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Emergent freeze and fire disturbance dynamics in temperate rainforests

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Abstract The coastal temperate rainforests of South and North America are part of the most biomass dense forest biome on the planet. They are also subject to rapid climatic shifts and, subsequently, new disturbance processes – snow loss-driven mortality and the emergence of fire in historically non-fire-exposed areas. Here, we compare and contrast Southern and Northern Hemisphere coastal temperate rainforests of the Americas, two of the largest examples of the biome, via synthesis of current literature, future climate expectations and new downscaling of a global fire model. In terms of snow loss, a rapid decline in winter snow is leading to mass mortality of certain conifer species in the Northern Hemisphere rainforests. High-elevation Southern Hemisphere forests, which are beginning to see similar declines in snow, may be vulnerable in the future, especially bogs and high-water content soils. Southern Hemisphere forests are seeing the invasion of fire as an ecological force at mid-to-high latitudes, a shift not yet observed in the north but which may become more prominent with ongoing climate change. We suggest that research should focus on the flammability of seral vegetation and bogs under future climate scenarios in both regions. By comparing these two drivers of change across similar gradients in the Northern and Southern Hemispheres, this work points to the potential for emerging change in unexpected places in both regions. There is a clear benefit to conceptualising the coastal temperate rainforests of the Americas as two examples of the biome which can inform the other, as change is proceeding in similar directions but at different rates in each region.

Abstract in Spanish is available with online material.

Key words: climate change, coastal temperate rainforest, emerging disturbance regimes, fire, snow loss.

INTRODUCTION

Climate change is affecting global forests in multiple ways, often by altering the abiotic conditions forests experience. Direct effects include increasing water stress and associated drought-induced tree mortality (Adams *et al.* 2009; Holz *et al.* 2017), CO_2 fertilisation (Bolker *et al.* 1995) or lengthening of the growing season (Cleland *et al.* 2007), with these effects leading to altered productivity and/or range shifts (Krapek & Buma 2018). These changes may be punctuated, resulting from the crossing of climatic thresholds that drive major ecological changes related to species physiological tolerances (e.g. Allen *et al.* 2010). The existence of environmental thresholds may also cause shifts in or intensification of disturbance regimes (Brooks *et al.* 2004; Veblen *et al.* 2011; Buma 2015; Millar & Stephenson 2015), which can lead to sudden changes in ecosystem type when disturbance severity or frequency exceeds species, community and ecosystem tolerances (Buma & Wessman 2011). As a result, significant shifts in ecological relationships – such as the establishment of

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novel functional relationships (Gilman *et al.* 2010) or the formation of no-analogue communities (Williams & Jackson 2007) – are widely anticipated.

Precipitation – including its phase, amount, intensity and timing – is one such climate factor expected to potentially drive significant, threshold-like change. The phase of precipitation (snow or rain) represents only a small shift in winter temperatures but results in a very large change in the physical environment that forests inhabit. For example, the loss of a winter snowpack results in decreased soil insulation in winter (Groffman *et al.* 2001), loss of nival habitat (Pauli *et al.* 2013), altered plant communities (Bannister *et al.* 2005) and reduced summer streamflows (e.g. Mote 2003), among other factors. Changes in the amount and timing of precipitation also have major impacts. Several researchers have focused on forest health in relation to precipitation-associated physiological stress (Anderegg *et al.* 2013), winter high flow/summer low flow events (Surfleet & Tullos 2013), and erosion and flooding severity and timing (Klos *et al.* 2014).

Fire is also a well-known driver of rapid threshold-like change. Fire is a major disturbance agent in most of the world's forests (Rundel 1981; Scott 2000), burning ~348 Mha annually (Bowman *et al.* 2009; Giglio *et al.* 2013) and influencing vegetation (He *et al.* 2016), soil (Certini 2014), and a host of other ecological aspects of forest ecosystems. Fire occurrence responds rapidly due to climate or anthropogenic activity (Doerr & Santín 2016). Because of its near ubiquity, fire can be difficult to disentangle from the baseline functioning of the forest (Pausas & Keeley 2009). When excluded via modelling, it is apparent that whole biome distributions likely result from the presence (or absence) of fire (Bond *et al.* 2005). Anticipating changes to fire regimes – especially the emergence of fire in areas where it was not historically present, or rare enough to not be an evolutionary force – is important for management, conservation and prediction of future ecosystem dynamics and functioning.

Both snow loss and fire regime shifts are major concerns to forest managers, conservationists, researchers and culture bearers in forests worldwide. Here, we illustrate how the loss of snow and the emergence of fire may act as important agents of change. We focus on coastal temperate rainforests, a globally important biome that holds an immense amount of carbon in relatively intact forests (Keith *et al.* 2009), where snow loss is proceeding faster than anywhere else globally and where the fire regime is expected to intensify or even emerge in areas where it was previously essentially absent.

Objectives

The objectives of this review are to (i) synthesise and describe the significance of crossing precipitation and fire thresholds to the ecology and functioning of this globally important forest biome; (ii) discuss the spatial pattern of potential change within the regions; and (iii) use the analysis of drivers of the new disturbances in this ecosystem to anticipate new dynamics in other temperate rainforest systems. We hope to draw attention to the benefits of considering the southern and northern coastal temperate rainforest as two regions which can inform each other via direct comparison.

COASTAL TEMPERATE RAINFORESTS: A FRONTIER OF CHANGE

Coastal temperate rainforests (hereafter CTRFs) are globally important as the most carbon-dense forested areas on the planet, containing upwards of 1867 tons C ha^{-1} (Australian CTRFs, Keith *et al.* 2009), a result of generally low rates of decomposition, low water stress, moderate climate and relatively long growing seasons. They provide a multitude of ecosystem services, from significant cultural resources to wildlife habitat, and function as the headwaters of globally significant fisheries (Brandt *et al.* 2014; Rodriguez-Echeverry *et al.* 2018). These regions are also associated with high endemic biodiversity (e.g. South American forests) in terms of nonvascular plants and lichens (DellaSala 2011) and relatively low levels of human development in many places.

Despite occurring across a wide range of latitudes (~30° north to south), CTRFs have relatively consistent, moderate climate conditions due to their close proximity to the ocean (Alaback 1991; DellaSala 2011; Fig. 1). The mild, consistent climatic conditions favour evergreen tree species, fine-scale, infrequent disturbances and generally older, late-successional forests over much of the landscape. Average annual temperatures range between 4 and 12°C, with annual precipitation from as low as 1.5 m to as high as 5 m or more in some areas (DellaSala 2011). The historic disturbance regime was dominated by relatively frequent tectonic activity, landslides, windstorms, fine-scale tree mortality and infrequent fires (Veblen & Alaback 1996; Buma & Barrett 2015; Holz *et al.* 2016). Although observed and projected absolute warming rates in CTRFs are not as high as in polar or high-latitude interior regions, warming temperatures are crossing key climatic and ecological thresholds (Veblen *et al.* 2011; Shanley *et al.* 2015), notably: (i) a phase change from snow to rain as mean winter temperatures cross the 0°C threshold and (ii) the emergence or increased role of fire on the landscape (e.g. see DellaSala *et al.* 2018).

The snow-to-rain transition is an abrupt physical threshold driven directly by temperature. This

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fundamental shift in hydrology influences a variety of ecosystem properties and underlying processes, including subnival habitat (Pauli *et al.* 2013) and snow disturbance dynamics (Hennon *et al.* 2016). Large areas of high-latitude CTRFs are at or near the 0°C isotherm during winter, meaning that precipitation usually falls as snow. This climatological location makes CTRF snow regimes especially vulnerable to a loss of days below freezing given even minimal warming (Meehl *et al.* 2004), as illustrated by the crossing of the snow-to-rain threshold already reported in portions of the biome (Buma 2018).

Historically, fire in CTRFs was very infrequent, although large in extent, at lower latitudes (~40°–50°) but very rare at higher latitudes (>55°) due to climatological constraints, especially the relatively wet summer periods and limited natural ignition sources (Veblen & Alaback 1996; Kitzberger *et al.* 2016). Areas with continuous human habitation had a more frequent fire regime associated with land management (Hoffman *et al.* 2016; Méndez *et al.* 2016), though many mid- to high-latitude locations had fire return intervals >1000–10 000 years (Veblen & Alaback 1996; Gavin *et al.* 2003). At lower latitudes, fire was rare but a significant driver of landscape pattern (e.g. Washington State, USA, Agee 1993; Gavin *et al.* 2007). Paleoecological records from the higher latitude portions of North America's CTRF (>54° N) have recorded essentially no charcoal since approximately 7500 years before present and no widespread fires since the Holocene Climatic Optimum (Baichtal *et al.* 2008). The anticipated general increase in fire activity at temperate latitudes worldwide, where fuel is abundant, is tied to lower moisture availability resulting from predicted higher temperatures, reduced precipitation and/or longer fire season

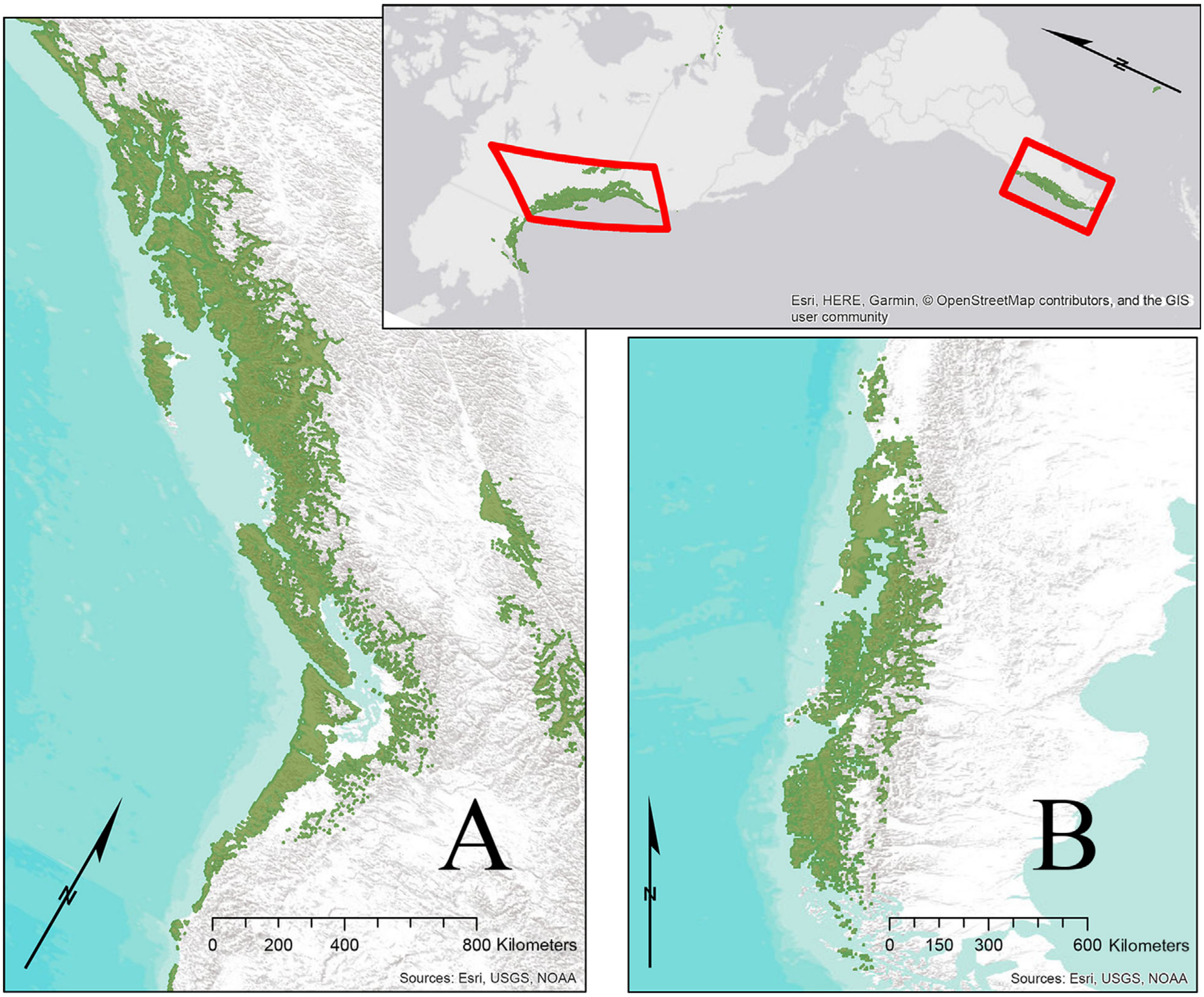

Fig. 1. The North Pacific coastal temperate rainforest (panel a) and the South Pacific CTR (panel b). The focus of the comparison is on the perhumid and seasonal zones of both forests. Biome map from DellaSala (2011). [Colour figure can be viewed at wileyonlinelibrary.com]

(Westerling *et al.* 2006; Bowman *et al.* 2009; Moritz *et al.* 2012; Abatzoglou *et al.* 2017). In addition, increasing temperatures generate higher water deficits (via increased evapotranspiration) even under potentially increased rainfall at higher latitudes. The lack of historical fire exposure combined with a likely increase in future fire activity makes CTRFs potentially vulnerable to novel change.

In sum, the particular climate and disturbance 'state space' in CTRFs makes them an ideal biome for studying how climate change-induced shifts in winter precipitation phase and the emergence of fire have direct and indirect, long-lasting consequences for ecosystem structure and function. Coastal temperate rainforests can serve as model systems for developing predictions about future changes in other forested regions, which are expected to undergo similar snow-to-rain and fire regime shifts in the future (Bowman *et al.* 2014; Holz *et al.* 2016).

We take advantage of the fact that the two largest examples of the biome, the North Pacific coastal temperate rainforest (NPCTR) of North America and the South Pacific coastal temperate rainforests (SPCTR) of Chilean South America (27.3 and 12.5 million ha, respectively), together represent 50.7% of all global temperate rainforests (DellaSala 2011). We focus on the perhumid and seasonal portions, which straddle the snow–rain and fire-presence/absence thresholds (Fig. 1; Veblen & Alaback 1996). Parallel characteristics result from adjacency to the highly moderating, cool Pacific maritime environment and continuously wet conditions that favour dense, contiguous evergreen forests (needleleaf in the Northern Hemisphere and broadleaf in the Southern Hemisphere) and a large abundance of temperate, peat-accumulating wetlands in areas of poor drainage. Both have high carbon (C) stocks, with slightly more in the Northern than the Southern Hemisphere (NPCTR: 568–794 tons C ha^{-1}, SPCTR: 326–571 tons C ha^{-1}; studies synthesised in Keith *et al.* 2009). Both regions of the CTRF exhibit a gradient of human impacts, from significant development/land cover change at lower latitudes to more intact landscapes at higher latitudes (DellaSala 2011). While the higher latitude areas are certainly impacted by extensive historical logging, often targeting large trees and vulnerable portions of the ecosystem (flood plain/riparian zones; Albert & Schoen 2013) with important negative impacts on fish, wildlife and habitat (Beier *et al.* 2008a), they still retain relatively high value in regard to cultural resources and biodiversity among other ecosystem services (Brandt *et al.* 2014; Rodriguez-Echeverry *et al.* 2018). The long north–south latitudinal extent of these CTRFs means that climate change is asynchronous across this gradient, with poleward regions warming faster and equatorward regions experiencing more rapid precipitation changes (IPCC 2014).

In contrast to many other well-studied biomes experiencing rapid changes in precipitation regimes and fire dynamics (e.g. Serreze *et al.* 2000), CTRFs are useful study systems in that climate change impacts can be examined concurrently and comparatively in both the Northern and Southern Hemispheres. A threshold may be crossed earlier in one region than the other, providing insights into how the slower changing area might respond. Comparative studies can provide a more robust test for hypothesised mechanisms and an indication of potential climate change impacts on local climatology and ecosystem responses to these and to other disturbances (Alaback 1991). We take advantage of that cross-comparison in the following discussion.

LOSS OF SNOW AND EMERGING FREEZE DISTURBANCE

Among the most visible environmental changes associated with a warming climate in these two regions are the reduced depth, extent and persistence of snow as average winter temperatures cross the rain–snow threshold of 0°C (Fig. 2). In CTRFs, where precipitation is ample year-round, precipitation phase and subsequent routing of runoff play important roles in forest functioning (Bisbing *et al.* 2016); this change in phase may be a more significant shift than any absolute change in the overall amount or seasonality. Because the CTRF regions have historically occurred along the 0°C isotherm in winter, the number of snow-covered days, there is decreasing faster than in any other biome (Meehl *et al.* 2004). Currently, the rain–snow boundary bisects the NPCTR, starting at approximately 2000 m by 50^{o} N and reaching sea level around 57^{o} N (Shanley *et al.* 2015). The more maritime southern SPCTR in Patagonia is generally already above this threshold at low elevations, and snow is transient in those areas, though areas at higher latitudes and elevations do remain snow and ice covered. While, to our knowledge, no research has been done on long-term changes in snow persistence in those higher elevation areas of the SPCTR, satellite-based observations in the Andes just north of the region (from ~28° to 36.5° S) identified significant declines in duration of snow persistence, approaching 2–3% per year, with the rate of snow loss highest at higher latitudes (Saavedra *et al.* 2018). Additionally, various ice caps in the region have been retreating rapidly over the last several decades, attributed to warming and subsequent raising of the 0°C isotherm (Davies & Glasser 2012), and this is expected to continue over the next decades (Fig. 2). Thus, research of climate

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change effects on the rain–snow threshold in the NPCTR may be instructive to the less studied snow dynamic SPCTR.

Observed effects of snow loss

The crossing of the rain–snow threshold can have significant ecological effects, especially among species adapted to reliable winter snow environments. In the NPCTR, yellow-cedar (*Callitropsis nootkatensis*) is experiencing extensive mortality over 9° of latitude (>400 000 ha; Buma *et al.* 2017). This species has a competitive strategy of fine root growth in the early spring when supplies of nitrogen are abundant in upper soil layers (Hennon *et al.* 2016); however, fine root death can occur during subfreezing weather events when snow is no longer present (Hennon *et al.* 2016). Snow is an effective insulator for soils, buffering soil temperatures from atmospheric variability; a lack of snow generally leads to colder soils in winter months (Groffman *et al.* 2001) and an overall increase in soil temperature variability (Jungqvist *et al.* 2014). Even in a warming climate with less snow, sporadic cold weather events have persisted in portions of the NPCTR (Beier *et al.* 2008b; Buma 2018), driving continued tree mortality. Ongoing mortality is likely to lead to shifts in community composition to a smaller suite of species more tolerant of snow-free winter conditions (Oakes *et al.* 2014). But, tree mortality is not the only effect of increasing soil freezing. Mobilisation of contaminants (Mohanty

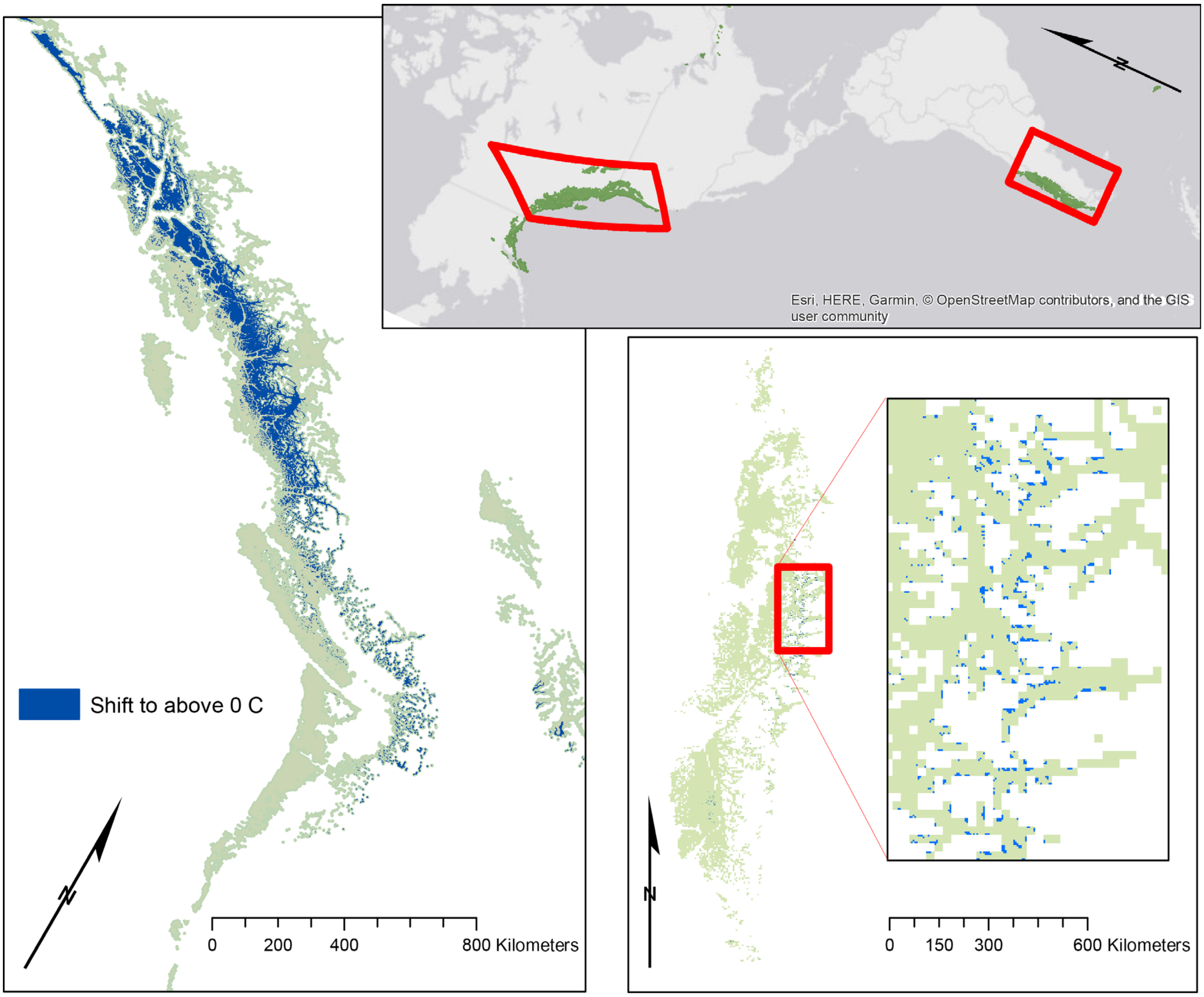

Fig. 2. Anticipated shifts in winter snow threshold in the South Pacific CTR (SPCTR) and North Pacific coastal temperate rainforest (NPCTR) using the HadGEM2-ES (RCP 8.5) climate model/emission scenario. No areas are expected to shift from above to below freezing. Due to substantial lower elevation/slope areas in the NPCTR, the spatial extent of change is large. In the SPCTR, shifts are likely along the higher altitudinal range edge throughout the forest, and the inset shows a subsection in detail to illustrate this pattern. Climate data from Hijmans *et al.* (2005) at 1-km resolution, HadGEM2-ES GCM. [Colour figure can be viewed at wileyonlinelibrary.com]

et al. 2014) and microbial communities (Larsen *et al.* 2002) can drive significant changes to nutrient cycling (Fitzhugh *et al.* 2001; Urakawa *et al.* 2014). These changes, triggered by increasing freeze–thaw dynamics in soils, may have significant downstream effects as well.

There are multiple pathways by which snow loss might cause continued plant mortality in the NPCTR and at higher elevations in SPCTR forests. Climate change is altering the phenology of forest species, leading to increased risk of cold-related damage in a warmer world (Gu *et al.* 2008; Rigby & Porporato 2008). The general ecological strategy of early spring activity as a means to gain competitive advantage is widespread (Polgar & Primack 2011). Apart from root freezing, warmer temperatures speed plant development earlier each year, making them vulnerable to frost (Gu *et al.* 2008). Increased cold damage associated with climate warming and earlier spring phenological development is well recognised (Gu *et al.* 2008; Inouye 2008) and is typically associated with aboveground bud mortality. Broadscale damage to sensitive bud tissue has already been noted in a variety of locations (Inouye 2008). The threat of root freezing due to a lack of snow has not been generally quantified outside of NPCTR, but it is expected to be a significant factor in areas where snow cover will shift from continuous to transient in temperate zones (Bannister *et al.* 2005). The risk would be highest in areas of the landscape prone to shallow rooting habits (e.g. wetlands and bogs). The most vulnerable species are likely to be those adapted to early-onset seasonal growth that historically occurred under reliable cover of snow.

It is possible that subfreezing-induced damages could decline after the transitional period, when temperatures rise above the freeze–thaw boundary (Henry 2008, Buma 2018), but this is dependent on freezing probability corresponding to average temperatures as they have in the past. Given the topography of both regions, with significantly colder areas located in close geographic proximity to these ecosystems (on the eastern sides of the Andes in South America and Coast Mountains of the United States and Canada), it is unclear whether that relationship will hold (Beier *et al.* 2008b). Areas of historically thin snowpack and winter temperature slightly below freezing in the SPCTR should be monitored for plant stress, root mortality and other emerging dynamics suggested by the NPCTR decline.

THE EXPANSION OF FIRE

The combination of decreasing winter snowpack resulting from precipitation phase change, earlier snowmelt and thaw, and increasing spring–summer evaporative demand (e.g. vapour pressure deficit) over longer, rainfall-free growing seasons is likely to result in an increase in the prevalence of fire in certain portions of CTRFs (Westerling *et al.* 2006; Littell *et al.* 2010; Moritz *et al.* 2012). As noted, the historic importance of fire in CTRFs has been relatively low, ranging from a nearly nonexistent fire regime at higher latitudes (Gavin *et al.* 2003) to infrequent, though stand-replacing, fires at lower latitudes (Agee 1993; Veblen & Alaback 1996; Holz *et al.* 2012; Walsh *et al.* 2015; Hoffman *et al.* 2016; Fig. 3). Although there is a substantial amount of highly contiguous vegetation that may act as fuel for a fire in CTRFs, vegetation is typically too wet to burn, and natural ignitions are very infrequent, as lighting is rare and generally accompanied by rain. Overall, fire across both CTRF regions has historically been driven by the confluence of atmospheric circulation patterns cycling at multiple temporal scales (Whitlock *et al.* 2008; Littell *et al.* 2010; Holz *et al.* 2017) and human presence (Hoffman *et al.* 2016; Méndez *et al.* 2016).

Under climate change projections, the poleward portions (>55 °N and >50° S) of both the NPCTR and the SPCTR are expected to experience significant annual warming, lower snowpack, a potential increase in spring–summer drought (Veblen *et al.* 2011) and increasing moisture deficits (40–50% at ~60°N; Haufler 2010). As a result, the equatorward portions of CTRFs are expected to become more flammable throughout the fire season (e.g. summer; Fig. 4), leading to more flammable conditions (Littell *et al.* 2010; Sheehan *et al.* 2015). Additionally, warmer coastal ocean temperatures are likely to create the potential for more ignitions via increased lightning activity (Garreaud *et al.* 2014). In several of the drier and mountainous areas in the SPCTR, increases in lightning-set fires have been observed in recent decades (Veblen *et al.* 2011), and increases in the frequency of dry, warm periods have been linked to global climate warming and ozone depletion in Antarctica (Holz & Veblen 2011; Holz *et al.* 2017). Recent research has identified the southern SPCTR as an area where wildfires might 'invade' as soon as ~2039 if ignitions are provided (Moritz *et al.* 2012).

Downscaled fire projections

Unlike global data related to the winter snow–rain temperature threshold (e.g. Meehl *et al.* 2004; Buma *et al.* 2017), comparable, high spatial-resolution fire modelling studies do not currently exist for northern and southern CTRFs. For the purposes of this synthesis, we used the global modelling framework of Moritz *et al.* (2012) to evaluate changes in climate-driven probability of fire across these regions. This framework integrates global fire datasets (NASA MODIS missions) and environmental covariates

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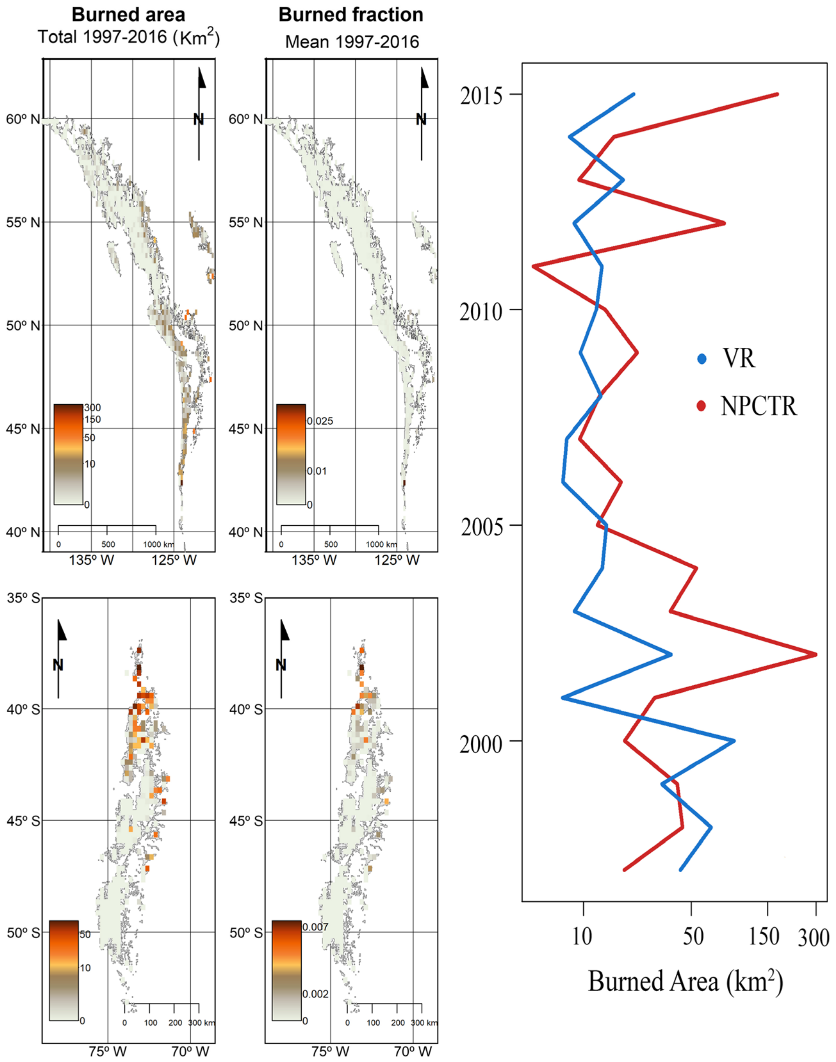

Fig. 3. Yearly burned area, cumulative burned area (per 0.25^0) and per cent burned (mean fraction of each pixel burned per 0.25^0) from 1997 to 2016 in the South Pacific CTR and North Pacific coastal temperate rainforest. Fire statistics come from the Global Fire Emissions Database version 4 (Giglio *et al.* 2013). [Colour figure can be viewed at wileyonlinelibrary.com]

representing fire-conducive climate conditions over the reference period 1971–2000 to determine fire–climate relationships and assess the likelihood of fire under ongoing climate change. We used the framework to build spatial statistical models of relative changes to fire probability that describe the long-term potential of fire occurrence over the period 2071–2100. Using methods based on Moritz *et al.* (2012), we used projected changes in temperature seasonality, precipitation of the driest month and annual precipitation to describe potential alterations in the probability of fire over 0.5° latitudinal bands across CTRFs (Fig. 5). Projected future climate data were obtained from the WorldClim CMIP5 HadGEM2-ES (RCP 8.5; Hijmans *et al.* 2005, updated to CMIP5 in 2017) for the study region (for full details, see Appendix S1–S3).

Because the scope of this synthesis is focused on relative changes, modelling was limited to the Hadley climate projection. The Hadley model performed the best in aggregate when compared to climate-precipitation values for five other GCM's at the seasonal level for the North Pacific forest region (SNAP 2009). To check the assumption that the climate–fire relationships quantified in Moritz *et al.* (2012) would remain valid with the Hadley climatic dataset, correlations between the WorldClim CMIP5 HadGEM2-ES data (used here) and CMIP3 data used in Moritz *et al.* (2012) were computed. We found very high Spearman rank coefficients for the variables used in the model (>0.9; Appendix S3) and considered the climate–fire relationships from the Moritz *et al.* (2012) ensemble fire model suitable to assess potential relative alterations in the CTRFs' likelihood of

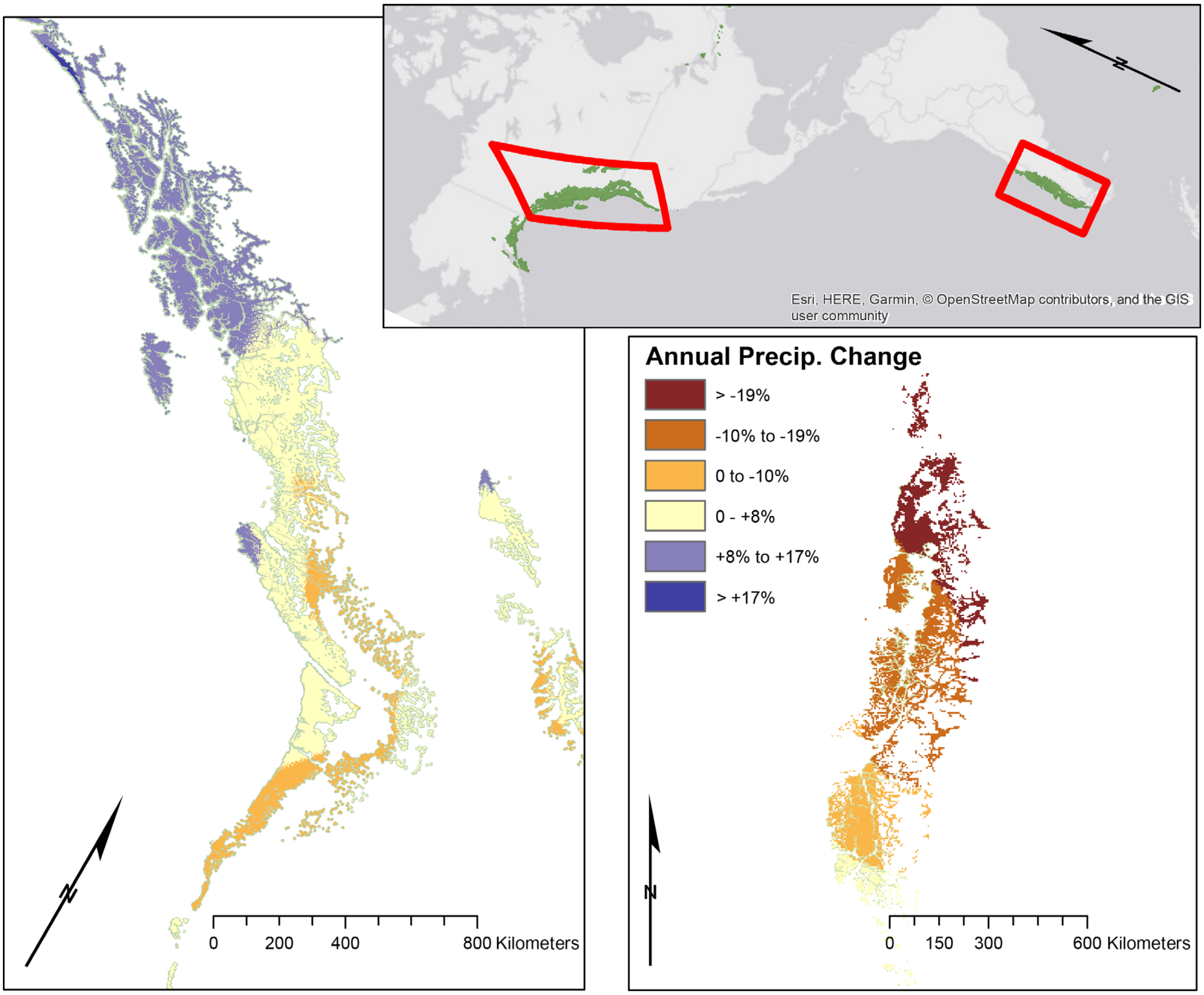

Fig. 4. Projected precipitation change. Relative change in summer precipitation (defined as warmest quarter of the year) by 2070 for the North Pacific coastal temperate rainforest (left) and the South Pacific CTR (right) using the HadGEM2-ES (RCP 8.5) climate model/emission scenario. Climate data from Hijmans *et al.* (2005) at 1-km resolution, HadGEM2-ES GCM (updated to CMIP5, see http://www.worldclim.org). [Colour figure can be viewed at wileyonlinelibrary.com]

fire for the period 2071–2100 driven by HadGEM2-ES climate projections. The purpose of this exercise was not to predict absolute changes in fire probability but rather to identify the portions of each region likely to see the largest relative change. For further details associated with this modelling methodology, see Appendix S1 and Moritz *et al.* (2012).

While the frequency of dry, warm conditions increases at low latitudes in both regions (where the majority of fire modelling work has been concentrated, for example Littell *et al.* 2010), the modelling results suggest that the central latitude portions of the biome in both hemispheres will see the largest relative increase in climate-driven fire probability. This is primarily due to projected changes in dry season precipitation (Fig. 5). The more equatorward portions of the biome will likely have higher rates of fire due to their higher baseline rates. However, a larger relative increase in fire activity indicates a more substantial departure from historical norms and is thus worth noting for future estimates of CTRF dynamics.

It should also be noted that these models are based on broadscale climatic trends and reflect general climate–fire relationships; the actual occurrence and behaviour of fires at regional and local scales is a result of finer scale weather patterns, topo-edaphic gradients and vegetation-fire feedbacks as well.

Effects of fire regime changes in the NPCTR

Fires have occurred historically in the southern and central portions of the NPCTR but with highly

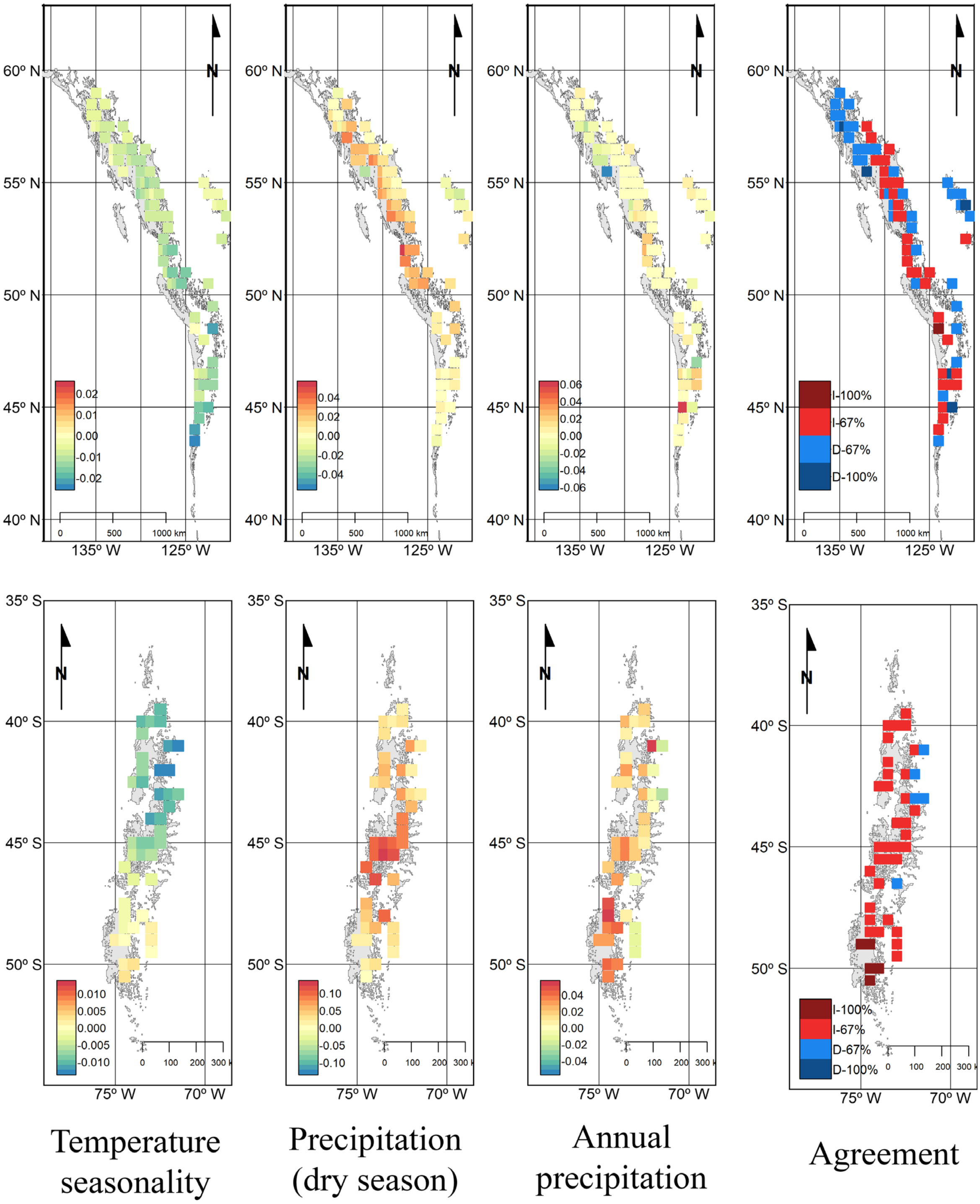

Fig. 5. Relative change in fire probability projected as a function of the major climate drivers in the North Pacific coastal temperate rainforest (NPCTR; top) and the South Pacific CTR (SPCTR; bottom) using the 2070 HadGEM2-ES (RCP 8.5) climate model/emission scenario. A negative (green or blue) value indicates the driver is expected to change in a direction that reduces relative fire probability, and a positive value (orange or red) indicates an increase in fire probability. Agreement between predictors: 100% indicates the three drivers had similar signs (i.e. all were positive), whereas 67% indicates that two-thirds were in agreement for either an increase (I) or a decrease (D) in fire probability. In general, there is strong agreement that fire frequency will increase throughout the SPCTR. Expectations are mixed in the NPCTR, but generally an increase is expected further north than historical fires. The extreme southern portion of the NPCTR is not modelled due to a lack of climate data at the proper scale; for climate locations used to create the probability graphs, see Fig. S1. Note differences of scale of axes and legends. [Colour figure can be viewed at wileyonlinelibrary.com]

variable return intervals (300–3000+ years, Fig. 4) and spatial heterogeneity due to variable ignitions and climatic conditions (Hoffman *et al.* 2018). Thin-barked, non-serotinous species dominate CTRFs, and fire-adapted species are generally absent (Veblen & Alaback 1996). In the southern NPCTR (<55° N), where fire has an infrequent but more significant role (Agee 1993; Tepley *et al.* 2013; Whitlock *et al.* 2014), a few seral thick-barked species occur (e.g. Douglas-fir, *Pseudotsuga menziesii*) that can survive low-to-moderate fire intensities (Agee 1993).

Anticipating the effects of both increasing and emerging fire (at lower and higher latitudes, respectively) is critical (Littell *et al.* 2010). Theory suggests that in wet systems, where flammability declines as forest structure develops, the introduction of fire-conducive conditions can lead to a cycle of increasing fire extents and subsequent widespread ecological changes. This positive feedback occurs because increases in the spatial extent and connectivity of the more flammable, early seral vegetation after each fire event lead, subsequently, to more extensive fires. Given sufficient ignition opportunities and a climate conducive to periodic fire (Perry *et al.* 2012), rapid and persistent threshold-like changes can occur when forests at the landscape scale cross critical flammable-connectivity thresholds and any fire event is likely to spread over the majority of the landscape. Increased NPCTR flammability associated with early successional species can lead to positive fire-vegetation feedbacks (Agee & Huff 1987) due to highly flammable early successional fine fuels that dry rapidly even in the relatively short fire season common to the region's climate. Thus, the emergence or acceleration of fire regimes is a significant concern and changes projected here should be considered conservative estimates. Recent events in mesic forest stands in the southern portions of the NPCTR (e.g. Eagle Creek Fire in the Columbia Gorge Scenic Area in Oregon and Norse Peak Fire in Washington, from a human ignition) remind us that the transformation of these forests by fire is likely as a potential result of the warming regional climate. To this point, the historical and already-underway expansion of fire into the SPCTR is instructive for the NPCTR.

The expansion of fire in the SPCTR

The expansion of fire is well documented in the SPCTR. Historically, humans were the ignition source for most SPCTR fires (Holz *et al.* 2016), with ignitions occurring primarily at the warmest and driest equatorward edge. Since the 1970s, there has been an increase in lightning-ignited fires in the northern and central regions of the SPCTR (Veblen *et al.* 2011), attributed to environmental shifts associated with climate change (Thompson *et al.* 2011, IPCC 2014, Garreaud *et al.* 2014). As biomass is not limiting and the climate is becoming more conducive to fire, the occurrence of fire is increasingly ignition limited (Paritsis *et al.* 2013). Emerging fires tied to climate change and increasing variability in climate have already been transforming ecological composition, structure and function, particularly in fire-sensitive *Pilgerodendron* forests (Holz & Veblen 2009; Bannister *et al.* 2012). These species are mostly fire sensitive, and the landscape has been relatively nonflammable historically – but is becoming less so today.

In addition to climate change driving increases in fire probability, tree plantations in the SPCTR have the potential to increase fire risk. Pine and eucalypts plantations, like other plantations in the southern NPCTR (Zald & Dunn 2018), facilitate fire spread due to homogeneous patch structure and connectivity, which in turn can result in higher fire frequency and severity (McWethy *et al.* 2018; Paritsis *et al.* 2018). While many historical and recent large fires in Chile occurred just north of the CTRF region in the more Mediterranean central valley, there are plantations of Eucalypts in the SPCTR as far south as 42^0 on Isla Chiloé, and at the Patagonian dry forest/steppe ecotone lodgepole pine (*Pinus contorta* var. *latifolia*), a fire-associated species has established from plantations even further south (at least 45.5^0; Taylor *et al.* 2017). There are concerns that invasion by fire-adapted species may alter the water balance, fuel type (Tng *et al.* 2012) and fuel structures (Cobar-Carranza *et al.* 2014) of the region.

When fires do occur, they can cause significant changes to forests and have the potential to initiate positive feedbacks that drive further increases in fire frequency (e.g. Paritsis *et al.* 2013; Taylor *et al.* 2017). In the SPCTR, invasion of shade intolerant *Sphagnum* species can result in subsequent waterlogging of the habitat due to an overall decline in evapotranspiration (Díaz *et al.* 2007). *Sphagnum* mosses, which dominate wetlands in the NPCTR as well, acidify substrates, outcompete tree seedlings, transform the plant community and potentially lock the system into an alternative stable state (Kitzberger *et al.* 2016; Zaret & Holz 2016). Preliminary results suggest that: (i) water table and substrate interact and best explain patterns in post-fire tree seedling abundance and plant community; (ii) small seedling abundance is best explained by water-table height and plant community type (Zaret & Holz 2016); and (iii) fine-fuel fibric peats are more likely to support a high-frequency, low-severity fire regime given an amenable climate for fire resulting in a positive feedback between fire and vegetation flammability (Holz 2009, Kitzberger *et al.* 2016).

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This observation of a rapid ecosystem shift triggered by the emergence of fire and explained by the expansion of more flammable, early seral vegetation coupled with increasingly favourable climates for fire is clearly instructive to the NPCTR. It also echoes observations from paleoecological reconstructions in temperate New Zealand (Perry *et al.* 2012) and recent events in Tasmanian temperate rainforests, where unprecedented fires in 2015 and 2016 burned fire-sensitive trees as well as vast tracks of peatland and alpine vegetation (~105 000 ha) during the driest season on record (Marris 2016). That the largest relative change in fire probability is not anticipated at the equatorward edge of the biome, but rather in the middle and at higher latitudes, is an unexpected finding and suggests research should consider emerging fire regimes beyond the drier, equatorward extents typically considered where adaptations to fire are minimal and resilience potentially low. The story of fire emergence clearly illustrates the value of linking the NPCTR and the SPCTR in a single analysis, as physical drivers are changing in similar directions, but at different times, in both areas – the emergence of fire in the south is a valuable case study for the forests in the north.

THE EMERGING BIOME EDGE

Much of the concern regarding climate change-driven mortality centres on changes at the trailing (lower latitude or elevation; Parmesan & Yohe 2003) or leading edges (higher latitude or higher elevation; Mason *et al.* 2015) of species and biome distributions. Generally, discussion in temperate regions has focused on increasing temperatures and declining precipitation on the southern boundary, as both are known to strongly structure species range edges and biome extents. At broad scales, species and biomes do generally track long-term climate conditions such as mean winter temperatures or annual water balance, though there may be lag after major climatic shifts (e.g. Ice Ages) due to slow migration rates (Krapek & Buma 2018). In the future, however, there is the potential for thresholds in species' tolerances to be crossed elsewhere within the current range of a forest ecosystem, because climate warming and precipitation changes are not synchronous and occur at different rates. 'Edges' of climatic tolerance may emerge within central portions of a range due to the intersection of climatic trends with important physical thresholds or biological tolerances.

The NPCTR and SPCTR regions demonstrate significant, climate change-driven changes occurring near the geographic middle of a biome – not just on the lower latitude portions. Loss of snow is causing the most significant ecological changes in the geographic middle of the NPCTR, where snow was reliably present but winter mean temperatures were near 0° (Buma *et al.* 2017). Higher elevations of the SPCTR and surrounding ecosystems are likely to be similarly susceptible in the future, as snow loss (although minimal in absolute terms) is reported in the central portion (Fig. 2). Further research on the role of snowpack changes in determining species ranges is a significant need (Pauli *et al.* 2013), either via direct mortality as in the case of yellow-cedar or via interactions with other stressors and disturbance agents (e.g. Poulos 2014). Similarly, the highest increase in relative fire likelihood is in the geographic middle latitudes of the biome in both hemispheres, where fire was historically rare and species are not well adapted to fire (this analysis, Fig. 5). Fire may emerge in unexpected locations, and the emergence – rather than simple intensification – is also a major research need, especially in landscapes where theory suggests rapid transformations due to seral changes in flammability.

Temperate rainforests, by virtue of their long latitudinal extent, exemplify these emerging edge phenomena at both the species and ecosystem levels. This suggests that climate change monitoring in a variety of regions should focus not only on leading or lagging edges, but also emerging edges driven by climatic shifts like precipitation phase.

CONCLUSIONS

The objectives of this synthesis and review were to draw attention to emerging disturbance phenomena in the coastal temperate rainforests of the Pacific Coast, discuss the causes and effects of those phenomena and utilise the cross-hemispheric comparison to enable more general predictions about change than can be done from single-system studies. This comparative examination of climate–ecosystem relationships across hemispheres of the CTRFs provides a framework within which to hypothesise the nature, geographic location and potential effects of emergent disturbances within similar systems.

The counter-intuitive nature of the processes being observed – root freezing due to warming and fire in wet forests – makes their prediction more difficult but the broad nature of the changes underway underlines the significance of these emergent trends. In particular, the sensitivity of forests to root freezing mortality in areas where snow will become transient should be investigated in other systems, especially those prone to late spring cold events. Emergence of fire, or increases in fire frequency and/or intensity, may constrain survival and self-replacement of dominant species, leading to long-lasting shifts in community composition or landscape structure, or the establishment of alternative ecosystem states. Both are resulting in community simplification by acting as filters – selective removal of freeze-susceptible trees and selection for more fire-tolerant species; longer term implications of this shift clearly need more research.

Temperate rainforests are undergoing novel change largely driven by climate change. Change in these systems is particularly important given the two regions we examined are well recognised for their global biodiversity importance and relative intactness, which provides opportunities to proactively respond to emerging conditions relative to highly disturbed areas. Their role as major storehouses of carbon at the global scale underlines the importance of these shifts. Finally, the use of coastal temperate rainforests as early indicators of change is valuable and can lead to predictive capabilities for similar functional groups and responses in forests elsewhere.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Fire modelling.
Appendix S2. Red dots depict the *x–y* coordinates used to extract the values of each bioclimatic variable in each region.
Appendix S3. Spearman rank correlation coefficient between WorldClim CMIP5 HadGEM2-ES (RCP8.5; Hijmans et al. 2005) and the CMIP3 climate projections used to build the ensemble fire models in the Moritz et al. (2012) global fire framework.