no native mammalian herbivores in this region. The snow tussock lands (*Chionochloa* spp.) in the southeastern South Island are known to intercept large amounts of fog that contribute substantially to the water yield from these uplands (Mark et al., 2013). Above the high alpine zone lies the permanent snowline, which is the lower limit of the nival zone (Mark et al., 2000). Areas of permanent snow are extensive along the central Southern Alps and in the southern part of the range (Fig. 1). Over 3000 glaciers have been identified, and

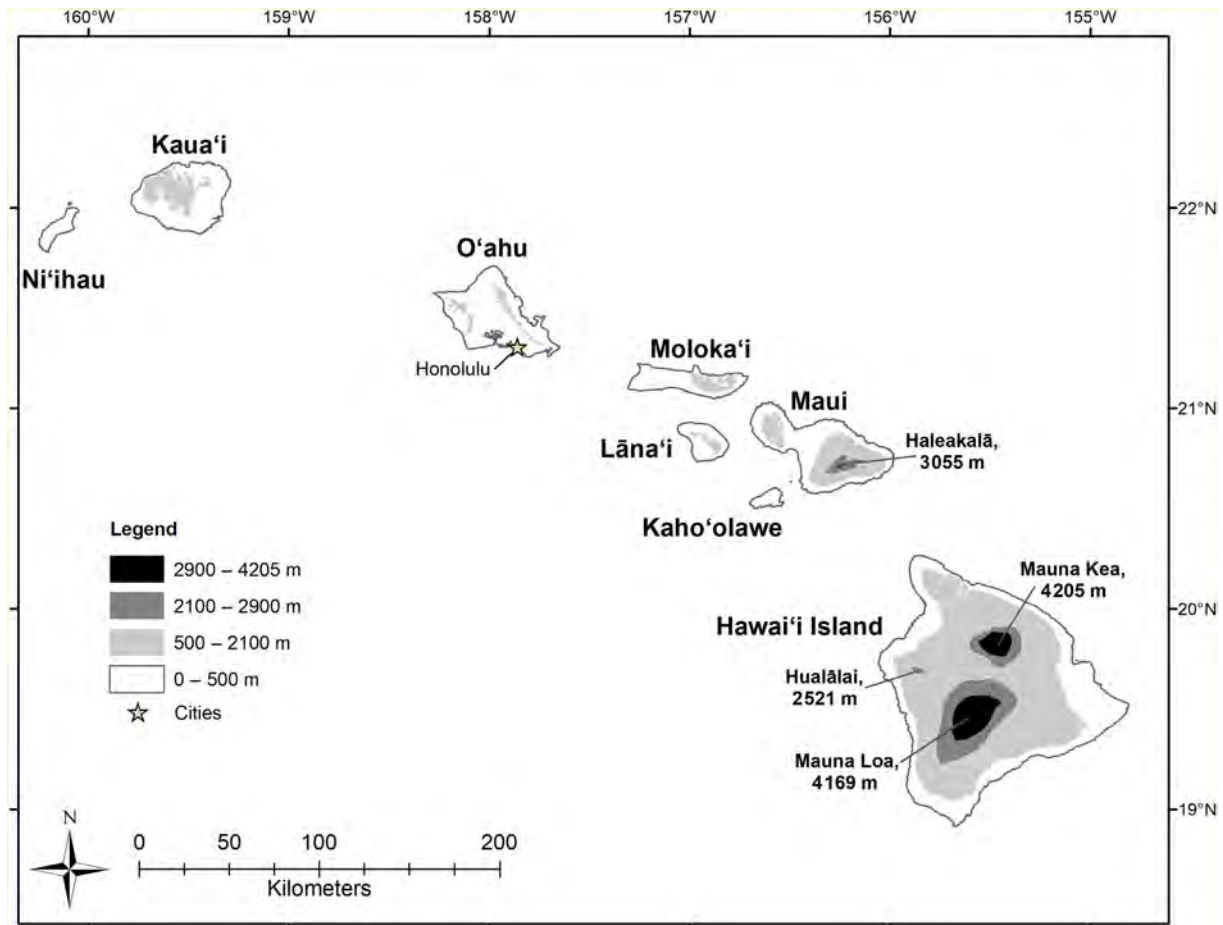


Fig. 2 Elevation zone map of the main Hawaiian Islands showing land above the approximate treeline elevations. Some individual summits discussed in the text are labeled.

as a result of the strong precipitation gradient they range in elevation from ~ 1600 m in elevation in the west to ~ 2500 m in the east (Chinn, 2001). Terminal alpine lakes are frequently present at the base of glaciers (Fig. 3A). Permafrost is found at the higher elevations in the central part of the range (Sattler et al., 2016).

In Hawai'i, between ~ 2000 and 3000 m are subalpine forests, woodlands, and shrublands. The treeline of Mauna Kea is typically defined as the upper extent of the māmane (*Sophora chrysophylla*) woodland and is located ~ 2900 m above sea level (Gerrish, 2013; Leuschner, 1996). The treelines of Mauna Loa and Haleakalā are at least 450 m lower than on Mauna Kea, which may be due to soil-dependent factors (Leuschner, 1996). Along parts of the northeastern slope of Haleakalā, the treeline occurs around 2100 m and is delineated by plantations of conifers that were introduced in the early 1900s. In other areas, treeline elevation varies and is made up of native subalpine cloud forest dominated by ōhia (*Metrosideros polymorpha*), which gives way to alpine shrublands, herbs, and tussock grasslands that form a fog-drip community of alpine scrub (Crausbay and Hotchkiss, 2010). Alpine desert conditions exist on Maui and Hawai'i Island above ~ 3000 m. These are dry and semibarren, with dwarf native shrubs dominated by pūkiawe (*Styphelia tameiameia*), ōhelo (*Vaccinium reticulatum*), 'āhinahina or Hawai'i silversword (*Argyroxiphium sandwicense*), and na'ena'e (*Dubautia* species). At the summits, eolian deserts (also called stone deserts, Fig. 3C) are populated with grasses, mosses, and lichens (Gerrish, 2013; Juvik and Juvik, 1998).

Mauna Kea was home to a 70 km^2 ice cap until 15,000 years ago, which left conspicuous, preserved moraines (Anslow et al., 2010). Despite mean annual temperatures well above freezing, perennial ice is present as permafrost inside two cinder cones on Mauna Kea and two lava tube ice caves on Mauna Loa (Schörghofer et al., 2018). Hawai'i's only alpine lake, Lake Waiau (3970 m) (Fig. 3D), is found in the Pu'u Waiau cinder cone on the slopes of Mauna Kea and is fed primarily by winter storms (Ehlmann et al., 2005), though there is concern over recent declining lake levels (Patrick and Kauahikaua, 2015). Pu'upōhaku pond (4000 m) is a nearby sporadic pond that was only recently recognized (Leopold et al., 2016). Given the porous nature of basaltic lava (which cannot hold water to form lakes), the causes of these permanent water bodies on Mauna Kea remain unknown.



Fig. 3 Alpine summits, glaciers, and lakes: (A) Mueller Glacier and Mount Cook, Aoraki/Mount Cook National Park, New Zealand; (B) Tongariro Alpine Crossing, Tongariro National Park, New Zealand; (C) Mauna Kea Summit, Hawai'i; (D) Lake Waiiau, Mauna Kea, Hawai'i. Photo credits: (A) Vern (CC, Flickr); (B) Andrea Schaffer (CC, Flickr); (C) Laura Brewington; (D) Thomas Tunsch (CC, Flickr).

Cultural Significance and Human Impacts

Globally, alpine environments are associated with cultural identity, spiritual practices and religious ceremonies, and the provision of ecosystem services such as food and water, natural hazards regulation, and tourism and recreation (Palomo, 2017). The mountains of New Zealand are immensely important to the Māori way of life and sense of place, with individual peaks seen as representations of ancestors (Pawson and Egli, 2001). Human impacts on the vegetation since the arrival of the Māori ~1000 years ago, however, have been pervasive. Fires in the region significantly altered the vegetation composition, allowing high-alpine plants to extend their ranges into low-alpine tussock grasslands (Halloy and Mark, 2003). European discovery and settlement of this region occurred in the 17th century (Pawson and Egli, 2001) and subsequent economic interests in the region included a brief gold rush, logging, coal mining, and agriculture (Balcar and Pearce, 1996), followed by a tourism boom in the late 20th century. Hiking, hunting, fishing, and skiing/snowboarding are permitted in many of the country's high elevation parks, nature reserves, and scenic areas, although special protected areas of high conservation value have been designated within them (Fig. 3B, Fig. 4A,B) (Mark et al., 2013). Today New Zealand's nature tourism industry generates 6% of the country's GDP and attracts upward of 3 million international visitors a year; only the dairy industry contributes more to the national economy (Stats, 2017). "Glacier Country" in the Southern Alps alone receives over 600,000 visitors a year between Franz Josef and Fox Glaciers (Purdie, 2013).

Native Hawaiian tradition states that deities reside in the high mountain summit areas of the archipelago, and Mauna Loa, Mauna Kea, and Haleakalā are therefore regarded as sacred places of great spiritual importance. The summit of Mauna Kea, the tallest point in Hawai'i, is extremely culturally significant as its peak is considered the *piko* (umbilical cord) of the Hawaiian spiritual world, connecting the Earth, heavens, and stars (Ho'akea, 2009). Lake Waiiau is culturally significant to Native Hawaiians as a source of healing water used for ceremonies and worship (Ho'akea, 2009). Most of Hawai'i's alpine regions fall into various conservation zones, which have historically shielded them from development and other human impacts. Nevertheless, Haleakalā National Park on Maui is visited by 1–2 million people a year, established roadways and trail networks provide relatively easy access to all alpine sites, and the construction and operation of astronomical observatories—particularly those near the summit of Mauna Kea—have been the subject of debate for decades due to their impacts on native ecosystems and culturally important sites (Fig. 4C,D) (Hilberg et al., 2018).

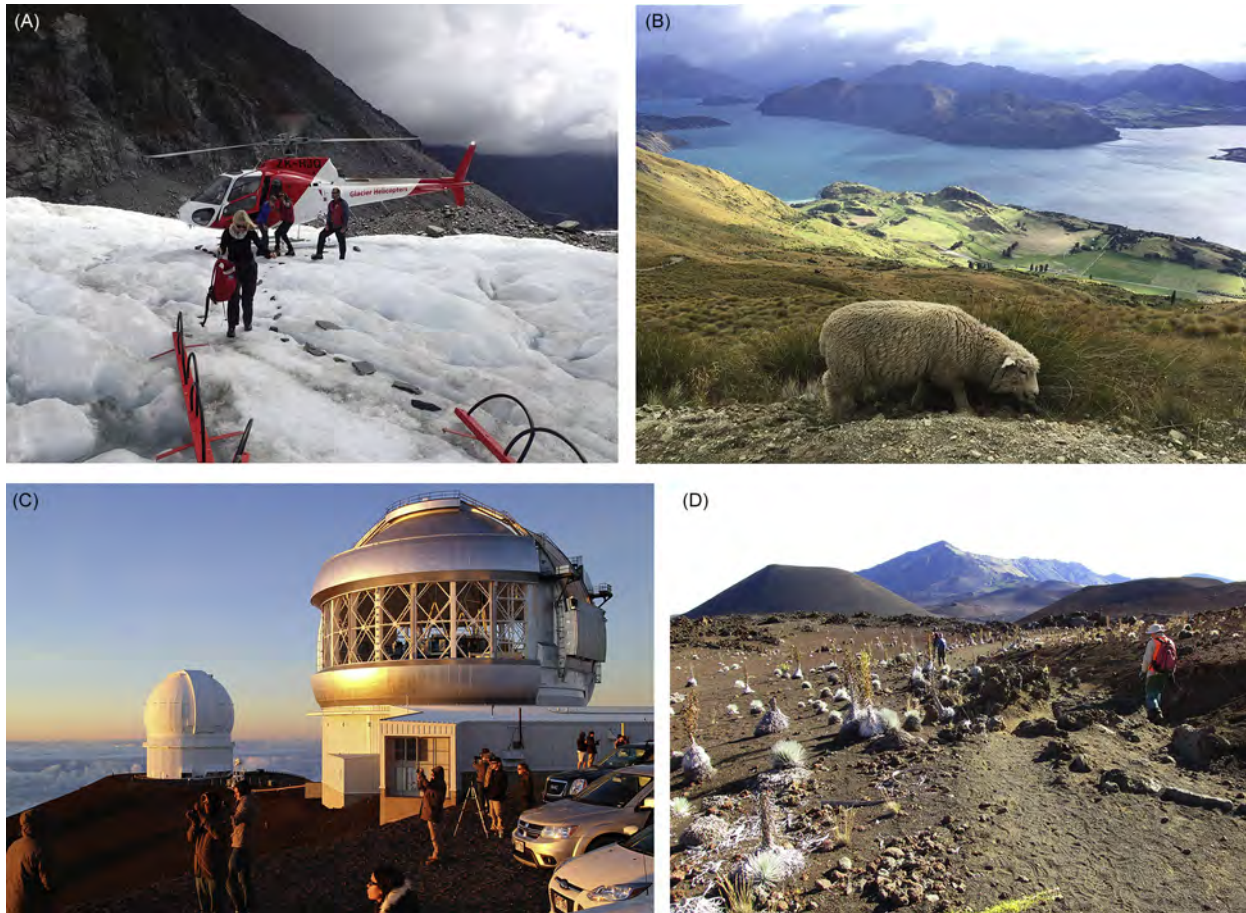


Fig. 4 Human interactions with alpine regions: (A) helicopter tourism operation, Fox Glacier, New Zealand; (B) grazing sheep near Wanaka, New Zealand; (C) tourism and astronomical observatories, Mauna Kea, Hawai'i; (D) popular hiking trails through Haleakala crater, Maui, with many flowering silverswords. Photo credits: (A) Abby Frazier; (B) Laura Brewington; (C) Laura Brewington; (D) Forest & Kim Starr.

Current Changes

Changes in Native and Invasive Species

In New Zealand's Southern Alps, extensive radiations of vertebrate and invertebrate alpine communities have been facilitated by the relatively recent tectonic activity and partial glaciation (Wallis and Trewick, 2009), most notably plants and some birds, such as the kea (*Nestor notabilis*) and rock wren (*Xenicus gilviventris*) (Fig. 5A,C). Like other oceanic islands, New Zealand has very high rates of endemism (around 30% of plants and 82% of animals; Gordon, 2013); many of the endemic birds are partially or completely flightless (e.g., South Island takahē (*Porphyrio hochstetteri*), Fig. 5B). In the alpine region, over 90% of plants are endemic (Halloy and Mark, 2003). O'Donnell et al. (2017) recently identified 24 native alpine bird species that are characteristic of the Southern Alps region, 17 of which are considered to be at risk. Cold-tolerant lizards (including geckos and skinks), invertebrates like the wētā (*Deinacrida* species) (Fig. 5D), cicadas, giant carnivorous land snails, butterflies, moths, giant wingless stoneflies, and freshwater fish are among the other indigenous biota found at these high altitudes (O'Donnell et al., 2017). The kea, the world's only alpine parrot, was the target of an official campaign from the late 1800s until 1971 to reduce their numbers due to attacks on farm animals (Young et al., 2012), and the New Zealand Department of Conservation (2017) estimates that there are fewer than 7000 today. During the growing season, kea feed extensively on fruiting plant species in the alpine region and as the only species that is known to fly long distances between mountains and ranges, they are significant contributors to alpine plant dispersal in New Zealand (Young et al., 2012).

In the alpine and subalpine ecosystems of Hawai'i, 84% of floristic species are endemic, with more species on Maui than Hawai'i Island despite a much smaller land area and elevational range (Price, 2004). One of the most iconic endemic alpine species, the Hawaiian silversword, is extremely vulnerable to warmer and drier conditions that have been experienced in recent decades (Krushelnycky et al., 2013). The Hawaiian alpine Wēkiu bug (*Nysius wekiuicola*), first discovered in 1979, is a rare endemic, flightless insect species found within a narrow elevation range (3415–4205 m) in the alpine stone desert zone of Mauna Kea that survives on wind-borne insect carcasses blown up from lower elevations (Stephenson et al., 2017). Seabirds, such as the 'ua'u (Hawaiian petrel,



Fig. 5 Endemic alpine and subalpine fauna. New Zealand: (A) Kea; (B) Takahē; (C) Rock Wren; (D) Alpine Scree Wētā (*Deinacrida connectens*). Hawai'i: (E) Nēnē; (F) Palila. Photo credits: (A) Tomas Sobek (CC, Unsplash); (B) Larry Koester (CC, Flickr); (C) Francesco Veronesi (Wikimedia Commons); (D) Danilo Hegg; (E) Forest & Kim Starr; (F) Jack Jeffrey, USGS (Wikimedia Commons).

Pterodroma sandwichensis), are also observed throughout Hawai'i's alpine regions (Banko et al., 2001), and alpine grasslands and shrublands also provide habitat for the endangered state bird of Hawai'i, the nēnē (Hawaiian Goose, *Branta sandvicensis*) (Fig. 5E).

The Hawaiian Islands once had abundant endemic avian biota. Mosquito-borne avian pox and avian malaria, however, have resulted in widespread mortality of forest birds and a shift to higher elevations where colder temperatures inhibit mosquito reproduction (Liao et al., 2015). 'Ōma'o (*Myadestes obscurus*), one of only two remaining species of endemic solitaire birds, have been observed in the scrub alpine environments of Hawai'i Island where they are vulnerable to predation by cats and rats (Judge et al., 2012). They, like most of Hawai'i's native forest birds, have lost an enormous proportion of their native range (estimated 70%) due to land cover change and nonnative species invasions, impacts that are expected to be exacerbated by projected changes in climate (Fortini et al., 2015). The palila (*Loxioides bailleui*), a species of critically endangered Hawaiian honeycreeper (Fig. 5F), is almost entirely dependent on the endemic subalpine māmane tree for its food, and has experienced drastic range reductions due to

browsing pressure from introduced ungulates that have degraded its habitat. This species is at high risk for extinction with the simultaneous threats of drought, wildfire, and invasive ungulates (Banko et al., 2014).

The alpine regions of the world are often viewed as being relatively resistant to biological invasions, due to their extreme climate and inaccessibility to humans (Pauchard et al., 2016). However, climate change, human-driven environmental degradation, and land use change facilitate species invasions, to which the isolated alpine ecosystems in the Pacific Islands are particularly vulnerable. The first known mammalian predator to arrive to New Zealand was the Polynesian rat around 800 years ago, but the vast majority of pests were introduced after European settlement in the 1800s (Wallis and Trewick, 2009). Feral populations of red deer (*Cervus elaphus scoticus*) and rabbits (*Oryctolagus cuniculus*) exert significant pressure on New Zealand's alpine grasslands above the treeline, while grazing livestock (primarily sheep, *Ovis aries*) also influence the vegetation cover and species makeup. In particular, native tussocks have declined in favor of invasive herbs in areas with a long history of summer livestock grazing (Norton and Young, 2016). Significant reductions in red deer populations in the Southern Alps have led to the recovery of native shrublands and grasslands in both number and size, however, suggesting that long-term management practices and exclusion of ungulates from sensitive areas can lead to successful restoration (Tanentzap et al., 2009). Himalayan tahr (*Hemitragus jemlahicus*) (Fig. 6A) was introduced to New Zealand's Southern Alps in 1904 as a hunting resource, which reproduced rapidly and reduced native tussock plant species to bare ground. While some efforts to reduce their numbers have been made, the population has continued to increase with long-term impacts on native alpine grassland communities (Cruz et al., 2017). New Zealand's ground-dwelling native alpine birds are particularly susceptible to predation by invasive mammals, including feral cats, stoats, and mice, which have been primarily responsible for their decline (Weston et al., 2018). Alpine populations of endangered takahē and rock wren have been extensively reduced by stoats (*Mustela erminea*) (Fig. 6B) (O'Donnell et al., 2017). Almost half of the country's endemic birds have gone extinct, while limited remaining populations are more vulnerable to changes in climate, extreme events, and disease (Innes et al., 2010).

Invasive ungulates, including pigs, cattle, and goats, have also severely impacted Hawaiian alpine ecosystems at various times over the last 200 years, particularly above the TWI in grassland-dominated areas (Daehler, 2005). This has coincided with soil erosion and nonnative plant invasions that have further reduced alpine plant community regeneration (Daehler, 2005). While goat and cattle populations have been greatly reduced on Hawai'i Island, feral sheep and mouflon have not yet been eradicated. Goats were eradicated from Maui in 1989 but axis deer are increasing in number (Hess, 2016). Removal of ungulates from a subalpine region of East Maui resulted in significant increases in relative cover of native shrubs and ferns, and a decrease in alien grass cover



Fig. 6 Invasive Species: (A) Himalayan Tahr near Cameron Glacier, Canterbury, New Zealand; (B) Stoat, New Zealand; (C) *Pinus radiata* (Monterey pine) in the subalpine shrubland, Haleakalā, Maui; (D) National Park Service installing an 8 km long cat-proof fence to protect endangered Hawaiian petrel habitat on the slopes of Mauna Loa, Hawai'i, 2400–3000 m elevation. Photo credits: (A) Jake Osborne (CC, Flickr); (B) Soumyajit Nandy (Wikimedia Commons); (C) Abby Frazier; (D) NPS.

(Hughes et al., 2014). Other invasive mammals, such as cats and mongooses, are rarely observed in Hawai'i's alpine locations, but are still a concern (Fig. 6D). Mice and rats, however, persist at all elevations and are especially abundant near food sources and visitor sites (Vanderwoude et al., 2015). Invasive social insects, such as the Argentine ant (*Linepithema humile*) that has been documented at Haleakalā National Park for the past 25 years (Hartley et al., 2010), have the potential to alter alpine native invertebrate communities and may enter new habitat ranges as the climate continues to warm, disturbing native ecosystems as well as visitor sites (Vanderwoude et al., 2015).

Transportation networks are a main driver species introductions to mountain systems (Alexander et al., 2016), and recreational tourist visitation to Haleakalā National Park, Mauna Kea, and Mauna Loa has facilitated the introduction of invasive plant seeds, pathogens, and insects into higher elevations in Hawai'i (Daehler, 2005). Backcountry huts in New Zealand have also been identified as important sites for invasion by nonnative plant species into remote alpine areas (Lloyd et al., 2006). The area around Lake Waiau on Mauna Kea experiences high levels of visitation via trail and has been invaded by common dandelion (*Taraxicum officinale*) and two species of beetle (*Agonum c.f. muelleri* and *Trechus obtusus*; Vanderwoude et al., 2015). Vegetation surveys along roadsides at Mauna Loa's upper elevations conducted 50 years apart (1958–2008) revealed a significant increase in the number of both native and invasive plant species. The reasons for the establishment of new species remain unclear, but are more likely due to increased human impacts and access than climate warming in this arid and sparsely vegetated environment (Juvik et al., 2011). On Mauna Kea, invasive grasses pose a serious threat to the ecosystems, both in terms of composition and fire risk (Banko et al., 2014), and introduced weeds are abundant in the alpine zone in New Zealand, including hawkweed (*Hieracium* species) (Steer and Norton, 2013). Conifers introduced to the windward slopes of Haleakalā as part of an early 20th century forestry initiative are moving into higher elevations and outcompeting native shrub species (Fig. 6C) (Pauchard et al., 2009). Introduced *Pinus contorta* (lodgepole pine) in New Zealand has also increased at high elevations by 180% over the past 20 years and is now found up to 270 m higher than previously established (Tomiolo et al., 2016). Planted *Pinus radiata* (Monterey pine) was found to reduce water yield by 43% compared to native snow tussock (Mark and Dickinson, 2008).

Observed Climate Changes and Impacts

Since 1900, New Zealand's mean annual temperatures have risen at a rate similar to the global mean, with most of the warming occurring after 1946 ($0.12\text{--}0.14^\circ\text{C decade}^{-1}$, 50-year trend ending in 2006, Dean and Stott, 2009). However, irregularities in observations and poor station coverage in alpine areas result in uncertainties in warming rates for high elevation areas (de Freitas et al., 2014). What is known, however, is that warming has reduced New Zealand's glacier volume since 1850 (Mark et al., 2006). In a recent glacier inventory, Chinn et al. (2012) found that the melting of the region's 12 largest glaciers accounts for 71% of total glacial volume loss in the last 30 years, while the melting of thousands of small- and medium-sized glaciers accounts for the remaining 29%. In total, ice volume in the Southern Alps has been reduced by 18.4 km^3 , or 34%, since 1977 (Chinn et al., 2012), and glacier retreat and reductions in snowfall have impacted tourism operations, with a shift to helicopter-oriented glacier tours (Purdie, 2013) and increased artificial snow-making for skiing and snowboarding (Hopkins, 2014). Despite the expectation that climate-induced warming will cause an upward shift in treeline in alpine locations worldwide, study of treeline areas dominated by *Nothofagus* (beech) in the Southern Alps has shown little response to recent temperature increases (Harsch et al., 2012). Precipitation over the past three decades has trended toward drier conditions on the west coast of the South Island, while wetter trends are found for the east coast (Salinger and Mullan, 1999).

Hawai'i's highest elevations have experienced rapid warming in the last four decades (Giambelluca et al., 2008). The Mauna Loa Slope Observatory (MLO) station, located at 3341 m elevation, has experienced a mean warming trend of $0.19^\circ\text{C decade}^{-1}$ between 1955 and 2016 (McKenzie et al., 2019). This strong warming trend has been linked to degradation of the permafrost on Mauna Kea, which has shrunk by an order of magnitude between 1973 and 2015 (Schorghofer et al., 2017). Based on historical accounts, snowfall used to be much more common on Mauna Kea, but in the modern climate snow occurs only a few times in winter and rarely in summer (Schorghofer et al., 2014). High elevation areas have experienced significant drying since 1920, particularly in the dry season (May to October; Frazier and Giambelluca, 2017). This is consistent with the observed increases in high elevation solar radiation and decreasing cloud cover since 1988, driven by changes in the TWI (Longman et al., 2015a). An abrupt shift in TWI in 1990 resulted in a 20% increase in mean TWI frequency, likely driven by increased intensity of Hadley Cell subsidence near the Hawaiian Islands (Longman et al., 2015a). This shift in TWI has been linked to ecological responses, such as the decline in the Haleakalā silversword population (Krushelnycky et al., 2016).

Future Projected Climate Changes

Alpine ecosystems may be the most affected by global climate change. Alpine climates are extremely complex due to the interactions between mountains and atmospheric circulation. A lack of high spatial and temporal resolution observations, coupled with the limitations of general circulation models (GCMs) in representing the complex terrain, restricts our understanding of these climates (Beniston et al., 1997). Representing complex topography on small islands in climate models is even more challenging, as the differences between land and ocean climates are stark. In Hawai'i, the entire state may fit into only a few grid cells in a GCM, and these coarse-resolution products are not able to simulate the complex processes that operate on relatively small scales (Elison Timm et al., 2015). To overcome these limitations in Hawai'i and New Zealand, various downscaling methods are employed to generate local- and regional-scale projections from the global models.

According to mid-range scenario projections for New Zealand's climate, by 2040, temperatures are expected to increase by 0.8°C, doubling again to 1.6°C by 2110, with the strongest warming over higher elevations. Rainfall will likely increase in the west and decrease in the east and north due to an increase in westerly winds; extreme daily wind speeds will be stronger, especially in the Southern Alps (Ministry for the Environment, 2018). Model projections for snowfall in popular ski destinations suggest dramatic cuts in the number of snow days averaged across all sites by 2040 (up to 24%, depending on the climate scenario) and catastrophic reductions (up to 68%) by 2100 (Hendriks and Hreinsson, 2012). As in other glaciated areas of the world, New Zealand may lose 88% of ice volume by the end of the century, driven largely by reductions in snowfall (Shannon et al., 2019); by 2100 Franz Josef Glacier could lose 38% of its volume (Anderson et al., 2008). In addition to the gradual loss of alpine glaciers and permafrost as indicators of climate change, there may be a greater risk of landslides and rockfalls associated with short-term temperature extremes, although this has not been confirmed in New Zealand's Southern Alps (Allen and Huggel, 2013). Species-area modeling results show that a 3°C rise in temperatures could lead to a loss of 33%–50% of native alpine plant species, and >100 new exotic species (Halloy and Mark, 2003). The loss of snow cover due to a warming climate may impact the frost-resistance of alpine plant species (Bannister et al., 2005). Reduced snow cover will likely result in more thermal stress for alpine cockroaches (*Celatoblatta quinque-maculata*) (Sinclair, 2001), while warmer temperatures are expected to reduce and displace populations of alpine grasshoppers (*Paprides nitidus*) (White and Sedcole, 1991). A recent transplant experiment found that some alpine plant communities had inherent resilience to altered snow cover, while novel biotic interactions such as herbivory and competition affected survival (Lord et al., 2018). In addition to warming, patterns of rainfall, wind, and snow cover as well as human disturbances and invasive species behavior will also change in complex ways, and there is still much that is unknown about the response of native species to these changes (Halloy and Mark, 2003).

For Hawai'i, future projections of temperature indicate robust warming statewide, with the greatest warming also at the highest elevations (projections range from 3.5°C to 5°C warmer temperatures by 2100; Elison Timm, 2017; Zhang et al., 2016). Future projections of rainfall are less certain. General patterns indicate that windward areas will become wetter or stay the same, while leeward areas will become drier by the late 21st century (Elison Timm et al., 2015; Zhang et al., 2016). TWI projections indicate a robust increase in the frequency of TWI days, from 82% to 91% on Hawai'i Island, and a decrease in mean base height (Zhang et al., 2016). End-of-century snowfall simulations indicate that snow will nearly disappear on the summits of Mauna Kea and Mauna Loa, with implications for the Hawaiian language name "Mauna Kea," which means "white mountain" (Zhang et al., 2017). As for the ecological impacts of these changes, very little is known about species- or community-level impacts of climate change on alpine ecosystems in Hawai'i. However, given the evidence for a moisture-driven treeline (e.g., Crausbay et al., 2014), a lower and more frequent TWI combined with an increase in El Niño event frequency could depress any upward movement, possibly resulting in downslope migration of the treeline.

Concluding Remarks

Climate change, introduced species, and human impacts have independent and interacting effects on alpine ecosystems globally. On the one hand, the harsher climate of alpine environments and reduced anthropogenic disturbance have historically prevented the establishment of nonnative biota (Alexander et al., 2016), but warming temperatures are alleviating those unfavorable conditions (Pauchard et al., 2016). Similarly, human influence can exacerbate the impacts of climate change while facilitating further introduction and establishment of introduced organisms into new ranges. Native species in these regions—especially those in low densities—may also lack adequate baseline information and are uniquely vulnerable to major threats such as global climate change and human impacts. Resource managers are therefore challenged with accommodating multiple-use natural areas (conservation, public hunting, tourism, cultural use, etc.) while monitoring and managing for ecosystem change with limited information.

The need to track changes in Pacific Island alpine environments is clear: they are rare, isolated (geographically and by elevation), and are uniquely sensitive to the threats posed by climate change, introduced species, and human impacts. Two field sites in the Southern Alps were recently incorporated into the Global Observation Research Initiative in Alpine Environments (GLORIA) project, which was founded in 2001 to monitor vegetation and climate in target high elevation regions worldwide (Mark et al., 2006). The Haleakalā Climate Network (HaleNet), established in 1988, monitors 13 climate variables at eight stations along two transects (windward and leeward) in Haleakalā National Park from 960 to 2990 m elevation (Longman et al., 2015b). The 30-plus years of data gathered here provide an invaluable monitoring dataset for the State of Hawai'i. Other alpine areas, however, are severely lacking climate information. Additional monitoring and research are needed to better understand the sensitivity of these diverse ecosystems to the simultaneous threats of climate change, invasion, and human-driven degradation.

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