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New Zealand Fern Distributions from the Last Glacial Maximum to 2070: A Dynamic Tale of Migration and Community Turnover

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Abstract.—The coming decades are predicated to bring widespread shifts in local, regional, and global climatic patterns. Currently there is limited understanding of how ferns will respond to these changes and few studies have attempted to model shifts in fern distribution in response to climate change. In this paper, we present a series of these models using the country of New Zealand as our study system. Ferns are notably abundant in New Zealand and play important ecological roles in early succession, canopy biology, and understory dynamics. Here we describe how fern distributions have changed since the Last Glacial Maximum to the present and predict how they will change with anthropogenic climate change – assuming no measures are taken to reduce carbon emissions. To do this, we used MaxEnt species distribution modelling with publicly available data from gbif.org and worldclim.org to predict the past, present, and future distributions of 107 New Zealand fern species. The present study demonstrates that ferns in New Zealand have and will continue to expand their ranges and migrate southward and upslope. Despite the predicted general increased range size as a result of climate change, our models predict that the majority (52%) of many species' current suitable habitats may be climatically unsuitable in 50 years, including the ecologically important group: tree ferns. Additionally, fern communities are predicted to undergo drastic shifts in composition, which may be detrimental to overall ecosystem functioning in New Zealand.

Key Words.—New Zealand, ferns, climate change, species distribution modelling, last glacial maximum, species temporal turnover

Understanding how plants respond to fluctuations in climate has long been of significant interest to biologists. Much of this early interest focused on changes in deep time and has revealed fairly dramatic periods of extinction, migration, ecological constriction, and proliferation (DiMichele and Phillips, 1996; Lezine and Cazet, 2005; McElwain and Punyasena, 2007; DiMichele *et al.*, 2009; Shepherd, Perrie, and Brownsey, 2007, Shepherd *et al.,* 2017). Studies like these have greatly informed our understanding about how plants respond to climate change. This knowledge will help guide how we forecast future changes in plant distribution and ecological communities. Unfortunately, Earth's climate has only rarely experienced periods of rapid climate change comparable to what is predicted to occur over the coming decades (Joos and Spahni, 2008; Loarie *et al.,* 2009; Smith *et al.,* 2015). The Intergovernmental Panel on Climate Change (IPCC) is a body of the United Nations that

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has studied climate change and its impacts since 1988. The panel has developed multiple models to predict future shifts in global CO_2 emissions, temperatures, rainfall patterns, sea level rise, etc. No matter the model employed, their discoveries are clear: anthropogenic emission of greenhouses gasses is driving a rate of global climate change not seen in the last 65 million years (Diffenbaugh and Field, 2013). These changes are going to impact modern ecosystems in dramatic ways. In this study, we focus on how individual New Zealand fern species respond to climatic shifts from the Last Glacial Maximum (LGM) through 2070 using species distribution modelling (SDM) to inform conservation activists, governments, and biogeographers.

One important organismal response to climate change is migration. As local environments change, several studies hypothesize that organisms may have to migrate into environments that are climatically similar to their modern habitats to avoid extinction (Walther *et al.*, 2002; Pearson, 2006). Mountains are particularly important in the creation and maintenance of species richness and diversity (Moran, 1995; McCain and Grytnes, 2010; Kessler, Karger, and Kluge, 2016; Esquerré *et al.*, 2019; Perrigo *et al.*, 2020) and may provide climate refugia. Several studies suggest that as temperatures increase, montane organisms from diverse lineages may migrate upslope into climatic conditions that reflect their modern ecosystems (Colwell *et al.*, 2008; Loarie *et al.*, 2009; Gottfried *et al.*, 2012; Şekercioğlu *et al.*, 2012). While the marked complexity of new ecosystems, from differences in soil chemistry (Lafleur *et al.*, 2010) and canopy architecture (Asner *et al.*, 2014) to pollinator (Gómez-Ruiz and Lacher Jr, 2019) and disperser debt (Urban *et al.*, 2012) will definitively constrain the refuge capacity of montane systems, some studies show that species can successfully migrate into higher elevations (see Parmesan, 2006).

Naturally, ferns are not exempt from climate change impacts and the same ideas and hypotheses that have been attributed to other lineages likely apply to ferns. However, ferns will likely require novel scrutiny given their unique life cycles. With their reliance on independent gametophytes and unique sporophyte physiology, ferns might be expected to respond differently under models of climate change. While several studies demonstrate the relative sensitivity of fern species distribution to climatic conditions (Marquez *et al.*, 1997; Lehmann, Leathwick, and Overton, 2002; de Gasper, Eisenlohr, and Salino, 2015; Suissa *et al.*, 2021), soil dynamics (Tuomisto, 2006; Zuquim *et al.*, 2012; Jones *et al.*, 2013), canopy architecture (Fayle *et al.*, 2009; Watkins Jr. and Cardelús, 2009), etc., studies are emerging to test how ferns respond to factors that are predicted to change under climate models. Gabriel y Galán *et al.* (2018) showed that even moderate temperature increases can reduce spore germination in some species. While gametophytes can be surprisingly stress tolerant, the gametophytes of some species are particularly impacted by increases in temperature and desiccation. Testo and Watkins (2013) demonstrated that gametophyte sensitivity to increased temperature and desiccation play an important role in the rarity of *Asplenium scolopendrium*, an endangered fern distributed throughout North America. However, there is at least initial evidence that gametophytes can exhibit local-scale adaptations to changes in microclimate (Chambers and Emery, 2016). Myriad studies have also found that gametophytes can grow beyond the range of sporophytes, often encroaching on hotter, drier, colder, or otherwise more stressful habitats than is suitable for their sporophytic counterpart (Sato, 1982; Ebihara *et al.*, 2013; Harrington and Watts, 2021; Nitta *et al.*, 2021). Reproductive strategy also contributes to a fern's ability to survive stressful environments. For example, some fern species have apomictic haplotypes that inhabit drier habitats than their sexual haplotypes (Ohlsen *et al.,* 2020). This gametophyte-level adaptation and ability to disperse long distances via spores (De Groot *et al.*, 2012; Almeida *et al.*, 2021) may differentially influence fern migration rates under changing climatic conditions. Data accessing fern sporophyte response to changing climatic conditions are complex. While increased temperature may negatively influence distribution (Hsu, Oostermeijer, and Wolf, 2014), increased levels of CO_2 predicted by many models may pose a greater benefit to ferns compared to angiosperms because of their strongly limiting mesophyll conductance (Flexas *et al.*, 2014). A great deal more work needs to be done to examine the complex array of responses across the fern life cycle to adequately assess climate change impacts on ferns.

While work on ferns may seem esoteric, the need to understand these plants is more urgent now than ever. Ferns play critical roles in forest ecosystem function across biomes; yet we have very little understanding of how perturbations of fern populations impact these systems (George and Bazzaz, 1999; Montgomery, 2004; Coomes *et al.*, 2005; Engelman and Nyland, 2006; Liu *et al.*, 2012). For example, in New Zealand, tree ferns (Cyatheales) are exceptionally diverse, represented by 11 native species (Brownsey and Perrie, 2015; Brock *et al.*, 2016). In habitats where these species occur, tree ferns are often important drivers of understory diversity. Brock *et al.* (2018) showed that the distance to the nearest tree fern was the most important determinant of understory seedling abundance, hypothesizing that increased shading and litter accumulation limited seedling recruitment below tree ferns. As such filters, tree ferns can reduce angiosperm competition and facilitate the long-term stability of conifer forests in New Zealand (Brock *et al.*, 2020). Epiphytic and herbaceous terrestrial ferns are also prominent in New Zealand forests. The importance of ferns stretches beyond plant interactions. Although little studied in New Zealand, studies elsewhere have shown that some fern epiphytes host remarkable insect interactions (Tanaka and Itioka, 2011; Watkins Jr. *et al.*, 2008) and harbor an impressive diversity of animals and insects (Ellwood, Jones, and Foster, 2002; Ellwood and Foster, 2004; Karasawa and Hijii, 2006; Donald, Clegg, and Ellwood, 2017) and may actually serve as refugia themselves for the animals they host (Scheffers *et al.*, 2014; Seidl *et al.*, 2020). Thus, extinction, migration, range expansion, or reduction of fern functional or phylogenetic diversity could have whole-scale impacts on ecosystem functioning that we cannot yet predict. The consequences of fern range shifts may be particularly important in New Zealand as ferns play an ecologically prominent role in structuring New Zealand's ecosystems.

While long-term common garden experiments may be the gold standard for examining how climate change impacts plants, species distribution models provide a useful context through which we can predict how species may change over time. For example, stacked species distribution models (SSDMs), where individual SDMs are aggregated to estimate local species richness (SR), are often used to model natural communities through time (Del Toro *et al.*, 2019; Zellmer *et al.*, 2019). SSDMs are conceptually simple, require little computational power, and provide useful data to characterize both individual species response to climate change and community dissimilarity through time (known as Species Temporal Turnover: STT). In combination, SR and STT can summarize how a community will change over time. STT can be driven by two fundamentally different processes: nestedness and replacement (Baselga, 2010; Albouy *et al.*, 2012). Nestedness is the gain or loss of species in a community with no replacement by another species, and replacement is the substitution of one species by another in a community.

The goal of this study is three-fold. 1) To use species distribution models to describe how fern diversity in New Zealand has shifted since the Last Glacial Maximum (LGM) (22,000 ya) (Newnham *et al.,* 2007) and predict how diversity will shift into 2070 under various models of anthropogenic climate change. This will allow us to compare the effects of future climatic changes on species migration and shifts in community composition to those that have already occurred from the LGM – present. 2) To describe spatial and elevational patterns of species temporal turnover (STT) between each time period. And finally, 3) to evaluate and describe spatial and elevational patterns in the proportion of STT that can be attributed to either nestedness or replacement.

Materials and Methods

Summary.—Using publicly available plant occurrence and climate data, we constructed species distribution models (SDMs) for 107 (approximately 54% of the estimated 200 native fern species) New Zealand fern species to elucidate distribution changes over time (Brownsey and Perrie, 2015). We used these models to predict the probability of occurrence (POC) for each species during the Last Glacial Maximum (LGM – 22,000 ya), the present, and in 2070 under a "business as usual" global climate model (GCM). We then calculated total suitable area, mean elevation, and mean latitude for each species and time period. For between time periods (LGM – present and present – 2070) we also determined the percent area gained, stable, and lost for each species. SDM predictions were stacked to estimate community composition and SR in each grid cell across time periods and STT was between time periods. All data processing, model fitting, and statistical analyses were done in R version 4.1.2 (R Core Team, 2021).

Data Collection and Cleaning.—A total of 464,058 occurrence points from all species that have records in New Zealand were downloaded from the Global Biodiversity Information Facility (gbif.org; GBIF) (*Download*, n.d.). To limit the inaccuracies associated with "human observations" on GBIF, we limited our download to only "preserved specimens," or specimens collected and identified by professionals and deposited in herbaria then digitized. Preserved specimen records are more accurately identified and exhibit less sampling bias (Sporbert *et al.*, 2019). Inaccurate occurrences were removed using the R package "CoordinateCleaner" (Zizka *et al.*, 2019). CoordinateCleaner works by automatically removing 1) any outlier occurrences using an algorithm, 2) rounded geographic coordinates, and coordinates with equal latitude and longitude, 3) coordinates with high reported inaccuracy, 4) coordinates in the sea or in the country capital, coordinates for all known herbaria, and coordinates inaccurately contributed to the country centroid. Additionally, to reduce sampling bias, occurrences were thinned to one per grid cell following (Williams and Blois, 2018) and (Jarnevich *et al.,* 2018). Species with fewer than 100 cleaned and thinned occurrences were excluded from the analysis to avoid poorly fit or inaccurate SDMs (van Proosdij *et al.,* 2016; Soultan and Safi, 2017). This left 115 species with sufficient occurrence data.

For environmental data, we used a combination of climatic and topographic variables. LGM, present, and 2070 climate data for the 19 bioclimatic variables were downloaded from worldclim.org at 2.5 minutes spatial resolution (about 4.5 km at the equator) (Fick and Hijmans, 2017). We used Community Climate System Model version 4 (CCSM4) at 2.5 minutes spatial resolution to model LGM climate in New Zealand. This model is widely used and has been shown to be representative of past climate refugia compared to other models in southern Australia (Worth *et al.,* 2014), the Pacific coast of the US (McGuire and Davis, 2013), Europe (Smith *et al.,* 2013), and New Zealand (Linder *et al.,* 2014) and is sensitive to changes in glacial forcing parameters (Brady *et al.,* 2013). For future climate we used CNRM-CM5 2070, Relative Concentration Pathway (RCP) 8.5 (Voldoire *et al.,* 2013), because in a study of the performance of 40 GCMs in Southeast Asia, CNRM-CM5 performed best over land areas (Kamworapan and Surussavadee, 2019). RCP 8.5 represents "business as usual" anthropogenic climate change – how the climate will be if no mitigative action is taken. A digital elevation model (DEM) for New Zealand was also downloaded from worldclim and used to compute the Topographic Ruggedness Index (TRI) of each grid cell using the "spatialEco" R package (Evans, 2021).

Species Distribution Models.—We built MaxEnt SDMs using the "SDMTune" package workflow in R. First, we collected 5000 random pseudoabsence points within 200 km of the nearest presence point. Pseudoabsences were also thinned to mirror presence points. For each species, we used data-driven variable selection to reduce the 21 climatic and topographic variables while maximizing model performance as measured by the Area Under the Curve (AUC) metric (Fielding and Bell, 1997; Jiménez-Valverde, 2012). Once variables were selected, we tuned MaxEnt model parameters using a genetic algorithm (population size: 15, generations: 2). Models were trained on a random subset of 80% of the data and tested on 20%. After gathering test AUC metrics, we retrained the models on 100% of the data. Underperforming models (AUC < 0.75) were removed from the analysis following Swets (1988) which describes any model with an AUC > 0.7 as fair, > 0.8 as good, and > 0.9 as excellent. This left 107 species in the final analysis. Models were trained using the present climate and projected into the LGM and 2070 climate space. Binary present-absent predictions for each species were defined from POC rasters using equal training sensitivity and specificity thresholds (Tessarolo *et al.,* 2014). Mean elevation, mean latitude, and total suitable area were calculated for each species' model at each time period using the "raster" R package (Hijmans, 2022). Between each time step (LGM – present and present – 2070) we also determined the percent area gained, stable, and lost for each species following Vila-Viçosa *et al.* (2020). Migration rates were calculated by determining the distance between the center of the mean suitable area (latitude and longitude for geographic distance, elevation for upslope migration), then dividing by the time in years between time periods.

We stress that our methods are fundamentally limited by the limitations of SDMs and the uncertainty associated with LGM GCMs; however, using these methods, we aim to represent general patterns of species richness of ferns in New Zealand over time as accurately as possible.

Stacked Species Distribution Models and Community Dissimilarity Metrics.—We utilized SSDM techniques to model communities through time and space in New Zealand. Species Temporal Turnover (STT) (eq. 1) is a common metric used to estimate community dissimilarity and is derived from Jaccard's dissimilarity index space (Albouy *et al.*, 2012; Swenson *et al.*, 2012). In eq. 1, G is the number of species gained and L is the number of species lost. STT ranges from zero to one and describes the community dissimilarity between two time periods with one indicating complete turnover and zero indicating no change in species number or composition.

$$\text{eq. 1: } STT = \frac{G+L}{SR+G}$$

STT can be separated into the proportion of community similarity accounted for by 1) replacement – STT due to the replacement of a lost species by a new species in a community (no change in SR) or 2) nestedness – STT due to the gain or loss of species within a community (positive or negative change in SR) (see Baselga (2010) for details and equations). STT Ratio is the proportion of STT driven by nestedness (values $> .5$ indicate that STT is driven by nestedness; $< .5$ indicates STT driven by replacement). Here, we use STT and STT Ratio to describe fern community dynamics in New Zealand.

RESULTS

Based on the results from 107 SDMs, ferns in New Zealand are predicted to have migrated southward – away from the equator – and upslope since the LGM. They are predicted to continue southward migration through 2070. New Zealand ferns have been expanding in total suitable area during this time as well, despite anthropogenic climate change. Figure 1A, B, C shows predicted

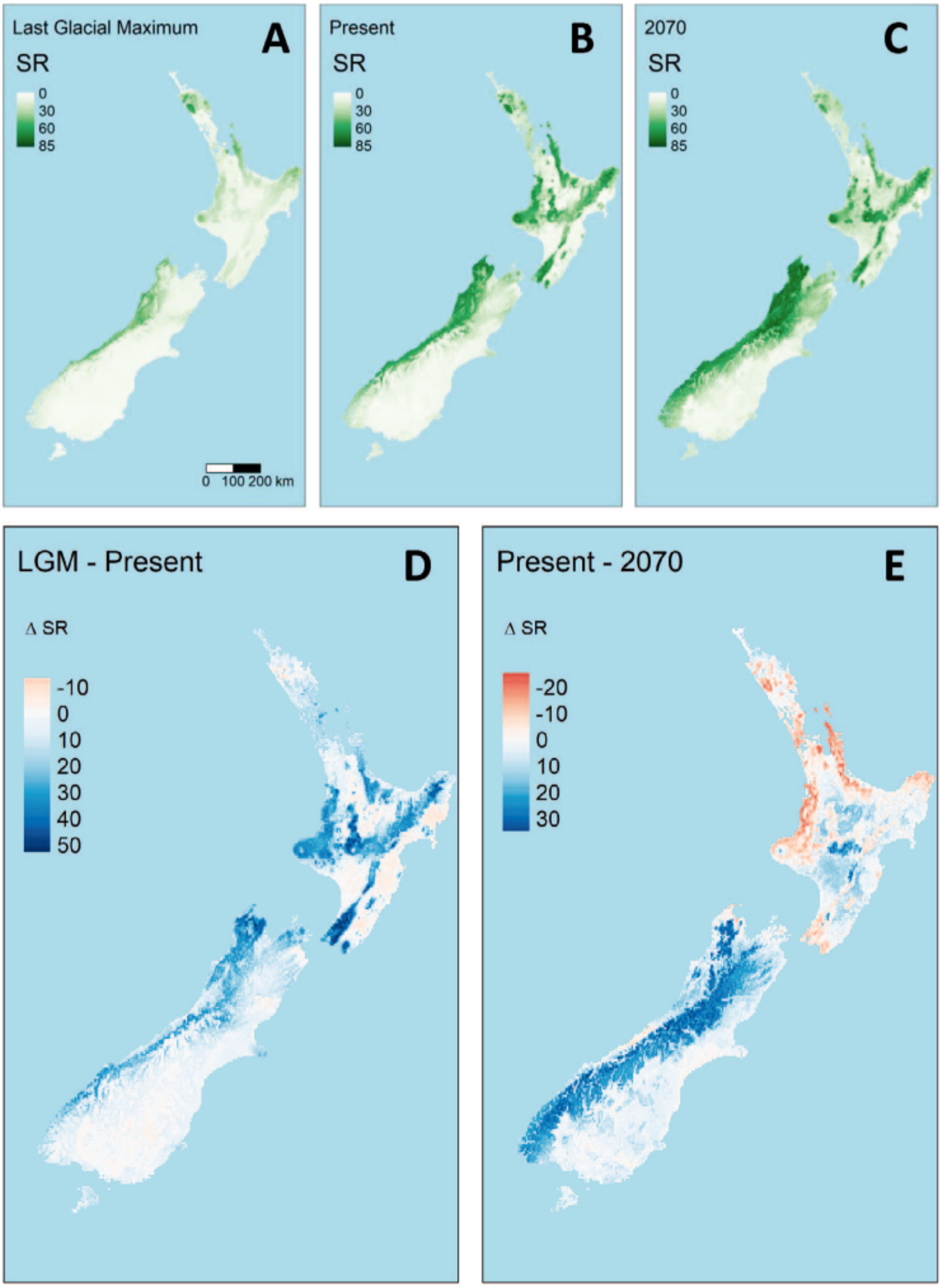

Fig. 1. Modeled fern Species Richness (SR) (107 species) during the Last Glacial Maximum (LGM) (A); the present (B); and 2070 under 85 rcp global climate model (C). Darker greens indicate higher SR. Change in SR (Δ SR) between time periods: LGM to present (D) and present to 2070 (E). Reds indicate a decrease in SR and blues indicate an increase in SR.

total fern diversity (of the 107 species modelled) at the LGM (Fig. 1A), the present (Fig. 1B), and 2070 (Fig. 1C). Careful examination of these figures reveals that the center of diversity for the ferns of New Zealand (included in this study) is presently dispersed throughout the North Island and in the northwestern corner of the South Island (Fig. 1A). During the LGM, areas with high fern species richness were constrained to the northern tip of the North Island and the west coast of the South Island (Fig. 1A). In 2070, fern SR is predicted to increase in northwestern South Island, and in the mountainous regions of the North and South Islands (Fig. 1E). The center of diversity will expand considerably down the west coast of the South Island while the low elevation areas of the North Island will lose species. Since the LGM, fern SR has increased across the majority of New Zealand (Fig. 1D).

The mean modeled range size of fern species in New Zealand increased from 31,000 km^2 to 57,000 km^2 from LGM – present and to 72,000 km^2 in 2070 (Supplementary Table 1). Additionally, species are predicted to have to migrate upslope and away from the equator to stay within favorable climate conditions. Between the LGM and the present, ferns in New Zealand migrated upslope at an average rate of 0.002 m yr^{-1} while they are predicted to have to migrate 1.16 m yr^{-1} between now and 2070. Similarly, our data suggest that southward migration rates must be orders of magnitude higher between now and 2070 than they have been in the past (0.003 km yr^{-1} and 2.35 km yr^{-1}, respectively) to keep up with climate change.

Fern communities across New Zealand have and will continue to experience high STT (Fig. 2A, B). From the LGM to the present, the global average STT value is 0.76, indicating that the average fern community in New Zealand is only 24% similar to its LGM analogue. From the present to 2070, the global average is 0.58 (Fig. 3B). The majority of STT in most of New Zealand can be attributed to replacement, the replacement of an old species by a new species in a community (Fig. 2C, D). The LGM – present STT Ratio global average is 0.27 and the present – 2070 average is 0.39, indicating 27% and 39% of STT due to nestedness (73% and 61% replacement) respectively.

The proportion of STT driven by nestedness is largely driven by species gain. On average, between the LGM and the present, species are predicted to have gained 60.4% suitable area and lost 13.5%, while 26.0% remained stable. Between now and 2070, species are predicted to gain 32.4%, lose 19.7%, while 47.9% will remain stable. According to our models, species' ranges have been and will continue to expand and move up in elevation. This range expansion through time has formed a strong mid-elevation species richness peak (Fig. 3A). Our models also indicate a mid-elevation peak in STT Ratio. Mid-elevation communities are gaining species (resulting in STT due to nestedness) while low and high elevation communities are exhibiting high degrees of species replacement (Fig. 3C).

When species' responses to climate change are grouped by family (a good estimate of phylogenetic and functional diversity), our study demonstrates that family-wide responses to changes in climate are variable through time (Fig. 4). For example, the Nephrolepidaceae, Gleicheneaceae, and Psilotaceae exhib-

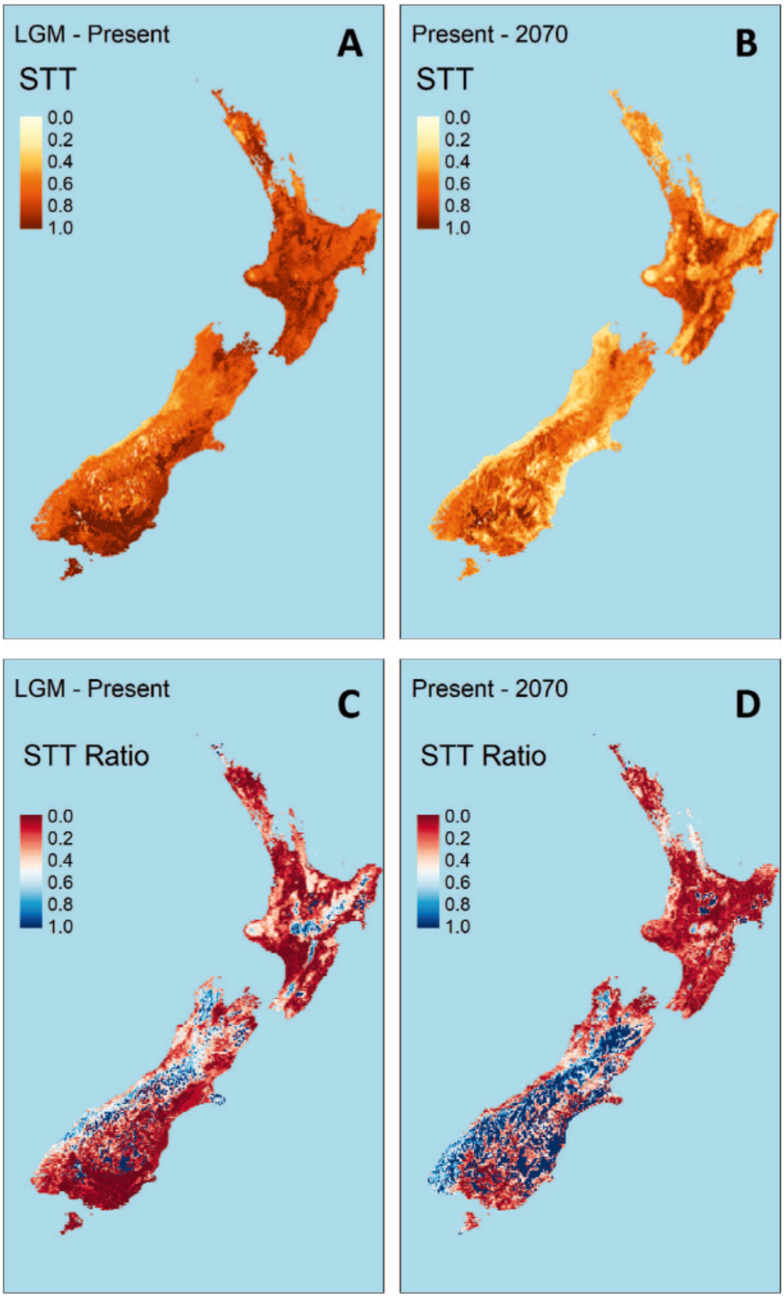

FIG. 2. Species Temporal Turnover (STT) between the LGM and the present (A) and the present and 2070 (B). Darker reds indicate higher STT (communities more dissimilar). STT Ratio between the LGM and the present (C) and the present and 2070 (D). Blues indicate increasingly high proportion of STT attributed to nestedness (species loss or gain); reds indicate higher proportions of replacement.

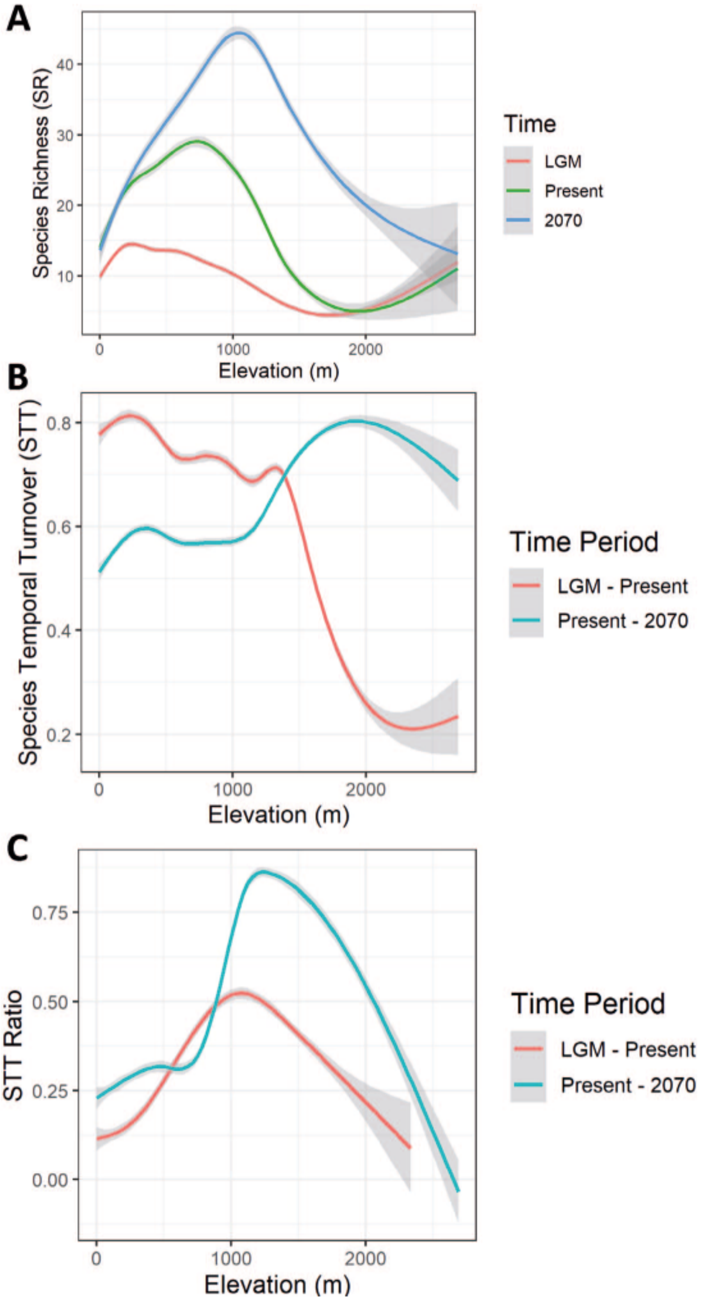

FIG. 3. Generalized Additive Model (GAM) of elevational gradient in SR (A), STT (B), and STT Ratio (C). From the present to 2070, there is a positive relationship between elevation and STT but a negative relationship between the LGM and the present (B). Our models demonstrate the development of a pronounced mid-elevation species richness peak over time as temperatures warm (A); additionally, they suggest a mid-elevation peak in STT Ratio for both time periods (C). Mid-elevation STT is driven by nestedness while low and high elevation STT is driven by replacement.

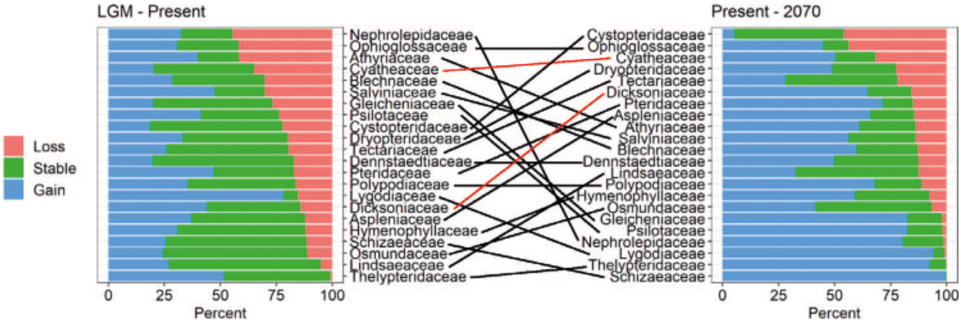

FIG. 4. Modeled percentage of species' ranges lost, gained, or stable (grouped by family and ordered by percent loss) between the LGM and the present and the present and 2070 under an 85 rcp GCM. Red indicates loss, green, stable, and blue, gain. Lines connect families across time periods. Red lines indicate the tree fern families: Cyatheaceae and Dicksoniaceae. The high degree of line crossing suggests that phylogenetic diversity within New Zealand's ecosystems has been shifting to favor some families over others at different periods of time.

ited high percent loss from LGM – present, but are predicted to exhibit universally high gain from present – 2070. Alternatively, the Ophioglossaceae, a high latitude specialist family characterized by small plants and subterranean gametophytes, exhibits consistently high levels of range loss. The Cyatheaceae and Dicksoniaceae, which make up the ecologically important tree fern clade. exhibit consistent ratios of gain, loss, and stability between the two time periods characterized by high percent gain and loss coupled with little stability (Fig. 4). The relative difference in family-level diversity through time will fundamentally alter the phylogenetic and functional diversity of New Zealand ecosystems.

DISCUSSION

Earth's climate has always been dynamic, often changing on macro timescales of tens or hundreds of thousands of years. In response, some species have the capacity to migrate across geographic space and over time (Moritz *et al.*, 2008; Vila-Viçosa *et al.*, 2020). The present study uses the 107 most common New Zealand fern species as a case study to elucidate relationships between past, present, and future communities during this dynamic period of climate warming. Specifically, we investigate the influence of individual species' range expansion, contraction, and migration on species richness, species temporal turnover, and phylogenetic and functional diversity of New Zealand's ecosystems.

Our results indicate an overall increase in average individual species range size from the LGM through 2070, from 31,000 to 72,000 km^2 during the LGM and 2070, respectively. Patterns of present species richness predicted by our models are consistent with other modelling papers which focus on New Zealand ferns (Lehmann, Leathwick, and Overton, 2002; Zaniewski *et al.*, 2002). However, this study is the first of its kind to model fern diversity during the LGM. During the LGM, SR was likely greatest on the Northern tip of the North Island and the far-northwest coast of the South Island (Fig. 1A). These results are consistent with spore fossil studies from this period which describe the Northern North Island as dominated by wet, tall podocarp, broadleaf forest and beech forest and the Western South Island as mixed shrubland and beech forest where many fern species are likely to thrive (Sandiford *et al.,* 2003; Suggate and Almond, 2005; Newnham *et al.,* 2007; 2013). Shepherd, Perrie, and Brownsey (2007) found that *Asplenium hookerianum* likely survived the LGM in large, widespread populations on the North Island. This is reflected in our model results which predict a large suitable area for *A. hookerianum* during the LGM (Supplementary Table 1).

Additionally, species are predicted to migrate upslope and away from the equator. However, it is important to note that the LGM period to the present is 22,000 years compared to the 50 years between today and 2070. Experimental evidence suggests that species are unlikely to migrate with sufficient speed to maintain their preferred climate as anthropogenic climate change is so rapid (Corlett and Westcott, 2013). Between the LGM and the present, our results suggest an average upslope migration rate of 0.002 m yr^{-1} and 1.16 m yr^{-1} between now and 2070 in order to keep up with climate changes. Similarly, our data suggest that southward migration rates will be orders of magnitude higher between now and 2070 than they have been in the past (0.003 km yr^{-1} and 2.35 km yr^{-1}, respectively). Despite New Zealand being highly mountainous with much available upslope habitat to inhabit, this modeled rate is double the estimate derived from previous work which estimated a migration rate of 1 km yr^{-1} required to "keep up" with climate change (Corlett and Westcott, 2013). However, some fern species have been shown to be very effective long-distance dispersers, albeit on a geological timescale, which may become increasingly beneficial in the coming decades as the climate changes rapidly (Perrie and Brownsey, 2007; Shepherd *et al.*, 2009). Whether ferns in New Zealand will be able to migrate fast enough remains to be understood and needs further long-term observational study.

SSDMs may overestimate SR when compared to community composition data (Dubuis *et al.*, 2011; Del Toro *et al.*, 2019). Consequently, other methods such as macroecological modelling have been suggested as more effective than SSDM at modelling communities over time; however, our study provides important insights into temporal community dynamics. SSDMs do not account for biotic interactions such as competition, facilitation, or ecological succession. Instead, they only account for the climatic drivers of species distributions such as temperature and moisture. Thus, as biotic interactions are not included in SSDMs, they can be used to inform how climate may potentially mediate fundamental biotic interactions through time. Our data suggest that high STT in New Zealand is driven by nestedness at mid-elevations and replacement at high and low elevations across both time periods (Fig. 3C). High nestedness is driven by increased SR at mid-elevations (Fig. 3A). These results suggest that as the climate changes, middle elevation environments will become *climatically* suitable for an *increased* number of fern species. On the one hand, this could lead to a general increase in competition at mid-elevations as more than one species vies to fill each functional role in the ecosystem which could drive extinction or displacement of local, mid-elevation species or the extirpation of low elevation species that fail to compete. On the other hand, high replacement in high and low elevation environments with little change in SR could lead to fundamentally different processes governing the formation of the final community. These environments will become *climatically* suitable for a *different* set of fern species. Depending on the functional diversity of these new communities, this could lead to less competition for some niches, more competition for others and, if a species filling an important functional role is forced to migrate, reduced ecosystem functioning and reduced facilitation and/or succession.

An example of how shifts in functional diversity could impact forest-level dynamics can be hypothesized through tree ferns. With their rough, fissured mantel texture, tree ferns provide essential habitat for many epiphytic species (Moran *et al.*, 2003; Newnham *et al.,* 2007), their dense crowns shade the understory, and their litter filters understory communities (Brock *et al.*, 2018). A reduction in tree fern species richness (and/or density if climate is only marginally favorable for tree fern growth) may impact understory light levels and could impact many shade-tolerant species. While this study does not explicitly investigate these interactions, it does reveal broad elevational patterns in STT Ratio under changing climate regimes. Future studies should investigate these ideas further across a larger study area and by splitting species into functional groups to investigate functional diversity across elevations and through time. New Zealand's mountains show one potential elevational pattern of STT Ratio but may not be representative of the larger role of mountains in species' responses to changing climates.

Here, we also show that different families may exhibit different responses to climatic change through time (Fig. 4). Families span a remarkably large range of percent gain, loss, and stability. The present – 2070 is characterized by less overall range stability and more novel habitat gain when compared to LGM – present. However, the ratio of gain:loss:stability is not set across the phylogeny. Families with lower stability values may consist of species with small, rapidly changing climatic niches. Such small-range species may be at an increased risk to extinction imposed by rapid climate change. In contrast, families with high stability values may consist of generalist species with larger climatic niches. The large degree of rank change from one time period to the next (indicated by crossing lines in Fig. 4) may indicate that the overall phylogenetic composition of New Zealand ecosystems has been and will continue to change as the climate changes. It may otherwise not spell functional changes for New Zealand's ecosystems, as within a family, there may be a species adapted to every climate that can fill the functional role left behind by the species that left. For example, the warm-loving *Cyathea medullaris* may be able to replace the more cold-loving *Dicksonia fibrosa* as *D. fibrosa* is forced out as the climate warms. In this example, the phylogenetic diversity of the ecosystem has technically changed with little to no consequences for functional diversity save for small differences in the traits, phenology, microclimatic preferences, etc. between the two species.

This study is one of the most comprehensive of its kind to model fern response to climate change in New Zealand (but see modelling papers (Lehmann, Leathwick, and Overton, 2002; Zaniewski *et al.*, 2002; Syfert *et al.*, 2013)). Here, we demonstrate that fern SR in New Zealand is likely to continue migrating both upslope and southward, away from the equator to keep pace with climate change. We also show that STT Ratio is greatest at mid-elevations where SR is predicted to increase across New Zealand. Finally, we explore the response of different fern families to these climate changes through time. While such modelling studies will always make assumptions and have limitations, they are useful as hypothesis generators for biologists and information for policy makers. To extend our predictions, future work should set up a series of common garden experiments across rainfall and temperature gradients to examine the ecological plasticity of New Zealand tree ferns as this group clearly plays a disproportionate influence on these forests. According to our predictions, conservation efforts are likely best focused on lowland areas on the North Island where climate change is predicted to have the greatest negative effect on fern species richness in New Zealand.

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