Forests in a changing world: conifer leaf traits, community shifts, and climate change adaptation

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Abstract

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Climate change is increasing forest vulnerability worldwide. While forest management has been an integral part of human history, climate change poses a new challenge. Mitigating and adapting to the impacts of this novel challenge likely requires the use of novel methods alongside tried-and-true management strategies. But to properly implement these methods, we need a robust understanding of the patterns of functional biodiversity in current forests, the degree of changes they have experienced in response to climate change, and the synergy between more traditional and more novel management techniques. In this dissertation, I present work that addresses these knowledge gaps in the coniferous forests of the Pacific Northwest. In chapter 1, I examined the variation and covariation of leaf traits of conifer communities across a climatic gradient. I found that the contribution of species turnover to community-level trait values was tightly linked to climate while the contribution of intraspecific trait variation, despite being more important, was

not. This suggests that species turnover will likely be the main mechanism by which these communities respond to climate change, as least as it pertains to leaf traits. In chapter 2, I compared historical and modern montane plant communities (both overstory and understory) to assess whether they had shifted towards more novelty and increased biotic similarity. I found that both overstory and understory communities had indeed shifted towards more novel species combinations over time, and had also become more differentiated from one another across space. This, in combination with our finding of potential disequilibrium between modern plant communities and climate, suggests that while organisms are responding to climate change, they are doing so individualistically resulting in increased potential for novelty in future communities. Finally, in chapter 3, I assessed whether thinning forest stands for old-growth restoration reduces landscape buffering capacity (in the form of climate change refugia) in a watershed-level experimental forest. I found that variation in remote sensing vegetation indices can be good proxies for climate change refugia and that strategic forest thinning does not have negative impacts on landscape buffering capacity. Overall, this body of work highlights the importance of examining community-level biodiversity from multiple perspectives and demonstrates the value of testing the efficacy of combining old and new methods to achieve multiple management goals.

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DEDICATION

To Hema Chema

INTRODUCTION

Climate change is dramatically impacting life on earth, with projected biodiversity losses that parallel previous mass extinctions (Ceballos et al., 2015). These biodiversity losses will likely lead to significant perturbations in ecosystem functions (Hooper et al., 2012; Pecl et al., 2017). To effectively address these challenges posed by our changing world, ecologists have been seeking insight into the relationship between organisms and their environment. One useful framework to examine organism-environment relationships has been functional traits, organismal characteristics that strongly impact organisms' ecological roles and can therefore provide insight towards causal mechanisms that drive ecologically relevant species-environment relationships (Funk et al., 2017). Next, we need to assess whether anthropogenic climate change is indeed leading to changes in biodiversity and whether these changes are at a rate fast enough to keep up with the changing climate (Essl et al., 2015). Finally, given the novel challenge of anthropogenic climate change, we need to consider novel management solutions alongside traditional ones to support climate change adaptation in across ecosystems.

In this dissertation, I look at the present, compare it to the past, and consider the future of forests in the Pacific Northwest in the face of climate change to help fill knowledge gaps and support climate-smart forest management. Forests are excellent ecosystems for addressing these knowledge gaps due to their cultural, socioeconomic, and ecological significance (Bonan, 2008; Watson et al., 2018). Importantly, they also provide habitat and buffering from climate change to other organisms (De Frenne et al., 2019), and function as a considerable carbon sink (Pan et al., 2011; Pugh et al., 2019). However, changing temperature and precipitation patterns are likely to impact forests, thereby changing their dynamics and increasing vulnerability (McDowell et al., 2020; Reich et al., 2022). While warmer spring temperatures have lengthened the growing season (due to an earlier onset of budburst and leaf out) raising the potential for increased growth in forests, increased temperature and altered precipitation patterns can lead to increase forest vulnerability to drought and water stress (Allen et al., 2015; Brodribb et al., 2020; Park Williams et al., 2013). In addition to this, climate change has altered disturbance regimes, degrading forest resilience globally (Forzieri et al., 2021, 2022; Seidl et al., 2017). These effects of climate change are compounding the already concerning loss of forests globally (Curtis et al., 2018). Within the Pacific Northwest, the conifer dominated forests provide habitat (Betts et al., 2018; Frey et al., 2016), provide multiple ecosystem services (Brandt et al., 2014), and have tremendous carbon storage capacity (Law & Waring, 2015). But, like forests globally, PNW forests are experiencing increased drought stress, forest fires, changes to growth, mortality and forest composition (Case et al., 2021; Law & Waring, 2015) and forest management plans are already considering climate change adaptation (Spies et al., 2010).

Recent resurgence in the interest in intraspecific trait variation has allowed ecologists to explore functional trait across scales of organization, revealing inconsistencies in trait-trait and trait-climate relationships for well-known functional traits included in the leaf economics spectrum (Anderegg et al., 2018). Although the leaf economic spectrum has been valuable, plant functional traits can have many major axes of variation (Yang et al., 2019) and examining less studied functional traits can provide further insight into trait-environment relationships. In my first chapter, I look at the present and explore how (if at all) climate gradients are related to leaf functional traits of conifers. I asked how leaf level traits vary and covary across large climate gradients in the conifer dominated forests of the Pacific Northwest. In addition to the leaf economic spectrum, I found that another axis of trait variation associated with light use traits is an important contribution of intraspecific trait variation on community-level trait values. Despite the large contribution of intraspecific trait variation to community level trait patterns, I found that this intraspecific trait variation was not related to climate variables, with species turnover playing the strongest role in climate-community-level traits. In other words, there is a tight link between patterns in community-level traits driven by species turnover and climate variables. This suggests that species turnover will be required for communities to respond to the changing climate and maintain ecosystem functions.

But have plant communities shifted in response to climate change? In my second chapter, I look to the past to answer this question**.** Specifically, I examined historical and modern plant communities to assess whether they have shifted and changed in response to ~40 years of climate change, and whether these shifts are fundamentally altering community structure, for example through novel co-occurrences of species not seen in the past and more homogenous community composition. Given increasing temperatures and changing precipitation regimes, the projected proliferation of no-analog climatic conditions (Ordonez & Williams, 2013; Williams et al., 2007), and species specific responses to climate change, I expected plant communities to become more homogenous (as generalists spread and specialist face local extirpation) (Olden & Poff, 2003; Rolls et al., 2023) and more novel (i.e., combinations of species not previously seen in a community) (Williams & Jackson, 2007). Addressing these hypotheses in response to anthropogenic climate change is difficult given the short time frames of rapid climatic shifts and the much longer time scales of community change. However, novel communities are unlikely to arise *de novo*. Instead, they will likely result from gradual shifts in communities in response to the changing climate, driven primarily by individualistic species responses (or lack thereof).

Using historical (Franklin et al., 1988) and modern community composition survey of overstory and understory species in the forests of Mt. Tahoma (Mt. Rainier National Park), I found that these communities are indeed changing, with understory communities changing at a faster rate than overstory communities. Specifically, 40 years of climate change have resulted in the emergence of novel communities, as expected, and spatially more heterogenous communities, which was not expected. However, alongside changes in community composition, community-climate relationships have also changed indicating a disequilibrium of vegetation dynamics with climate (Svenning & Sandel, 2013) .

Given these changes in plant community composition and alterations of community-climate relationships, climate change poses a new challenge for forest management. Managers are increasingly interested in management strategies that include new approaches taking climate change adaptation into account (Prober et al., 2019; Stein et al., 2013). However, there is considerable uncertainty in whether these new management strategies can be used synergistically with existing management strategies, or if there is a trade-off. In my final chapter, I look towards the future and consider forest management in the face of climate change. Here, my collaborators and I assessed whether tried-and-true approaches for hastening the development of old-growth structure in secondary forests can be combined with new approaches identifying landscape level opportunities for climate change buffering (microclimate refugia). In response to declining forest resilience (Spies et al., 2010), restoration efforts in the Pacific Northwest (PNW) have focused on promoting the development of old-growth forest characteristics in secondary forests. One method to speed up succession in secondary forests involves managing stand density by restoration thinning. However, removing canopy cover has the potential to alter understory microclimate and impact the landscape buffering capacity; as canopy cover can cool forest understories (De Frenne et al., 2019) and buffer understory species responses to climate change (Zellweger et al., 2020). So, does restoration thinning alter landscape buffering capacity through its influence on canopy cover? In this chapter, I used variation in remotely-sensed vegetation indices to identify climate change refugia (areas of the landscape that are more buffered from climate change) (Morelli et al., 2016) in an experimental forest with control and thinned (restoration) stands. Unexpectedly and positively, I found that restoration thinning did not negatively landscape buffering capacity. Restoration thinning can therefore be combined with management for climate change refugia. This and other findings from this chapter indicate that there is potential to synergistically manage forests for both restoration and climate change adaptation.

Works Cited

Allen, C. D., Breshears, D. D., Mcdowell, N. G., Allen, C. :, Breshears, D. D., & Mcdowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 1–55. https://doi.org/10.1890/ES15-00203.1

Anderegg, L. D. L., Berner, L. T., Badgley, G., Sethi, M. L., Law, B. E., & HilleRisLambers, J. (2018). Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters*, *21*(5), 734–744. https://doi.org/10.1111/ele.12945

Betts, M. G., Phalan, B., Frey, S. J. K., Rousseau, J. S., & Yang, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions*, *24*(4), 439–447. https://doi.org/10.1111/DDI.12688

Bonan, G. B. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, *320*(5882), 1444–1449. https://doi.org/10.1126/science.1155121

Brandt, P., Abson, D. J., DellaSala, D. A., Feller, R., & von Wehrden, H. (2014). Multifunctionality and biodiversity: Ecosystem services in temperate rainforests of the Pacific Northwest, USA. *Biological Conservation*, *169*, 362–371. https://doi.org/10.1016/j.biocon.2013.12.003

Brodribb, T. J., Powers, J., Cochard, H., & Choat, B. (2020). Hanging by a thread? Forests and drought. *Science*, *368*(6488), 261–266. https://doi.org/10.1126/science.aat7631

Case, M. J., Johnson, B. G., Bartowitz, K. J., & Hudiburg, T. W. (2021). Forests of the future: Climate change impacts and implications for carbon storage in the Pacific Northwest, USA.

Forest Ecology and Management, *482*, 118886. https://doi.org/10.1016/j.foreco.2020.118886

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5). https://doi.org/10.1126/sciadv.1400253

Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers of global forest loss. *Science*, *361*(6407), 1108–1111. https://doi.org/10.1126/science.aau3445

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution 2019 3:5*, *3*(5), 744–749. https://doi.org/10.1038/S41559-019-0842-1

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Pyšek, P., Wilson, J. R. U., & Richardson, D. M. (2015). Delayed biodiversity change: no time to waste. *Trends in Ecology & Evolution*, *30*(7), 375–378. https://doi.org/10.1016/j.tree.2015.05.002

Forzieri, G., Dakos, V., McDowell, N. G., Ramdane, A., & Cescatti, A. (2022). Emerging signals of declining forest resilience under climate change. *Nature*, *608*(7923), 534–539. https://doi.org/10.1038/s41586-022-04959-9

Forzieri, G., Girardello, M., Ceccherini, G., Spinoni, J., Feyen, L., Hartmann, H., Beck, P. S. A., Camps-Valls, G., Chirici, G., Mauri, A., & Cescatti, A. (2021). Emergent vulnerability to climate-driven disturbances in European forests. *Nature Communications*, *12*(1), 1081. https://doi.org/10.1038/s41467-021-21399-7

Franklin, J. F., Moir, W. H., Hemstrom, M. A., Greene, S. E., & Smith, B. G. (1988). *The Forest Communities of Mount Rainier National Park*. U.S. Department of the Interior, National Park Service.

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4). https://doi.org/10.1126/SCIADV.1501392/SUPPL_FILE/1501392_SM.PDF

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L., & Wright, J. (2017). Revisiting the <scp>H</scp> oly <scp>G</scp> rail: using plant functional traits to understand ecological processes. *Biological Reviews*, *92*(2), 1156–1173. https://doi.org/10.1111/brv.12275

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L., & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*(7401), 105–108. https://doi.org/10.1038/nature11118

Law, B. E., & Waring, R. H. (2015). Carbon implications of current and future effects of drought, fire and management on Pacific Northwest forests. *Forest Ecology and Management*, *355*, 4–14. https://doi.org/10.1016/j.foreco.2014.11.023

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., … Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, *368*(6494). https://doi.org/10.1126/science.aaz9463

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/JOURNAL.PONE.0159909

Olden, J. D., & Poff, N. L. (2003). Toward a Mechanistic Understanding and Prediction of Biotic Homogenization. *The American Naturalist*, *162*(4), 442–460. https://doi.org/10.1086/378212

Ordonez, A., & Williams, J. W. (2013). Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: implications for community disaggregation. *Climatic Change*, *119*(3–4), 659–675. https://doi.org/10.1007/s10584-013-0752-1

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, *333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Park Williams, A., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., Swetnam, T. W., Rauscher, S. A., Seager, R., Grissino-Mayer, H. D., Dean, J. S., Cook, E. R., Gangodagamage, C., Cai, M., & McDowell, N. G. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*(3), 292–297. https://doi.org/10.1038/nclimate1693

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332). https://doi.org/10.1126/SCIENCE.AAI9214/SUPPL_FILE/PECL.SM.PDF

Prober, S. M., Doerr, V. A. J., Broadhurst, L. M., Williams, K. J., & Dickson, F. (2019). Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecological Monographs*, *89*(1), e01333. https://doi.org/10.1002/ecm.1333

Pugh, T. A. M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., & Calle, L. (2019). Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences*, *116*(10), 4382–4387. https://doi.org/10.1073/pnas.1810512116

Reich, P. B., Bermudez, R., Montgomery, R. A., Rich, R. L., Rice, K. E., Hobbie, S. E., & Stefanski, A. (2022). Even modest climate change may lead to major transitions in boreal forests. *Nature*, *608*(7923), 540–545. https://doi.org/10.1038/s41586-022-05076-3

Rolls, R. J., Deane, D. C., Johnson, S. E., Heino, J., Anderson, M. J., & Ellingsen, K. E. (2023). Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews*. https://doi.org/10.1111/brv.12958

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*(6), 395–402. https://doi.org/10.1038/nclimate3303

Spies, T. A., Giesen, T. W., Swanson, F. J., Franklin, J. F., Lach, D., & Johnson, K. N. (2010). Climate change adaptation strategies for federal forests of the Pacific Northwest, USA: Ecological, policy, and socio-economic perspectives. *Landscape Ecology*, *25*(8), 1185–1199. https://doi.org/10.1007/S10980-010-9483-0/TABLES/1

Stein, B. A., Staudt, A., Cross, M. S., Dubois, N. S., Enquist, C., Griffis, R., Hansen, L. J., Hellmann, J. J., Lawler, J. J., Nelson, E. J., & Pairis, A. (2013). Preparing for and managing change: climate adaptation for biodiversity and ecosystems. *Frontiers in Ecology and the Environment*, *11*(9), 502–510. https://doi.org/10.1890/120277

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266–1286. https://doi.org/10.3732/ajb.1200469

Watson, J. E. M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J. C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J. G., Painter, M., Wilkie, D., Filardi, C., Laurance, W. F., Houghton, R. A., … Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, *2*(4), 599–610. https://doi.org/10.1038/s41559-018-0490-x

Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, *5*(9), 475–482. https://doi.org/10.1890/070037

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, *104*(14), 5738–5742. https://doi.org/10.1073/pnas.0606292104

Yang, Y., Wang, H., Harrison, S. P., Prentice, I. C., Wright, I. J., Peng, C., & Lin, G. (2019). Quantifying leaf-trait covariation and its controls across climates and biomes. *New Phytologist*, *221*(1), 155–168. https://doi.org/10.1111/nph.15422

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Chapter 1. FOLIAR TRAITS IN PACIFIC NORTHWEST CONIFER SPECIES ACROSS AN ENVIRONMENTAL GRADIENT

1.1 ABSTRACT

An increased understanding of the magnitude of intraspecific plant trait variation (ITV) has led ecologists to focus on disentangling the relative contributions of intraspecific trait variation and species turnover to community-level traits. Most studies exploring ITV focus on well-known traits like those in the Leaf Economics Spectrum (LES), but recent studies have demonstrated that LES only represents one axis of functional variation. Exploring additional foliar functional traits, like light-use ability and chlorophyll content (Light Use Traits-LUT), can give us additional insight into trait-environment relationships. As such, we assessed how leaf level traits vary and covary across large climate gradients in the conifer dominated forests of the Pacific Northwest. We examined trait-trait covariation across three levels of organization (within species, across species, and across communities) for seven foliar traits. Then, we decomposed the contribution of species turnover, ITV, and their covariation to community-level patterns. Finally, we examined the relationships between climate variables and community-weighted means (CWMs) influenced solely by species-turnover and that influenced by both species turnover and ITV. We found two major axes of variation in foliar traits – one associated with the leaf economics spectrum and one associated with light-use – illustrating that exploring multiple functional traits can reveal multiple plant strategies. Importantly, although ITV had a larger contribution to CWMs than species turnover for most of the traits we studied, this variation was not well explained by climate variables. This surprising lack of trait-climate relationships, especially given the high degree of ITV, indicates that there are additional traits that might be

important for a complete picture of intraspecific contribution to community-level climate change responses. Instead, climate variables did a much better job in describing patterns of regional CWM, showing a tight link between patterns in community-level traits driven by species turnover. Taken together, our results suggest that if these trait-climate relationships reflect important functional differences, unfortunately local communities will not be able to adapt through ITV. Instead, species turnover will be required for communities to respond to the changing climate and maintain ecosystem functions.

1.2 INTRODUCTION

Plant functional traits are a useful framework to examine organisms' relationships with their environment, as species-level structural and physiological differences in functional traits influence which parts of the climate space are optimal for their growth, and thus, where they can occur and are most abundant (Violle et al., 2007). Over the last two decades, functional trait frameworks have been used to examine ecological strategies (Adler et al., 2014), biodiversity-environment relationships (Asner et al., 2016; Cui et al., 2020), and community assembly (Ackerly & Cornwell, 2007; Lasky et al., 2015; Marteinsdóttir et al., 2018). These assessments have led to the discovery of several cross species trade-offs linked to ecological strategies in foliar (Pan et al., 2020; Wright et al., 2004) , wood (Chave et al., 2009), root (Freschet et al., 2021; Kong et al., 2019; Prieto et al., 2015), and whole plant traits (Díaz et al., 2016; Freschet et al., 2010; Reich, 2014; Verbeeck et al., 2019). Despite the success of these studies in exploring broad patterns of trait diversity across species, ecologists are still gaining insight on the ability of these plant functional traits and associated trait syndromes to describe patterns at other levels of organization (like across communities or within species) and across environmental gradients.

The first challenge in understanding how functional traits vary with environment lies in identifying relevant axes of functional trait variation. The Leaf Economic Spectrum (LES) is an example of a set of commonly measured traits that form a core framework across which leaf level traits vary in a way that characterize species-level trade-offs between growth and persistence (Wright et al., 2004). These traits describe global patterns of trait variability (Díaz et al., 2016), are well studied from the perspective of intraspecific trait variation (ITV) (Westerband et al., 2021), and have been linked to climatic and edaphic characteristics (Joswig et al., 2021; Simpson et al., 2016a). However, recent studies have identified other axes of functional trait variation that do not line up with LES, and yet, also vary across climatic environmental gradients (Díaz et al., 2016; Joswig et al., 2021). Similarly, studies have documented that LES is just one axis of foliar trait variation, with other axes describing photosynthetic capacities, leaf area and internal-to-ambient CO_2 ratios (Yang et al., 2019). Traits that are generally not included in LES but are associated with stress-response are an important avenue to explore as they can be relevant to our understanding of how plant communities might respond to climate change. For example, traits obtained from measuring chlorophyll content and fluorescence (hereafter, LUT-Light Use Traits) have the potential to provide insight into plant stress response as they have been previously linked to drought, heat, and nutrient stress (Swoczyna et al., 2022). These photosynthetic functional traits have been used extensively in plant phenotyping and screening for agricultural applications as they reflect photosynthetic performance and sensitivity to environmental stressors but are less commonly applied in ecology and global change studies.

Understanding trait patterns at multiple levels of organization can provide insight beyond those provided by species-level explorations. Studies of intraspecific trait variation have revealed that strong trait-trait correlations across species may be weaker when examined at intra-specific or community level scales (Anderegg et al., 2018; Dong et al., 2020). For instance, studies of trait-trait covariation across levels of organization have demonstrated inconsistency in expected covariation patterns for foliar traits (Anderegg et al., 2018; Laughlin et al., 2017; Osnas et al., 2018). Even in cases where patterns at the community level reflect patterns expected from species level analysis, the relationship of plant traits to climatic conditions can be weak at large scales (Bruelheide et al., 2018). Trait-environment patterns at the species-level have also been shown to diverge over other levels of organization (Dong et al., 2020). Thus, understanding how LES and LUT traits vary within species, between species, and across communities experiencing different climates can guide our expectations for the relevance of these traits as well as their future patterns given climate change.

A second challenge for better understanding the relationship between plant functional traits and environmental gradients, lies in disentangling the influence of ITV and species turnover on community-level traits. Community-level trait-environment patterns can allow us to understand co-existence mechanisms and community assembly processes (Adler et al., 2013; Kraft et al., 2015), as well as identify potential optimal trait strategies (Muscarella & Uriarte, 2016). In addition to this, community level traits can be scaled-up and used to describe and predict ecosystem-level processes like productivity and biodiversity-ecosystem function relationships (N. He et al., 2023; Lavorel & Garnier, 2002). Trait-environment patterns across communities can be the result of either species turnover, ITV, or both. Different interactions between these intra-specific and species-sorting responses to environmental gradients can result in differences in trait-climate relationships across communities (Tautenhahn et al., 2020). Across communities, discrepancies between expectations and observations in trait-environment relationships can be driven (at least in part) by intraspecific trait variation (ITV) (Anderegg, 2023; Tautenhahn et al., 2020; Westerband et al., 2021). Individual organisms may either have coordinated responses, species-specific responses, or no responses to changes along an environmental gradient leading to different contributions of ITV vs. species turnover to community-level trait patterns along the same environmental gradients (Tautenhahn et al., 2020). Studies that have examined the relative contributions of ITV vs species turnover have found that in even though ITV is important, species turnover plays a large role in community-weights trait values (Auger & Shipley, 2013; Derroire et al., 2018; Kazakou et al., 2014; Kichenin et al., 2013; Siefert et al., 2015). However, this importance of species turnover over ITV can depend on the trait in question (Auger & Shipley, 2013; Derroire et al., 2018; Fajardo & Siefert, 2018; Kazakou et al., 2014) and the spatial scale at which these traits were studied (Albert et al., 2011; Kumordzi et al., 2019b; Messier et al., 2017; Siefert et al., 2015)

Thus, to effectively characterize foliar functional traits in our focal Pacific Northwestern coniferous forests, we explore how leaf level traits vary and covary across spatial and climate gradients in the conifer dominated forests of the Pacific Northwest. To address this overarching topic, we collected leaf level traits for 10 conifer species common in the montane forests of the Pacific Northwest across temperature and precipitation gradients, and used this data to address the following specific questions:

1. Are foliar traits coordinated such that they covary along the same axes across levels of organization (within species, across species and across communities)? We expect covariation in traits will be less evident at intraspecific levels of organization than at species and community levels, as ITV is likely to be high.
2. Can climate variables explain the variation of leaf level traits across environmental gradients within species, across species and across communities? We expect to see an increase in more acquisitive traits in LES, as well as a shift away from stress-tolerance traits in LUT in warmer and wetter regions.
3. What is the contribution of species turnover and intraspecific trait variation to variation in leaf level functional traits along climatic gradients? Here we expect to see a stronger influence of species turnover compared to intraspecific variation due to the large changes in environmental conditions across our study sites as we expect ITV to be more important in cases of higher environmental heterogeneity and smaller scales and the contributions

of turnover to be more important at larger scales (Siefert et al., 2014, 2015; Westerband et al., 2021).

The montane evergreen conifer forests in the Pacific Northwest are an excellent study system in which to examine how foliar traits vary with species and across communities along large environmental gradients. Montane conifer forests in the PNW occur across both temperature (energy-limited) and precipitation (water-limited) gradients induced by elevation and rain shadow effects, respectively. These large spatial differences in climate can serve as proxies for the climatic changes Pacific Northwestern forests, which are expected to warm and dry (Dalton et al. 2013), will experience. Coniferous forests are relatively species poor (compared to tropical or eastern deciduous forests), making it feasible to assess ITV across all dominant tree species in these forests. Pacific Northwestern forests are also important to global carbon dynamics, so understanding the capacity of forest communities to adjust functional traits through ITV vs. species turnover may additionally help ecologists appreciate climate change impacts on forest processes associated with functional traits, including carbon uptake, in an important biome.

1.3 MATERIALS AND METHODS

1.3.1 *Study area*

Our study sites are located in the North Cascades region and Mt. Rainier (Tahoma) National Park (MRNP; Fig 1), with most of our data collection and sampling concentrated along two elevational transects in the North Cascades region. While the regional climate consists of generally cool wet winters and warm dry summers there is a distinct rain shadow effect leading to a drier east side and a wetter west side of the Cascade range. The west transect (Fig 1-1a) is located in the Mt. Baker-Snoqualmie National Forest in the Mt. Baker Ranger District. These forests are dominated by western hemlock with some western red cedar (Thuja plicata) at lower elevations and increasing presence of firs (*Abies amabilis* and *Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations. The east transect (Fig 1-1b) is located in the Okanagan-Wenatchee National Forest in the Methow Valley Ranger District. The forests at lower elevations tend to be more open and are dominated by Douglas Fir (*Pseudotsuga menzesii*) and Ponderosa pine (*Pinus ponderosa*) and tend to shift to a fir (*Abies amabilis* and *Abies lasiocarpa*) and hemlock (*Tusga heterophylla* and *Tsuga mertensiana*) dominated forests at higher elevations with some *Larix occidentalis* at the highest elevations. Supplemental trait sampling took place in Mt. Rainier (Tahoma) National Park (Fig 1-1 c) to cover more elevational sampling for some species.

1.3.2 *Environmental variables*

As we were interested in the patterns of traits variation across gradients of energy and moisture limitation, we focused on environmental variables that describe temperature and moisture gradients. Specifically, we obtained data on elevation, and 30 year normal (1991-2020) growing degree days (GDD), climatic moisture deficit (CMD), mean annual precipitation (MAP), precipitation as snow (PAS), and mean annual temperature (MAT) from ClimateNA (T. Wang et al., 2016) . To reduce dimensionality, we examined these variables using a principle components analysis and selected GDD and CMD as they were orthogonal to one another and were associated with other climate variables we had originally considered important.

1.3.3 *Foliar traits data*

We collected foliar traits for 11 conifer species (see Fig 1-1 for where locations for trait data collection). To collect trait data from conifer species, we first selected one individual per species at each site that was mature (was large or we could see evidence of cones) and had a low-mid canopy branch that was exposed to light. We then followed protocol outlined in Youngentob *et al*. (2016) to secure a branch from each selected individual. We used an arborist's throwline launcher (essentially a giant sling shot) to throw a line with an arborist's throw weight on one end over the target branch. After lowering the weight-bearing end of the line to the ground we removed the weight and attached a double-sided flexible chainsaw to it. The other end of the flexible chainsaw was then attached to another line and both ends of the chainsaw were marked with flagging tape for visibility. While one person held onto the free end of the line, another person raised the chainsaw to the branch after which we used a back-and-forth motion to saw through the branch. Once the branch (hereafter main branch) was sawed from the tree and lowered to the ground, we collected data in situ and prepared three sub-branches along the main branch for transport to our lab for the rest of the data collection.

We collected three foliar traits associated with the LES specific leaf area (SLA; fresh leaf area/leaf mass), nitrogen content (N_{mass}), and carbon to nitrogen ratio (C:N). These trait data were collected in the lab following standard protocol (Pérez-Harguindeguy et al., 2016) . Since our species set consisted of both needle-leaved and scale-leaved conifer species, we approached SLA calculation for these sets of species in slightly different ways. For the needle-leaved species, we collected 50 needles from each sub-branch (150 needles per individual) from the previous year to ensure that they were fully unfolded. We then scanned and measured the dry weight of these 50 needles and calculated the SLA for each needle before averaging them. For the scale-leaved species, we collected ~ 0.5 g worth of leaves in sections, scanned and weighed (dry weight) them all together and then calculated the SLA. We also did not constrain the leaves of the scale-leaved species to the previous year but attempted to sample from end of the branches as much as possible. We ground all the scanned leaf samples into fine powder using liquid nitrogen and a mortar and pestle and then put them in the drying oven once again for 72 hours. Finally, we got the carbon and nitrogen content of these samples using a CHN Analyzer 2400 Model, Perkin Elmer Co. at the University of Washington's Soil Analytics Lab and Analytical Service Center.

In addition to LES traits, we also collected four foliar traits that we collectively refer to these traits as Light Use Traits (LUT) as these traits are associated with chlorophyll content and fluorescence: relative chlorophyll content, Phi2 (proportion of incoming photosynthetically active radiation (PAR) going to photosynthesis), PhiNPQ (non-photochemical quenching; proportion of incoming PAR that is dissipated as heat) and PhiNO (absorbed light energy going into photoinhibitive processes). These traits were collected using a Multispeq (Kuhlgert et al., 2016), with up to 30 measurements taken per main branch across different leaves. Phi2, PhiNPQ and PhiNO are dependent on the amount of PAR incident on the leaf, which means that these measurements do not tell us about the light use and photoprotection ability of a leaf/leaves. We therefore calculated the slope of the relationship between the log10 of the trait and log10 of PAR. We refer to the slope of these relationships as photoefficiency (slope of Phi2), photoprotection (slope of PhiNPQ), and photoinhibition (slope of PhiNO).

1.3.4 *Foliar traits across levels of organization*

Because we were interested in covariation and variation of foliar traits across three levels of organization (within species, across species and across communities), we aggregated trait data to individual (average of all samples collected from the 3 sub-branches or a main branch), species (average of all individuals of a particular species), and community levels (community weighted means, CWMs). To calculate community weighted means (CWMs), we also needed information on tree community composition. We therefore surveyed vegetation communities at each location we sampled traits by establishing 500 m^2 circular plots at 28 sites (14 on the east transect and 14 on the west transect), identified (to species) all standing and live trees that were taller than 140 cm in height and collected their diameter at breast height. We used the abundance of each species per site, as weights to calculate community weighted trait means. We calculated two types of CWMs to disentangle the influence of species turnover and intraspecific trait variation – 1) "regional" CWMs (using means of traits by species), and 2) "local" CWMs (using locally observed trait means in plots). First, we calculated regional CWMs using mean trait values for each species based on trait values of all trees we sampled. To calculate local CWMs we used site-specific (local) trait values for each species. In combination, regional and local CWMs can give us insight into of the relative contribution of species turnover vs intraspecific trait variation. For individuals for which we had missing site-specific trait values (~6%, 36 out of 567 individual trait values), we substituted species mean trait values.

1.3.5 *Data analysis*

To determine how traits covary, addressing our first question, we examined trait covariation from a bivariate and a multivariate perspective at all levels of organization (within species, between species, across communities). Specifically, we looked at these relationships within species, across species (using species means), and across communities (using both local and regional community-weighted means separately). For bivariate trait covariation, we conducted a standardized major axis regression (SMA) using the smatr package (Warton et al.,

2012) for each trait-trait combination and organizational level to calculate Pearson's correlation coefficients. For a multivariate perspective, we conducted a PCA across all traits to examine multivariate trait associations, using the vegan package (Oskanen *et al*. 2022).

To address our next question, how traits at different organizational levels vary with climate, we used ordinary least squared regression. We focused on GDD and CMD as explanatory variables, as they represent both water and energy limitation (important to our study system) and also described climatic variation along elevation and rain shadow gradients within our study sites. We assessed linear relationships between these climate variables and each trait individually at three levels of organization – within species, across species, and across communities. Within species we examined each species separately and used site-specific trait values for each species as the response variable. We then used species trait means and community-weighted means (both regional and local) as response variables to assess how species level traits and community-level traits varied with climate. For each individual model fit, we first fit a maximal model (Trait ~ GDD + CMD + GDD:CMD) and selected the model with the lowest Akaike Information Criterion (AIC).

To address our third question, whether ITV or species turnover contributes more to community level trait variation across climatic gradients, we decomposed community-level trait variation (separately for each trait) using methods introduced by Leps *et al*. (2011) using the cati package (Taudiere & Violle, 2016) in R. This approach is based on the premise that changes in CWM across communities can result either a change in species composition (turnover), a change in trait value of a species across some gradient within its population (intraspecific trait variation), or a combination of the two (covariation). Using this approach, we first decomposed the total variation in plant traits across communities into turnover (the sum of squares of the regional

CWM), covariation (the sum of squares of the local), and intraspecific (the sum of squares of the local – the sum of squares of the regional CWM) components by fitting intercept only models to CWMs. We then examined the total among plot variation of foliar traits explained by GDD, CMD, and GDD:CMD by fitting generalized linear models to the different components of CWMs and extracting their sum of squares. These sums of squares represent the total variation in each component explained by the predictor variables. This allows us to examine both the amount of variation in traits explained by species turnover, intraspecific trait variation and their combination as well as how much CMD, GDD and their interaction accounts for the variation in these three components.

All analyses were conducted in R (R Core Team, 2022).

1.4 RESULTS

1.4.1 *Bivariate and multivariate trait covariations*

We found that the strongest patterns of trait covariation emerged at the community level; with weak or non-significant patterns within and across species (Fig 1-2). Within species, traits associated with light use, i.e., photoinhibition and photoefficiency as well as photoprotection were significantly correlated with each other for some but not all species (Fig 1-2). Across species, the only traits that were significantly correlated were N_{mass} and SLA (slope = 0.49, $p < 0.01$) and N_{mass} and photoefficiency (slope = 1.80, $p < 0.05$). Across communities, community-level traits were generally correlated with one another when calculated using regional community-weighted means, but not for the local community-weighted means. There were a few exceptions to this pattern – traits associated with light use covaried for local but not for regional community weighted means.

For all multi-variate analyses, regardless of scale, traits spread out into two main axes of variation (Fig 1-3). Across the first axis of variation, N_{mass} and SLA were positively associated with each other and negatively associated with C:N, as is predicted and commonly found in studies of the Leaf Economics Spectrum (LES). A second axis of variation differentiated species in their light use traits and (to some extent) relative chlorophyll. Within species, photoefficiency and photoinhibition were strongly positively associated, and negatively associated with photoprotection. The nature of these multi-variate trait correlations and these general patterns did vary across some levels of organization. For example, at the interspecific level, photoefficiency was positively associated with C:N, and photoinhibition and photoprotection were negatively, not positively associated with one another (Fig S1).

1.4.2 *Trait-climate relationships*

Similar to trait-trait covariations and correlations, trait-climate relationships were not consistent in their direction across levels of organization, and generally not significant (except at the community-level). Within species, there were very few significant trait climate relationships (TableS1) and there was no consistency in the direction of these relationships across all species (Fig 1-4). Across species, only SLA was marginally significant ($p = 0.081$) in its relationship to the environment (Table S1), with a positive correlation with GDD ($p < 0.05$) and a marginally negative relationship with CMD ($p = 0.068$). By contrast, climatic explanatory variables significantly explained variation in community-level traits, but only when examined through the lens of regional community weighted means (Table 1-1). When examining local community weighted trait means and how they vary with climate, climate variables are significantly related to only Relative chlorophyll (adj $r^2 = 0.395$, $p <0.01$).

1.4.3 *Relative influence of turnover, intraspecific trait variation and their combination*

Trait decomposition analyses demonstrates that ITV contributes more to changes in community weighted means (CWM) for most of the traits we studied, but that the relative importance of ITV to CWMs differed by trait (Fig 1-3a). All three components of trait variation – species turnover, intra-specific variation, and their combination – contributed to variation in community weighted traits, with the relative contribution of ITV highest for the light response traits (i.e., photoefficiency, photoprotection, and photoinhibition). This pattern was different for N_{mass}, which was the only trait for which turnover explained more of the variation than ITV. When we examined the influence of climate variables, GDD was generally more important than CMD (Fig 1-3b). However, most traits responded only weakly to these climate variables which only significantly contributed to turnover, if at all (Table 1-1), reflecting what we found from our linear models of trait climate-relationships.

1.5 DISCUSSION

By examining foliar traits in conifers across environmental gradients, we add to the growing collection of studies that have highlighted the importance of examining sources of variation and covariation of traits within species and across communities. We found that traditionally relevant traits associated with the leaf economics spectrum (SLA, N_{mass} and C:N) were important, but that less-measured traits relating to foliar responses to light and photosynthetic performance formed an additional axis of variation of plant traits, suggesting that ecologists should consider measuring a greater variety of traits. We also found a high degree of ITV across community-level traits, which implies that we need to be cautious about approaches simply taking species means. Finally, we found that climate variables do a good job of explaining changes in community-level traits because of turnover, but perform poorly for the effects of ITV. We discuss these findings further, highlighting the importance of looking at traits beyond the LES and exploring the influence of ITV vs. turnover to fully understand plant functioning in forest communities experiencing climate change.

1.5.1 *Foliar traits represent two distinct axes of variation*

We found two distinct axes of foliar trait variation – one well-known and reflecting resource use (LES), and another that reflected differences among species in light use ability (LUT; Fig 1-3). The LES axis of variation described the positive covariation of SLA and N_{mass} and their negative association with C:N, reflecting a well-known LES tradeoff (Wright et al., 2004). The second axis of variation was independent of LES traits and demonstrated a transition of foliar function from photo-efficiency (more of the incoming radiation is used in photosynthesis) to photoprotection (more of the incoming radiation is dissipated as heat). In other words, leaves that used a lower fraction of incoming light in photosynthesis, have more light energy left over that then needs to be safely discarded, requiring more photoprotection. As such, our work adds to the growing body of evidence that exploring traits beyond those associated with LES can reveal additional axes of variation even within leaf traits (Anderegg, 2023; Westerband et al., 2021).

Our study adds to those finding variable relationships between LES and LUT. For instance, the lack of association between SLA and LUT in multivariate space (Fig 1-3) contrasts with findings of strong correlations between SLA and the proportion of N content allocated to photosynthesis (Luo et al., 2021a), and between chlorophyll fluorescence traits and LES traits (Guimarães et al., 2022). However, our results are similar to previous findings of independence between processes in the electron transport chain (represented in our study by photoefficiency) and SLA (Walker et al., 2014). We also found that N_{mass} and LUT are not correlated with one another (Fig 1-2) which contrasts with previous studies that have examined photosynthetic assimilation rates and their relationship to leaf N content (Wright et al., 2004). Such discrepancies could be a result of differences in nitrogen use strategies (Luo et al., 2021b), e.g., differences in allocation of leaf-level nitrogen to carbon assimilation vs. light-use ability, the two components of photosynthesis. In all, out study suggests that we need to explore relationships between not only LES traits and overall photosynthetic capacity, but also individual processes within photosynthesis (i.e., distinctions between the electron transport and the carboxylation components) across different taxonomic groups of plants to understand when these processes covary and when they do not.

Interestingly, we found that the association between LES traits with light use and chlorophyll fluorescence traits varied across levels of organization, in contrast to their consistent internal relationships to each other in multivariate space (Fig S1). For example, at the species-level, we found that lower photoinibition is positively associated with higher SLA and N_{mass} while relative chlorophyll content is the most orthogonal to LES traits. At the community level, photoinhibition, photoprotection, and photoefficiency were not associated with LES traits. This contrasts to the strong positive relationship between SLA and N_{mass} and their negative association with CN, which emerged in all our analyses. Differences in trait coordination across levels of organizations have been previously observed in bi-variate trait assessments (Anderegg et al., 2018), and are assumed to demonstrate the contribution of ITV (at both cross community and within species scales), and ITV and species turnover (at cross community scales) to trait diversity patterns.

1.5.2 *Intraspecific variation dominates overall trait variation across conifer communities*

For the most part, we found that ITV has a greater contribution to community weighted trait values than species turnover (Fig 1-5). Although this contrasts with a recent meta-analysis in which ITV only accounted for 32% of the total variation in traits across communities (Siefert et al., 2015), our results are consistent with recent studies that have found much higher contribution of ITV than across species trait variation (Tautenhahn et al., 2019) (Messier et al. 2010). The degree of ITV can depend on the scale of study and the characteristics of the study system itself (Westerband et al., 2021). According to the spatial variance partitioning hypothesis, the importance of ITV decreases as you increase spatial scale while the importance of species turnover increases (Albert et al., 2011). Our study is at an intermediate scale as we examine communities within an ecosystem, and we find that even at this scale, ITV is still very large. Another factor that may have contributed to higher ITV in our study is the topographic complexity and large environmental gradients our study sites covered. Other studies have found that higher heterogeneity at smaller scales is linked to higher ITV (Chalmandrier et al., 2017; Kumordzi et al., 2019a).

We also found that the relative contribution of ITV depended on the trait in question, suggesting that trait plasticity or local adaptation (both of which may generate ITV) are trait specific. For example, we found that relative chlorophyll and light use traits were generally more variable within species than the morphological and chemical content traits we measured across communities. This is consistent with previous findings that leaf morphological traits tend to have less ITV than photosynthetic traits (Siefert et al., 2015). This could be a consequence of the longer leaf lifespans of conifer leaves where photoefficiency and photoprotection can vary within the lifetime of a leaf in response to seasonal climatic variation (Ain-Lhout et al., 2004). Such

ITV is particularly relevant for evergreen species where changes in LUT traits can be a result of the need to upregulate photoprotection in dry seasons to protect longer-lived leaves (Adams et al., 2004; Ishida et al., 2006). We also found that N_{mass} was the only trait where turnover was a more important than ITV, contrasting with a previous finding that leaf chemical traits were more variable than leaf morphological traits (Siefert et al., 2015). One potential reason for this discrepancy could be that our study included one deciduous conifer (*Larix lyalii*) of ten total species sampled. Deciduous conifers are known to have much higher nitrogen content than the evergreen conifer species, and our communities are relatively low in species number, which could explain the importance of species turnover for this trait.

1.5.3 *Trait-climate relationships across plant communities*

Community-level trait-climate relationships suggest that multiple climatic variables affect the optimal plant strategies needed to maintain function, but also that these patterns may only be obvious when measuring multiple traits. For example, community level SLA (from regional CWM) tended to vary across the energy gradient (as measured by GDD) while community level light-use traits varied along both energy and water gradients. An increase in SLA with increasing energy availability aligns with expectations based on trait-climate relationships across species and across communities (Rosbakh et al., 2015) and a stronger effect of temperature than precipitation variables on LES traits (Anderegg et al., 2018; Moles et al., 2014). However, with increasing growing degree days and climatic moisture deficit, we observed a shift towards lower photoefficiency and relative chlorophyll, and increased photoprotection indicating greater stress in these environments. Taken together, these trait-environment relationships indicate that as the climate continues to get warmer and dryer, regional community weighted means will shift towards leaves with lower photoefficiency and relative chlorophyll, but greater SLA and photoprotection. Thus, forest communities will likely have a “faster” resource acquisition strategy morphologically while potentially being able to fine tune stress responses at the molecular level by adjusting their light-use traits.

Importantly, we found a stronger relationship between climate variables and regional CWMs than local CWMs (Table 1-1). We believe the stronger relationship we found between climate and regional CWMs results from individualistic species responses to climate (Anderegg, 2023). In addition to conflicting species-specific responses, the lack of synchrony between intraspecific responses and species sorting across environmental gradients can also result in weak trait-climate relationships (Tautenhahn et al., 2020). In our study, trait-climate relationships across levels of organization (Fig 1-4) show distinct species level responses including differences in the direction of trait-environment relationship at different levels of organization. Previous studies have also found differences in ITV among species along the same environmental gradient leading to different outcomes for productivity and resource use (Walters & Gerlach, 2013) or a lack of response to changing environmental conditions within species for traits that are relevant to performance at the across species levels (Hikosaka et al., 2021).

1.5.4 *Implications and future directions*

Taken together, we illustrate the utility of trait-based studies in exploring plant function across climate gradients, especially if these studies can incorporate intra-specific trait variation and consider large suites of traits. We found that taking ITV into account was essential in getting a full picture of how plants at different locations respond to the environment, as other studies have found (Violle et al., 2012). If our study had only focused on regional CWMs, we would have concluded that all cross-community trait patterns are well explained by GDD and CMD – instead, our results are not so clear. Decomposing CWM into its species turnover and ITV effects allows us to have a much more nuanced understanding of how community trait patterns arise. Specifically, the strength of the regional CWM-climate relationship indicates that community turnover is linked to climatic conditions, which implies that species turnover will be required for communities to respond and that phenotypic variation within species cannot buffer communities from these impacts. At the same time, the climatic variables we used were surprisingly poor predictors of ITV, despite their known importance to ecological processes in Pacific Northwestern forests – suggesting there is much room for improvement – in the measurement of traits, our choices of covariates to measure, and the even perhaps the choices of specific traits to focus on.

We have two suggestions that we believe would improve the strength of the trait-climate relationships in our study system, coniferous forests in summer dry and winter wet conditions. Many studies have shown that soil characteristics can be important for LES traits and, in some cases, have a higher explanatory power than climate variables (D. He et al., 2018; Maire et al., 2015; Simpson et al., 2016b). Because shade-tolerant and intolerant species tend to have different leaf morphological and molecular traits (P. He et al., 2019; Q. Wang et al., 2020), insolation is good additional environmental variable to consider. Finally, carefully exploring trait-environment relationships beyond traditional across-species analysis can provide additional insight into trait-patterns. As such, future studies should explicitly account for phylogenetic effects of sampling withing vs. across lineages as they can obscure and complicate trait assessments across communities (Anderegg, 2023).

Finally, we suggest the functional trait field embrace the measurement of additional traits beyond LES, for example by measuring relative chlorophyll and light-use traits in assessment of trait-climate relationships. This fits with recent calls for exploring multiple axes of trait variation and types of traits (Anderegg, 2023; Westerband et al., 2021). We especially suggest the incorporation of light-use traits, as they have improved models of photosynthesis (Pleban et al., 2020) due to their direct link to light response and light use by plants. Additionally, these traits may be more directly linked to remotely sensed spectral properties (Chou et al., 2017) and productivity, as they reflect a plants response to and fluorescence of light. Relative chlorophyll was also the only trait for which we found both a significant and strong relationship between both regional and local community weighted traits and a notable covariation between intraspecific and species sorting responses across environmental gradient. However, the lack of similar studies examining these traits in other natural systems across large environmental gradients hinders our ability to make more general comparisons. As such, future studies of trait-patterns should consider including relative chlorophyll and light-use traits in addition to other foliar traits.

1.6 CONCLUSIONS

Overall, our study contributes to the growing literature of the importance of disentangling different sources of variation to community level traits to better understand trait-climate relationships. As functional traits influence community and ecosystem structure and function, gaining a better understanding of foliar traits and their relationships to environmental gradients can help us improve predictive methods in biodiversity and ecosystem modeling. Our results imply that shifts in traits of these plant communities in response to climate change is likely to rely on species turnover, not intra-specific trait variation. This study also demonstrates that foliar traits beyond those associated with the leaf economic spectrum can help us gain a more fine-tuned understanding of variation in the efficiency and allocation of light energy in plants. Thus, further exploration of traits beyond the LES can support linkages between functional traits collected at leaf and organism level and ecosystem functions like light use efficiency and productivity.

1.7 REFERENCES

Ackerly, D. D., & Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, *10*(2), 135–145. https://doi.org/10.1111/j.1461-0248.2006.01006.x

Adams, W., Zarter, R., Ebbert, V., & Demming-Adams, B. (2004). Photoprotective Strategies of Overwintering Evergreens. *BioScience*, *54*(1), 41–49. https://doi.org/htthttps://doi.org/10.1641/0006-3568(2004)054[0041:PSOOE]2.0.CO;2

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*(10), 1294–1306. https://doi.org/10.1111/ele.12157

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences*, *111*(2), 740–745. https://doi.org/10.1073/pnas.1315179111

Ain-Lhout, F., Barradas, M. C., Zunzunegui, M., Rodríguez, H., Novo, F., & Vargas, M. A. (2004). Seasonal Differences in Photochemical Efficiency and Chlorophyll and Carotenoid Contents in Six Mediterranean Shrub Species under Field Conditions. *Photosynthetica*, *42*(3), 399–407. https://doi.org/10.1023/B:PHOT.0000046159.96228.49

Albert, C. H., Grassein, F., Schurr, F. M., Vieilledent, G., & Violle, C. (2011). When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(3), 217–225. https://doi.org/10.1016/j.ppees.2011.04.003

Anderegg, L. D. L. (2023). Why can’t we predict traits from the environment? *New Phytologist*, *237*(6), 1998–2004. https://doi.org/10.1111/nph.18586

Anderegg, L. D. L., Berner, L. T., Badgley, G., Sethi, M. L., Law, B. E., & HilleRisLambers, J. (2018). Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters*, *21*(5), 734–744. https://doi.org/10.1111/ele.12945

Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E., & Vaughn, N. (2016). Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proceedings of the National Academy of Sciences*, *113*(28). https://doi.org/10.1073/pnas.1604863113

Auger, S., & Shipley, B. (2013). Inter-specific and intra-specific trait variation along short environmental gradients in an old-growth temperate forest. *Journal of Vegetation Science*, *24*(3), 419–428. https://doi.org/10.1111/j.1654-1103.2012.01473.x

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrodt, F., Mahecha, M. D., Peet, R. K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., … Jandt, U. (2018). Global trait–environment relationships of plant communities.

Nature Ecology & Evolution, *2*(12), 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Chalmandrier, L., Münkemüller, T., Colace, M. P., Renaud, J., Aubert, S., Carlson, B. Z., Clément, J. C., Legay, N., Pellet, G., Saillard, A., Lavergne, S., & Thuiller, W. (2017). Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands. *Journal of Ecology*, *105*(1), 277–287. https://doi.org/10.1111/1365-2745.12658

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*(4), 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chou, S., Chen, J., Yu, H., Chen, B., Zhang, X., Croft, H., Khalid, S., Li, M., & Shi, Q. (2017). Canopy-Level Photochemical Reflectance Index from Hyperspectral Remote Sensing and Leaf-Level Non-Photochemical Quenching as Early Indicators of Water Stress in Maize. *Remote Sensing*, *9*(8), 794. https://doi.org/10.3390/rs9080794

Cui, E., Weng, E., Yan, E., & Xia, J. (2020). Robust leaf trait relationships across species under global environmental changes. *Nature Communications*, *11*(1), 2999. https://doi.org/10.1038/s41467-020-16839-9

Dalton, M.M., P.W. Mote, and A.K. Snover [Eds.]. 2013. Climate Change in the Northwest: Implications for Our Landscapes, Waters, and Communities. Washington, DC: Island Press.

Derroire, G., Powers, J. S., Hulshof, C. M., Cárdenas Varela, L. E., & Healey, J. R. (2018). Contrasting patterns of leaf trait variation among and within species during tropical dry forest succession in Costa Rica. *Scientific Reports*, *8*(1), 285. https://doi.org/10.1038/s41598-017-18525-1

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Dong, N., Prentice, I. C., Wright, I. J., Evans, B. J., Togashi, H. F., Caddy-Retalic, S., McInerney, F. A., Sparrow, B., Leitch, E., & Lowe, A. J. (2020). Components of leaf-trait variation along environmental gradients. *New Phytologist*, *228*(1), 82–94. https://doi.org/10.1111/nph.16558

Fajardo, A., & Siefert, A. (2018). Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology*, *99*(5), 1024–1030. https://doi.org/10.1002/ecy.2194

Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., & Aerts, R. (2010). Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, *98*(2), 362–373. https://doi.org/10.1111/j.1365-2745.2009.01615.x

Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., Bardgett, R. D., De Deyn, G. B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M. L., Meier, I. C., Pagès, L., Poorter, H., Prieto, I., Wurzburger, N., Zadworny, M., Bagniewska-Zadworna, A., … Stokes, A. (2021). Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*, *232*(3), 1123–1158. https://doi.org/10.1111/NPH.17072

Guimarães, Z. T. M., dos Santos, V. A. H. F., & Ferreira, M. J. (2022). Chlorophyll a fluorescence parameters are related to the leaf economics spectrum of tropical tree species in a mixed plantation. *Trees - Structure and Function*, *36*(2), 763–775. https://doi.org/10.1007/S00468-021-02248-Y/FIGURES/4

He, D., Chen, Y., Zhao, K., Cornelissen, J. H. C., & Chu, C. (2018). Intra- and interspecific trait variations reveal functional relationships between specific leaf area and soil niche within a subtropical forest. *Annals of Botany*, *121*(6), 1173–1182. https://doi.org/10.1093/aob/mcx222

He, N., Yan, P., Liu, C., Xu, L., Li, M., Van Meerbeek, K., Zhou, G., Zhou, G., Liu, S., Zhou, X., Li, S., Niu, S., Han, X., Buckley, T. N., Sack, L., & Yu, G. (2023). Predicting ecosystem productivity based on plant community traits. *Trends in Plant Science*, *28*(1), 43–53. https://doi.org/10.1016/j.tplants.2022.08.015

He, P., Wright, I. J., Zhu, S., Onoda, Y., Liu, H., Li, R., Liu, X., Hua, L., Oyanoghafo, O. O., & Ye, Q. (2019). Leaf mechanical strength and photosynthetic capacity vary independently across 57 subtropical forest species with contrasting light requirements. *New Phytologist*, *223*(2), 607–618. https://doi.org/10.1111/nph.15803

Hikosaka, K., Kurokawa, H., Arai, T., Takayanagi, S., Tanaka, H. O., Nagano, S., & Nakashizuka, T. (2021). Intraspecific variations in leaf traits, productivity and resource use efficiencies in the dominant species of subalpine evergreen coniferous and deciduous broad-leaved forests along the altitudinal gradient. *Journal of Ecology*, *109*(4), 1804–1818. https://doi.org/10.1111/1365-2745.13603

Ishida, A., Diloksumpun, S., Ladpala, P., Staporn, D., Panuthai, S., Gamo, M., Yazaki, K., Ishizuka, M., & Puangchit, L. (2006). Contrasting seasonal leaf habits of canopy trees between tropical dry-deciduous and evergreen forests in Thailand. *Tree Physiology*, *26*(5), 643–656. https://doi.org/10.1093/treephys/26.5.643

Joswig, J. S., Wirth, C., Schuman, M. C., Kattge, J., Reu, B., Wright, I. J., Sippel, S. D., Rüger, N., Richter, R., Schaepman, M. E., van Bodegom, P. M., Cornelissen, J. H. C., Díaz, S., Hattingh, W. N., Kramer, K., Lens, F., Niinemets, Ü., Reich, P. B., Reichstein, M., … Mahecha, M. D. (2021). Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. *Nature Ecology & Evolution*, *6*(1), 36–50. https://doi.org/10.1038/s41559-021-01616-8

Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J., & Garnier, E. (2014). Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*, *25*(1), 235–247. https://doi.org/10.1111/jvs.12066

Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, *27*(5), 1254–1261. https://doi.org/10.1111/1365-2435.12116

Kong, D., Wang, J., Wu, H., Valverde-Barrantes, O. J., Wang, R., Zeng, H., Kardol, P., Zhang, H., & Feng, Y. (2019). Nonlinearity of root trait relationships and the root economics spectrum. *Nature Communications*, *10*(1), 2203. https://doi.org/10.1038/s41467-019-10245-6

Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, *112*(3), 797–802. https://doi.org/10.1073/pnas.1413650112

Kuhlgert, S., Austic, G., Zegarac, R., Osei-Bonsu, I., Hoh, D., Chilvers, M. I., Roth, M. G., Bi, K., TerAvest, D., Weebadde, P., & Kramer, D. M. (2016). MultispeQ Beta: a tool for large-scale plant phenotyping connected to the open PhotosynQ network. *Royal Society Open Science*, *3*(10). https://doi.org/10.1098/RSOS.160592

Kumordzi, B. B., Aubin, I., Cardou, F., Shipley, B., Violle, C., Johnstone, J., Anand, M., Arsenault, A., Bell, F. W., Bergeron, Y., Boulangeat, I., Brousseau, M., De Grandpré, L., Delagrange, S., Fenton, N. J., Gravel, D., Macdonald, S. E., Hamel, B., Higelin, M., … Munson, A. D. (2019a). Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants. *Functional Ecology*, *33*(9), 1771–1784. https://doi.org/10.1111/1365-2435.13402/SUPPINFO

Kumordzi, B. B., Aubin, I., Cardou, F., Shipley, B., Violle, C., Johnstone, J., Anand, M., Arsenault, A., Bell, F. W., Bergeron, Y., Boulangeat, I., Brousseau, M., De Grandpré, L., Delagrange, S., Fenton, N. J., Gravel, D., Macdonald, S. E., Hamel, B., Higelin, M., … Munson, A. D. (2019b). Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants. *Functional Ecology*, *33*(9), 1771–1784. https://doi.org/10.1111/1365-2435.13402

Lasky, J. R., Bachelot, B., Muscarella, R., Schwartz, N., Forero-Montaña, J., Nytch, C. J., Swenson, N. G., Thompson, J., Zimmerman, J. K., & Uriarte, M. (2015). Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. *Ecology*, *96*(8), 2157–2169. https://doi.org/10.1890/14-1809.1

Laughlin, D. C., Lusk, C. H., Bellingham, P. J., Burslem, D. F. R. P., Simpson, A. H., & Kramer-Walter, K. R. (2017). Intraspecific trait variation can weaken interspecific trait correlations when assessing the whole-plant economic spectrum. *Ecology and Evolution*, *7*(21), 8936–8949. https://doi.org/10.1002/ece3.3447

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lepš, J., de Bello, F., Šmilauer, P., & Doležal, J. (2011). Community trait response to environment: Disentangling species turnover vs intraspecific trait variability effects. *Ecography*, *34*(5), 856–863. https://doi.org/10.1111/J.1600-0587.2010.06904.X

Luo, X., Keenan, T. F., Chen, J. M., Croft, H., Colin Prentice, I., Smith, N. G., Walker, A. P., Wang, H., Wang, R., Xu, C., & Zhang, Y. (2021a). Global variation in the fraction of leaf nitrogen allocated to photosynthesis. *Nature Communications 2021 12:1*, *12*(1), 1–10. https://doi.org/10.1038/s41467-021-25163-9

Luo, X., Keenan, T. F., Chen, J. M., Croft, H., Colin Prentice, I., Smith, N. G., Walker, A. P., Wang, H., Wang, R., Xu, C., & Zhang, Y. (2021b). Global variation in the fraction of leaf nitrogen allocated to photosynthesis. *Nature Communications*, *12*(1), 4866. https://doi.org/10.1038/s41467-021-25163-9

Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü., Ordonez, A., Reich, P. B., & Santiago, L. S. (2015). Global effects of soil and climate on leaf photosynthetic traits and rates. *Global Ecology and Biogeography*, *24*(6), 706–717. https://doi.org/10.1111/geb.12296

Marteinsdóttir, B., Svavarsdóttir, K., & Thórhallsdóttir, T. E. (2018). Multiple mechanisms of early plant community assembly with stochasticity driving the process. *Ecology*, *99*(1), 91–102. https://doi.org/10.1002/ecy.2079

Messier, J., McGill, B. J., Enquist, B. J., & Lechowicz, M. J. (2017). Trait variation and integration across scales: is the leaf economic spectrum present at local scales? *Ecography*, *40*(6), 685–697. https://doi.org/10.1111/ecog.02006

Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Díaz, S., Dickie, J. B., Freschet, G. T., … Bonser, S. P. (2014). Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science*, *25*(5), 1167–1180. https://doi.org/10.1111/JVS.12190

Muscarella, R., & Uriarte, M. (2016). Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20152434. https://doi.org/10.1098/rspb.2015.2434

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). vegan: Community Ecology Package. R package version 2.6-4, https://CRAN.R-project.org/package=vegan

Osnas, J. L. D., Katabuchi, M., Kitajima, K., Wright, S. J., Reich, P. B., Van Bael, S. A., Kraft, N. J. B., Samaniego, M. J., Pacala, S. W., & Lichstein, J. W. (2018). Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proceedings of the National Academy of Sciences*, *115*(21), 5480–5485. https://doi.org/10.1073/pnas.1803989115

Pan, Y., Cieraad, E., Armstrong, J., Armstrong, W., Clarkson, B. R., Colmer, T. D., Pedersen, O., Visser, E. J. W., Voesenek, L. A. C. J., & van Bodegom, P. M. (2020). Global patterns of the leaf economics spectrum in wetlands. *Nature Communications*, *11*(1), 4519. https://doi.org/10.1038/s41467-020-18354-3

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *64*(8), 715. https://doi.org/10.1071/BT12225_CO

Pleban, J. R., Guadagno, C. R., Mackay, D. S., Weinig, C., & Ewers, B. E. (2020). Rapid Chlorophyll *a* Fluorescence Light Response Curves Mechanistically Inform Photosynthesis Modeling. *Plant Physiology*, *183*(2), 602–619. https://doi.org/10.1104/pp.19.00375

Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H., Maeght, J. L., Mao, Z., Pierret, A., Portillo, N., Roupsard, O., Thammahacksa, C., & Stokes, A. (2015). Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology*, *103*(2), 361–373. https://doi.org/10.1111/1365-2745.12351

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reich, P. B. (2014). The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Rosbakh, S., Römermann, C., & Poschlod, P. (2015). Specific leaf area correlates with temperature: new evidence of trait variation at the population, species and community levels. *Alpine Botany*, *125*(2), 79–86. https://doi.org/10.1007/s00035-015-0150-6

Siefert, A., Fridley, J. D., & Ritchie, M. E. (2014). Community Functional Responses to Soil and Climate at Multiple Spatial Scales: When Does Intraspecific Variation Matter? *PLoS ONE*, *9*(10), e111189. https://doi.org/10.1371/journal.pone.0111189

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., L. Dantas, V., Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*(12), 1406–1419. https://doi.org/10.1111/ele.12508

Simpson, A. H., Richardson, S. J., & Laughlin, D. C. (2016a). Soil-climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography*, *25*(8), 964–978. https://doi.org/10.1111/geb.12457

Simpson, A. H., Richardson, S. J., & Laughlin, D. C. (2016b). Soil-climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography*, *25*(8), 964–978. https://doi.org/10.1111/geb.12457

Swoczyna, T., Kalaji, H. M., Bussotti, F., Mojski, J., & Pollastrini, M. (2022). Environmental stress - what can we learn from chlorophyll a fluorescence analysis in woody plants? A review. *Frontiers in Plant Science*, *13*, 4936. https://doi.org/10.3389/FPLS.2022.1048582/BIBTEX

Taudiere, A., & Violle, C. (2016). cati: an R package using functional traits to detect and quantify multi-level community assembly processes. *Ecography*, *39*(7), 699–708. https://doi.org/10.1111/ECOG.01433

Tautenhahn, S., Grün-Wenzel, C., Jung, M., Higgins, S., & Römermann, C. (2019). On the relevance of intraspecific trait variability—A synthesis of 56 dry grassland sites across Europe. *Flora*, *254*, 161–172. https://doi.org/10.1016/j.flora.2019.03.002

Tautenhahn, S., Migliavacca, M., & Kattge, J. (2020). News on intra-specific trait variation, species sorting, and optimality theory for functional biogeography and beyond. *New Phytologist*, *228*(1), 6–10. https://doi.org/10.1111/nph.16846

Verbeeck, H., Bauters, M., Jackson, T., Shenkin, A., Disney, M., & Calders, K. (2019). Time for a Plant Structural Economics Spectrum. *Frontiers in Forests and Global Change*, *2*. https://doi.org/10.3389/ffgc.2019.00043

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*(4), 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D., & Woodward, F. I. (2014). The relationship of leaf photosynthetic traits – Vcmax and Jmax – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and Evolution*, *4*(16), 3218–3235. https://doi.org/10.1002/ECE3.1173

Walters, M. B., & Gerlach, J. P. (2013). Intraspecific growth and functional leaf trait responses to natural soil resource gradients for conifer species with contrasting leaf habit. *Tree Physiology*, *33*(3), 297–310. https://doi.org/10.1093/treephys/tps134

Wang, Q., Robson, T. M., Pieristè, M., Oguro, M., Oguchi, R., Murai, Y., & Kurokawa, H. (2020). Testing trait plasticity over the range of spectral composition of sunlight in forb species differing in shade tolerance. *Journal of Ecology*, *108*(5), 1923–1940. https://doi.org/10.1111/1365-2745.13384

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLOS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). smatr 3– an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, *3*(2), 257–259. https://doi.org/10.1111/J.2041-210X.2011.00153.X

Westerband, A. C., Funk, J. L., & Barton, K. E. (2021). Intraspecific trait variation in plants: a renewed focus on its role in ecological processes. *Annals of Botany*, *127*(4), 397–410. https://doi.org/10.1093/aob/mcab011

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. https://doi.org/10.1038/nature02403

Yang, Y., Wang, H., Harrison, S. P., Prentice, I. C., Wright, I. J., Peng, C., & Lin, G. (2019). Quantifying leaf-trait covariation and its controls across climates and biomes. *New Phytologist*, *221*(1), 155–168. https://doi.org/10.1111/nph.15422

Youngentob, K. N., Zdenek, C., & van Gorsel, E. (2016). A simple and effective method to collect leaves and seeds from tall trees. *Methods in Ecology and Evolution*, *7*(9), 1119–1123. https://doi.org/10.1111/2041-210X.12554

1.8 TABLES

Table 1-1. Coefficients for models linking community-weighted traits (columns) to climatic variables (coefficients in rows). In each column, we show results community weighted traits calculated using fixed species mean values (Fixed) and for those calculated using site specific values (Local). Significant trait-climate relationships that align with our original expectations (in terms of direction) are shown in bold while significant models are present in grey.

$p < 0.1$; *$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Trait		Intercept	GDD	CMD	GDD:CMD	Adj R Sq	F value	p value
SLA	Fixed	0.001 (4.034e-03) **	7.273e-06 (2.949e-06) *			0.1585	6.084	2.06E-02
	Local	-2.784e-02 (2.190e-02) .	3.659e-05 (1.576e-05) *	2.485e-04 (1.283e-04) .	-1.655e-07 (8.081e-08) .	0.08152	1.799	0.1743
Nmass	Fixed	0.205 (0.002)***	-8.337e-06 (1.532e-05)			-0.02676	0.2962	0.5909
	Local	0.201 (0.001) ***		-3.227e-05 (4.707e-05)		-0.02002	0.4701	0.499
C:N	Fixed	52.172 (3.414) **	-0.001 (0.002)			-0.03375	0.1185	0.7334
	Local	55.719 (5.375) ***	-0.003 (0.004)			-0.008	0.7819	0.3847
Relative Chlorophyll	Fixed	32.59 (3.027) ***	-1.175e-02 (2.178e-03) ***	-3.083e-02 (1.773e-02) .	2.463e-05 (1.117e-05) *	0.653	17.96	2.51E-06
	Local	0.388 (6.462) ***	-1.656e-02 (4.650e-03) **	-5.422e-02 (3.786e-02)	4.054e-05 (2.384e-05)	0.395	6.874	0.002
Photoefficiencey	Fixed	-0.002 (9.646e-03) *	-3.864e-05 (6.941e-06) ***	-1.013e-04 (5.651e-05) .	9.871e-08 (3.559e-08) *	0.679	20.02	1.02E-06
	Local	-4.460e-02 (3.531e-02)	-2.128e-05 (2.581e-05)			-0.012	0.68	0.4173
Photoprotection	Fixed	-0.145 (7.384e-02) .	3.042e-04 (5.313e-05) ***	7.478e-04 (4.326e-04) .	-7.200e-07 (2.724e-07) *	0.684	20.48	8.36E-07
	Local	-0.028 (0.203)	0.0001749 (0.0001484)			0.014	1.388	0.2494
Photoinhibition	Fixed	7.119e-02 (1.406e-02) ***	-6.204e-05 (1.012e-05) ***	-1.820e-04 (8.238e-05) *	1.377e-07 (5.187e-08) *	0.705	22.51	3.71E-07
	Local	6.236e-02 (5.644e-02)	-5.225e-05 (4.126e-05)			0.022	1.604	0.2165

1.9 FIGURES

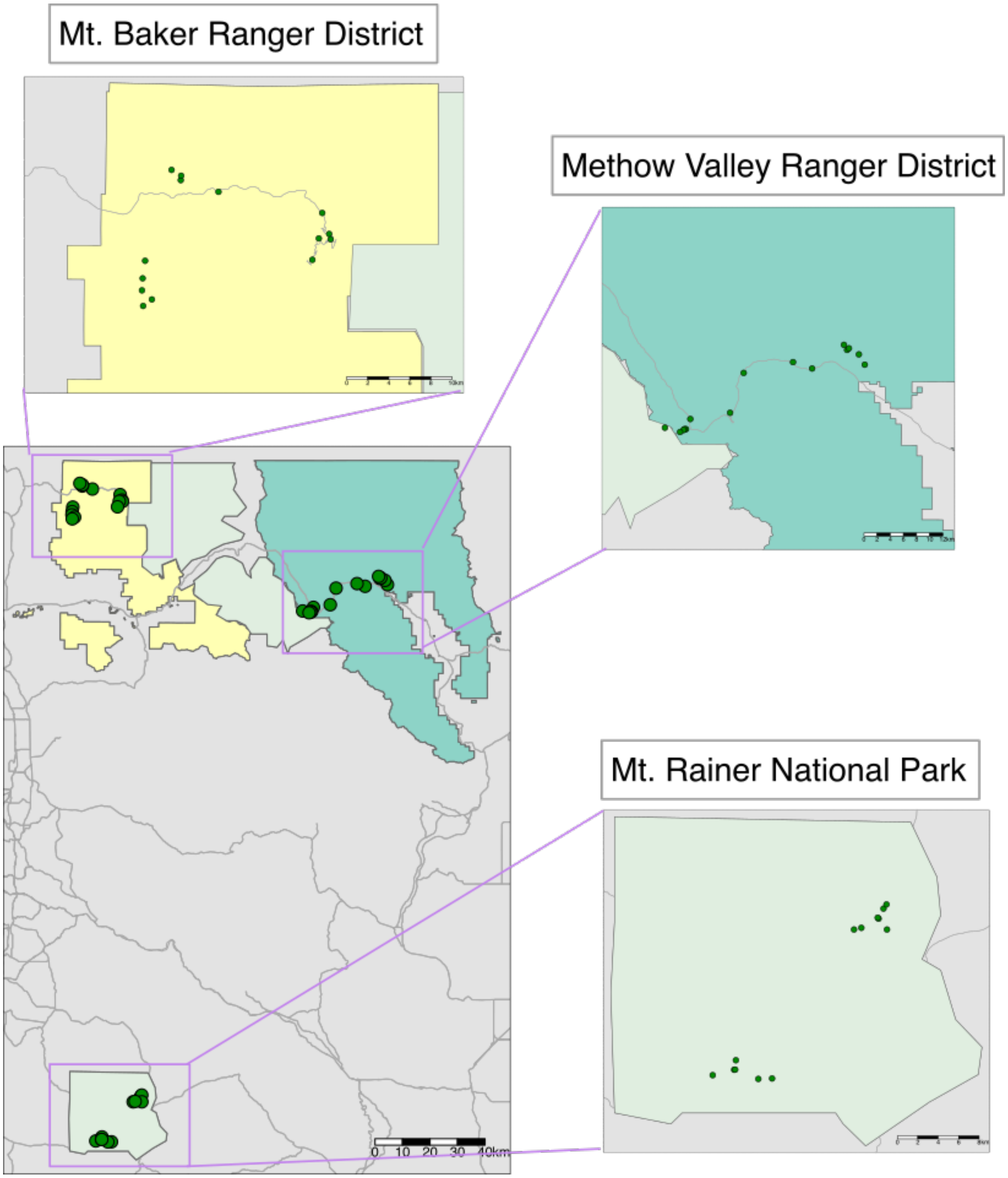


Figure 1-1. Study region and site locations where trait and/or community composition data was collected. Both tree community composition and foliar traits were collected from sites in Mt. Baker Ranger District (yellow polygon) and Methow Valley Ranger District (teal polygon). For sites in Mt. Rainier National Park, we only collected foliar trait data.

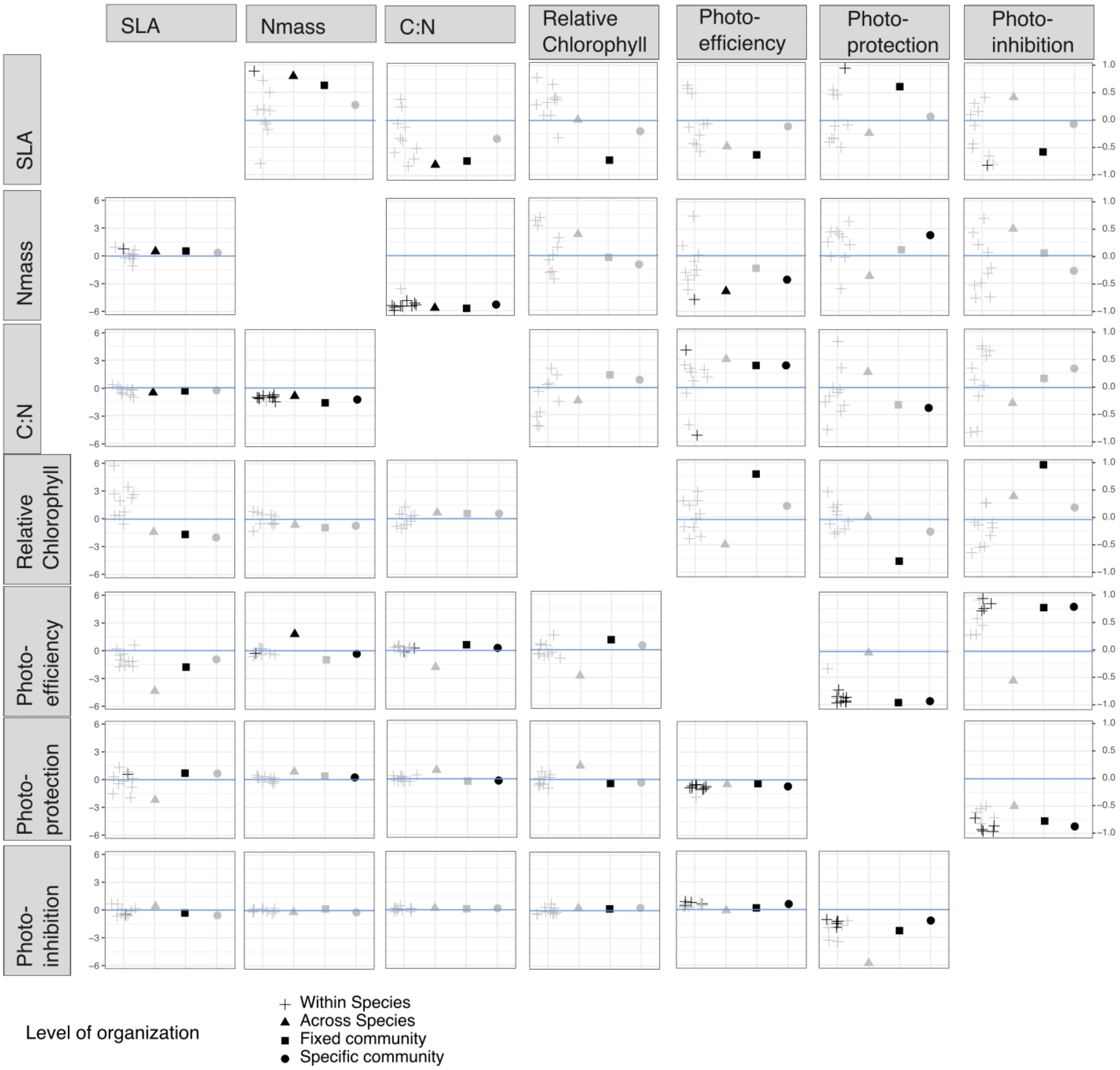


Figure 1-2. Bivariate trait relationships for all traits within species (crosses), across species (triangles), with regional community weighted means (squares), and with local community weighted means (circles). Upper triangle shows Pearson's correlation while lower triangle shows the slopes of the standardized major axis regressions. For all relationships, significant ($p < 0.05$) relationships are shown in black while non-significant relationships are shown in grey.

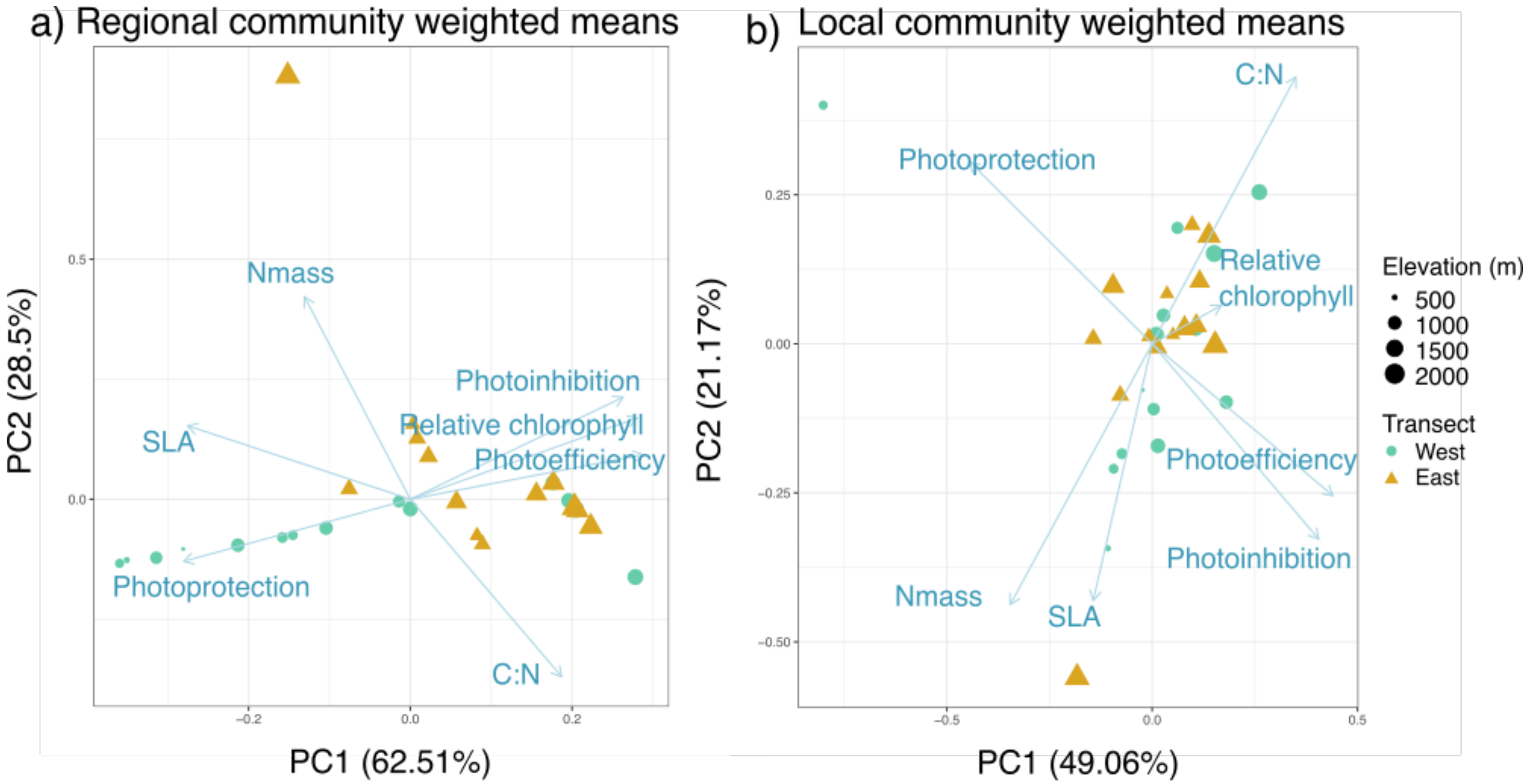


Figure 1-3. Associations between traits in multivariate space for community weighted means. The trait space for community weighted means calculated with the effect of (a) turnover only (regional CWMs) and (b) both turnover and intraspecific trait variation (local CWMs) show the location of each site with the size of the symbol representing the elevation.

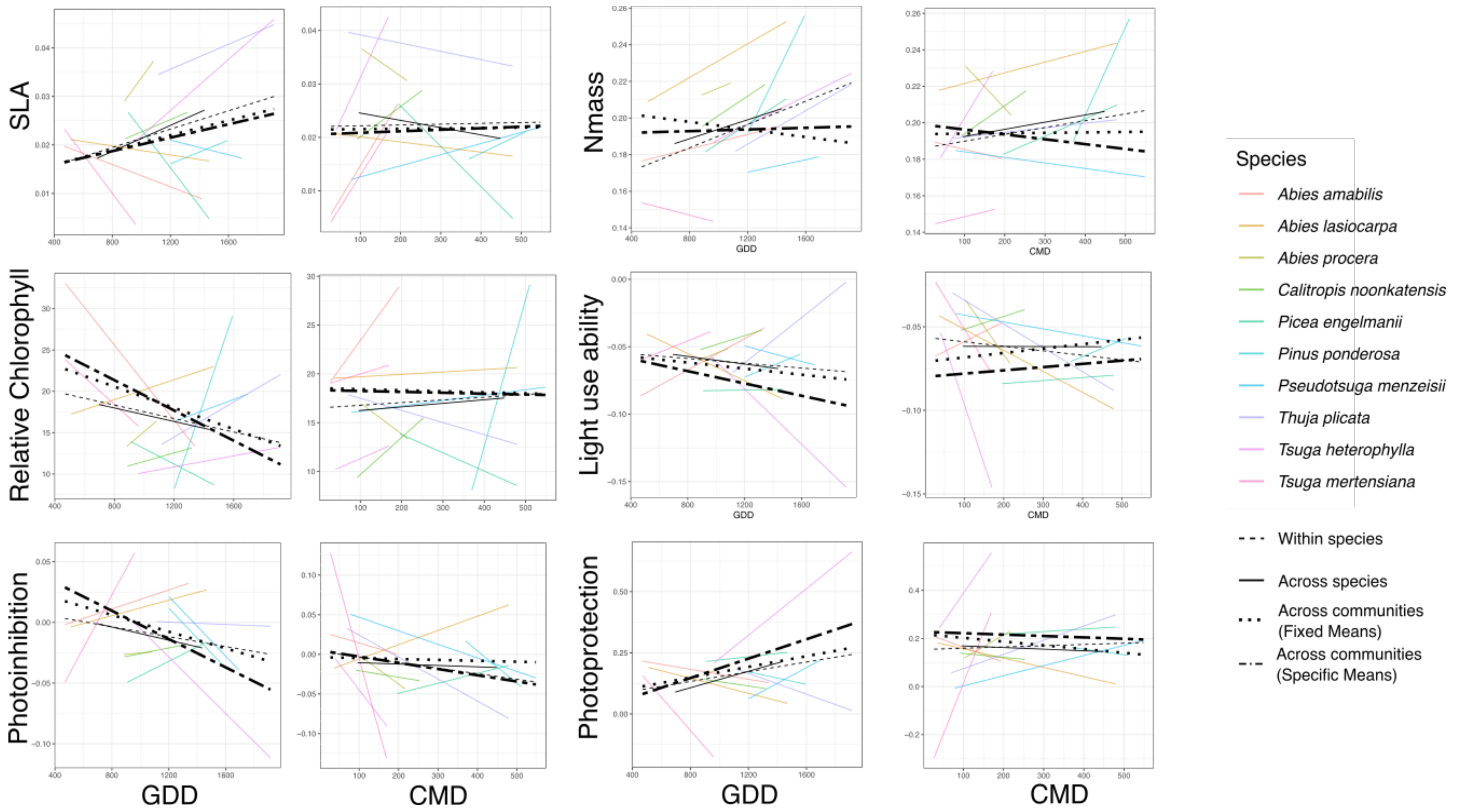


Figure 1-4. Relationships between traits and climatic conditions (CMD and GDD) across levels of organization.

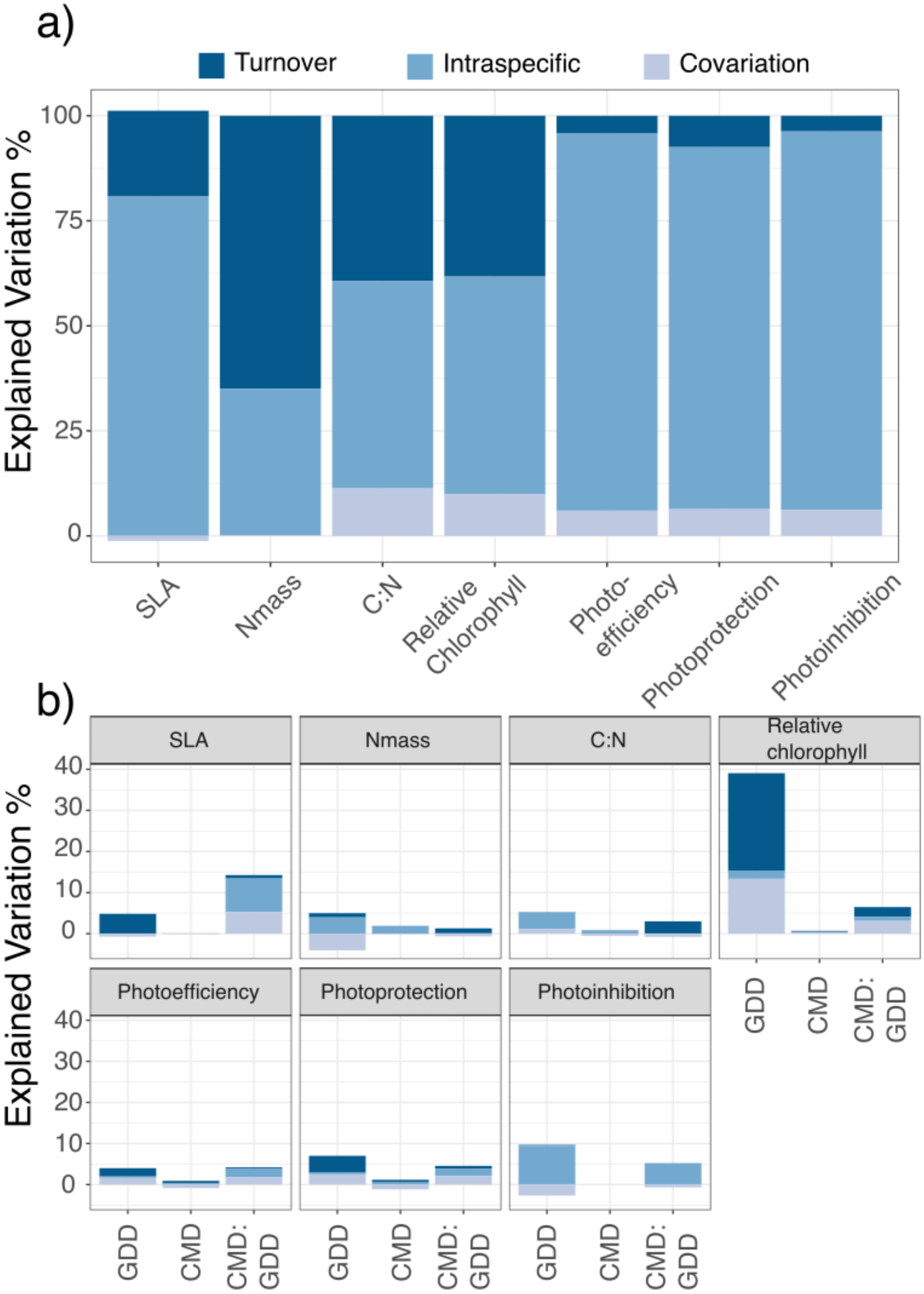


Figure 1-5. Explained variation in a) community weighted means of traits and b) traits across climate that can be attributed to turnover, intraspecific trait variation, and their combined effects.

1.10 SUPPLEMENTARY MATERIAL

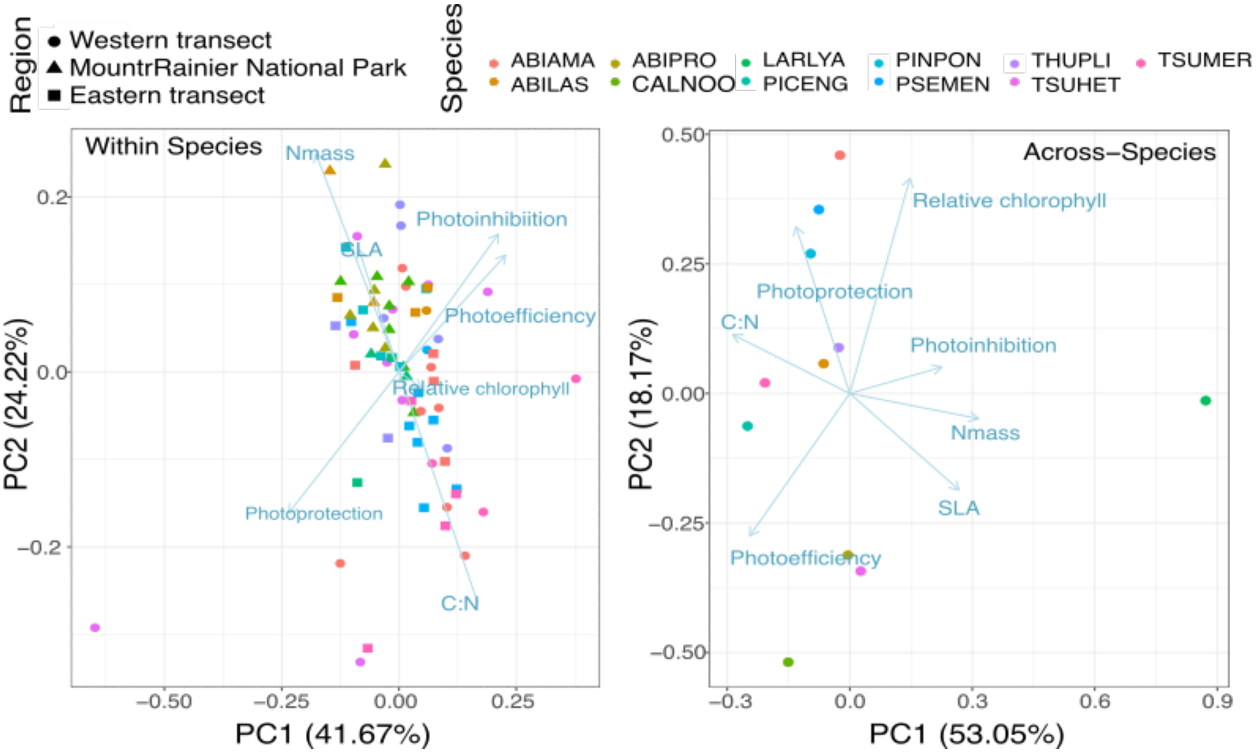


Figure S1. Associations between traits in multivariate space for foliar traits a) within species and b) across species (using species mean trait values). Within species, the color shows each species (ABIAMA = Abies amabilis; ABIPRO = *Abies procera*; ABILAS = *Ablies lasiocarpa*; CALNOO = *Callitropis nootkatensis*; LARLYA = *Larix lyalii*; PICENG= *Picea englemanii*; PINPON = *Pinus ponderosa*; PSEMEN = *Pseudotsuga menzeisii*; THUPLI = *Thuja plicata*; TSUHET = *Tsuga heterophylla*; TSUMER = *Tsuga mertensiana*) and each symbol represents an individual. Across species, each point represents the species mean while the color represents species (same as for within species plot).

Table S1. Across species trait-climate relationships. Coefficients for models linking community-weighted traits (columns) to climatic variables (coefficients in rows). Significant trait-climate relationships that align with our original expectations (in terms of direction) are shown in bold while significant models are present in grey.
·p < 0.1; *p < 0.05; ** p < 0.01; *** p < 0.001

Trait	**SLA**	**Nmass**	**C:N**	**Relative Chlorophyll**	**Photoefficiency**	**Photoprotection**	**Photoinhibition**
Intercept	2.37E-03	170.92**	1.03E+02**	5.13E+01*	-4.40E-02	-5.76E-01	1.70E-02
DD5	2.47E-05*	0.021	-3.64E-02	-2.62E-02*	-1.41E-05	6.00E-04 *	-2.33E-05
CMD	-4.65E-05·		-3.02E-01	-1.64E-01		2.60E-03	
DD5:CMD			1.98E-04	1.17E-04		-2.00E-06	
Adj R Sq	0.374	-0.058	0.1037	0.2753	-0.04741	-0.0004945	0.3829
F value	3.688	0.505	0.347	2.14	0.5927	0.9956	2.862
p value	0.081	0.498	0.3449	0.1965	0.4635	0.3476	0.1264

Chapter 2. EMERGING NOVELTY IN OLD-GROWTH FORESTS SPANNING LARGE CLIMATIC GRADIENTS

2.1 ABSTRACT

Species are responding to climate change, and often in predictable ways – for example shifting their ranges upwards and towards the poles. However, even subtle differences in how fast and how far species shift their ranges in response to changing climates, and which species increase and decrease in abundance, is likely to result in a reshuffling of communities under climate change. Community reassembly can therefore have a wide range of outcomes that are difficult to predict without studying entire communities – from the emergence of novel communities (unique combinations of species relative to the past) to biotic homogenization (the reduction in community dissimilarity). However, the timescales at which such changes may arise have made it difficult to assess how likely novelty and biotic homogenization are in response to the accelerated rate of anthropogenic climate change. In this study, we combined historical forest community surveys with contemporary resurveys to ask how overstory and understory plant communities in a montane coniferous forest have shifted over the last 40 years. We asked whether contemporary forest communities are novel (relative to historic communities) and more homogenous over large spatial scales, as might be predicted when combining rapid rates of warming, individualistic species responses, and the potential disproportionate loss or rare and specialized species. We also examined whether community-climate relationships have remained consistent over time. We found that both tree and understory communities have reassembled, with tree communities lagging behind understory communities. Contrary to our expectations,

contemporary overstory and understory communities are more biotically differentiated (differ more from each other than communities did in the past). However, we did find the emergence of novel communities in contemporary forests (combinations of species that were less likely to occur together in the past). Consistent with these results, we found that community-climate relationships are not static across time. Taken together, our results indicate that shifting communities are leading to increased novelty and a potential disequilibrium between organisms and their environment.

2.2 INTRODUCTION

Climate change is threatening biodiversity and has led to observable changes in species, populations, communities, and ecosystems (Blowes et al., 2019; Garcia et al., 2014; Grimm et al., 2013; Lenoir & Svenning, 2015; Moritz & Agudo, 2013; Pecl et al., 2017; Pörtner et al., 2023; Turner et al., 2020). One of the best-known examples of these changes are shifts in species ranges (Lenoir & Svenning, 2015), with species generally tracking their climatic niches and moving poleward in latitude and upward in mountains (Cavanaugh et al., 2014; Chen et al., 2011; Freeman et al., 2018; Parmesan, 2006; Rumpf et al., 2018). Increasing temperatures and changing precipitation regimes have also altered phenology (the timing of biological events). For instance, flowering phenology has been shifting in response to warming and changes in snow cover in montane meadows (Sethi et al., 2020; Theobald et al., 2017), and bud-burst and emergence of leaves are happening earlier (Cleland et al., 2012; A. K. Ettinger et al., 2020; Piao et al., 2019) with potential consequences for tree growth and carbon accumulation (Gao et al., 2022; Keenan et al., 2014). Plant responses to climate change can also involve shifts in physiology and functional traits. For example, drought can increase allocation to reproductive tissues in plants (Metz et al., 2020), reduce stem growth in conifers (Song et al., 2022), and shifts root strategy towards drought avoidance (Chandregowda et al., 2022).

While there is consensus and much empirical data supporting the effects of climate change on individual species, great uncertainty exists in how these effects will “add up” to influence communities. There are several reasons for this. First, as temperatures continue to increase, climate models project a loss of extant climates and a proliferation of no-analog climatic conditions in the future (Williams et al., 2007; Williams & Jackson, 2007). In addition to emergence of novel climates, more rapid changes in local climate variables (i.e., high climate change velocity) relative to species responses and asynchronous changes of different climate variables (in both direction and degree) can reshuffle and rearrange communities (Ordonez et al., 2016b). Second, there are inconsistencies in the rate and direction of species-level responses to these climate variables. For instance, while some species are keeping up with changes in climate, others show a lagged response with different degrees of lag (Chen et al., 2011). Similarly, while most species have moved poleward in latitude or upward in elevations, there are exceptions to this pattern with some species moving in the opposite/different directions and others not moving at all (Crimmins et al., 2011; Fei et al., 2017; Lenoir et al., 2010; Rapacciuolo et al., 2014). These differences in species level responses to climate change are not a novel response to the rates and types of global changes in the Anthropocene; responses of organisms to past changes in climate have also involved individualistic species responses (Davis & Shaw, 2001; Ordonez, 2013). Finally, other factors besides climate influence species level responses; for example canopy cover can modify understory organisms responses to climate change (Zellweger et al., 2020), interactions with mutualists like fungal endophytes and soil microbes can alter species range limits (Afkhami et al., 2014; Benning & Moeller, 2021), and negative effects of seed predators and novel competitors can reduce recruitment at range limits (Alexander et al., 2015; Brown & Vellend, 2014; A. Ettinger & HilleRisLambers, 2017). All these factors can result in a reshuffling of communities into new and novel combinations of species not seen before with climate change, even if most species are on average responding as expected.

Perhaps counter intuitively, species differences in their responses to climate change can lead to novel communities (compared to past communities) while at the same time resulting in communities that are more similar to each other regionally (i.e. biotic homogenization). Specifically, biotic homogenization can occur if species differ strongly in their abundance related responses to warming, such that local species introductions are weighted towards the same generalist species which are expanding their ranges, while less abundant species are more likely to go locally extinct. Changes in the biotic similarity of communities across spatial gradients are therefore not at odds with the emergence of temporally novel communities following rapid change. Biotic similarity has increased across various taxa globally (Baiser et al., 2012) and increases in biotic homogenization are largely driven by spread of more common species in plants and, in some cases, exacerbated by the loss of specialist species (Finderup Nielsen et al., 2019; Lôbo et al., 2011; Zwiener et al., 2018). Biotic similarity has also increased in response to climate change as more warm-adapted plant species from lower-elevation move upward along an elevational gradient (Savage & Vellend, 2015).

Palaeoecological data demonstrates that the spatial redistribution of predictable communities, the emergence of novel communities, and biotic homogenization are all possible responses to changing climates (Feurdean et al., 2010; Jackson & Overpeck, 2000; Ordonez & Williams, 2013a). However, our understanding of which of these possibilities is more likely in contemporaneous responses to our rapidly changing climate has been difficult. This is because although anthropogenic climate change is occurring at rates faster than historical climate change events, the time scales at which biotic changes arise, particularly novelty, are longer still. The few studies that have examined novelty in response to anthropogenic climate change so far have focused on projecting communities to future conditions based on current community-climate relationships to identify where we might expect to see novel assemblages (Fitzpatrick et al., 2018; Gougherty et al., 2021; Ordonez et al., 2016a; Ordonez & Williams, 2013b) providing valuable insight into regions of concern globally. However, to our knowledge, none have examined whether terrestrial communities have become more novel in response to climate change. Since, novel communities likely result from gradual shifts in communities, reexamination of historically surveyed communities can provide an excellent opportunity to assess community change. Using historical surveys as a baseline (Vellend et al., 2013) could allow us to assess whether communities are changing towards more novelty and homogeneity at relatively shorter time periods.

The response of montane forest communities to climate change may be particularly interesting, yet difficult to predict. On the one hand, the large climatic gradients provided by mountains allow researchers to better understand how ecological factors of interest, including communities, vary with climate (Duque et al., 2015; Gottfried et al., 2012; Steinbauer et al., 2022). Moreover, the relatively smaller climate velocities and shorter distances over which species have to disperse to maintain their climate niches in these montane environments may mean that lagged responses due to dispersal limitation are less likely (Dobrowski et al., 2013; Loarie et al., 2009). This may also allow more competitive species to spread and dominate under warming, leading to biotic homogenization. On the other hand, forests are composed of long-lived trees and shorter-lived understory species which could lead to differential range shift responses leading to community disassembly. Traits like lifespan (longer lifespans of trees leading extinction lags) and dispersal syndromes (shorter plants with shorter dispersal distances leading to dispersal lags) have been linked to lags in species shifts (Alexander et al., 2018; Angert et al., 2011). In addition to this, forest canopies are known to have a buffering effect on understory microclimates leading to mismatch between macroclimatic warming and modulating rates of shifts in understory species (Zellweger et al., 2020).

To assess whether climate change has already caused forest community shifts, and if so, whether greater novelty, biotic homogenization, or both occur, we examined overstory and understory plants in montane forests surveyed across ~40 years at Mt. Rainier National Park (Washington, USA). We used the plant composition in these historic and resurveyed communities to ask:

1) Have plant communities changed over this 40-year time period? We expect forest communities, both overstory and understory, to have shifted in response to changing climates. We expect these shifts to have differed between understory and overstory species, due to their differing generation times.
2) If communities have changed,
    a. Has biotic homogenization occurred? In other words, are communities in the present more similar to each other than those of the past were? We expect forest communities today to be more similar to each other (biotic homogenization) than forest communities in the past were, due to greater increases in generalist and widespread species.
    b. Are those communities 'novel' with respect to past communities? In other words, are the communities of today composed of different combinations of species than those of the past? We expected to detect the emergence of novel communities in both tree and understory communities.
3) Are community-climate relationships across space consistent across time? We expect to see differences in community-climate relationships between the two surveys due to species-specific responses to spatial climate gradients in the two time periods.

2.3 MATERIALS AND METHODS

2.3.1 *Study system and forest community composition data*

We studied the montane forests of Mt. Rainier (Tahoma) National Park located on the western side of the Cascade Range in Washington, U.S.A. Mt. Rainier is a volcanic peak with a temperate maritime climate with warm dry summers and cool wet winters. Mt. Rainier National Park was established in 1899 and since then has experiences minimal changes in land-use and land cover. This in combination with, the region's large temperature and precipitation gradients (due to rapid changes in elevation and complex topography as well as a rain shadow effect) make it an ideal "natural experiment" for studying impacts of climate change. The vegetation types at Mt. Rainier transition from closed moist coniferous forests at lower elevation, more open colder subalpine forests adjacent to subalpine meadows at mid-elevations, and alpine meadows as you go higher.

2.3.1 *Historical surveys*

To characterize these the forests, Franklin et al. (1988) conducted extensive community composition surveys at 518 plots within the park boundaries between 1975-1980 (hereafter historical survey). The goal of this historical survey was to describe and develop and classification of natural vegetation and forest habitat, and relate these communities to environmental factors like climate, elevation, and topography as prior to this study, little was known about these forests. The sampling design of these surveys consisted of circular plots (mostly 500 m^2 or 1000 m^2) in forest stands across the park. Within each plot, all trees greater than 1.4 m in height were identified to species and binned into 4 in diameter at breast height (DBH) intervals. For the understory, the percent cover of shrubs and herbs were visually estimated for the whole circular plot. This historic data was entered by the National Park Service and the locations of the historic survey plots were digitized from topomaps where the original locations were marked (for 463 of the 518 plots).

2.3.2 *Modern surveys*

Using the historical survey as our baseline, we resurveyed 331 plots to compare community composition across time. We refer to this survey as the "modern" community and these plots as the "modern" plots. Plots were not permanently marked; instead, we followed GPS coordinates digitized from topomaps and established a 500 m^2 circular plots with a smaller concentric 50 m^2 circular plot at each location. Within each plot we identified all trees taller than 140 cm and collected their exact DBH, i.e., unlike the historic survey we did not bin trees into DBH size classes. We recorded presence-absence of understory species (shrubs, herbs, ferns, and grasses) within the 50 m^2 plot.

2.3.3 *Environmental data*

To assess the impact of changes in climate on metrics of change in community composition we obtained climate data from ClimateNA, a software package that delivers locally downscaled data for North America (Wang et al., 2016). Specifically, we obtained 10-year normals (1971-1980 for historical and 2010-2020 for resurvey) data for growing degree days (GDD), climatic moisture deficit (CMD), mean annual precipitation (MAP), precipitation as snow (PAS), and mean annual temperature (MAT).

2.3.4 *Community data preparation*

To ensure the comparability of data collected in these two surveys, we first converted all community information into presence-absence data within each plot. For the tree communities, we constrained the list of tree species to 19 species as the two surveys had different categorizations for what is a tree. For understory species, we first removed any rare species (< 5 occurrences in either survey) and any individuals that were identified at a higher level of classification than the species level (e.g., genus level or family level). We then added back species that were rare in one survey period (< 5 occurrence) but were abundant in another (>=20 occurrences) to retain large changes in occurrences while minimizing noise from rare species. Finally, for any species that were present in the species pool of one survey but absent in the other, we examined and assessed whether these appearances or disappearances were likely to be real or an artefact of survey protocol and surveyor differences between the two periods.

2.3.5 *Statistical Analyses*

2.3.5.1 Change in forest communities across time

We computed 3 metrics of changes in community composition across time – 1) temporal beta-diversity, 2) change in similarity of communities, and 3) novelty – and assessed the statistical significance of these changes (if any) in community composition.

Our first metric, temporal beta-diversity, was used to assess whether community composition has changed across time (Q.1) – this metric was estimated from beta-diversity (in the form of Sorenson's dissimilarity) for the same plot across the two time periods (Fig. 2-1a). Turnover in communities can be a consequence of changes in turnover (replacement of species; hereafter turnover), nestedness (no replacement but only loss or gain of species) or a combination of both. In addition to this, whether temporal beta-diversity changes are due to loses or gains indicate different consequences for the communities over time.

The second metric we calculated, community biotic similarity, allowed us to assess whether communities in the two time periods were more (homogenization) or less (differentiation) similar to each other (Fig. 2-1b, Q2a). Specifically, we calculated the dissimilarity, i.e., the pairwise Sorenson's beta-diversity, across plots for the historical survey and the modern survey. We then averaged the pairwise dissimilarity for each plot within each survey period and, using the historical beta-diversity as the baseline, we asked whether there was a shift towards more biotic homogenization or more differentiation using a paired Wilcoxon signed rank test.

Finally, we assessed whether communities have shifted towards novelty (Fig. 2-1c, Q2b). To measure novelty in modern survey communities, we first calculated the pairwise dissimilarity of each plot in the modern survey and all plots in the historical survey. In other words, we examined how dissimilar a plot in the present was from all plots in the past. We then averaged the pairwise dissimilarity of each modern survey plot. Finally, we compared this measure of novelty in modern survey plots with our historical baseline dissimilarity (i.e., beta-diversity across space for historical survey plots) using a paired Wilcoxon signed rank test.

2.3.5.2 Influence of climate on community composition

Finally, we examined whether community-climate relationships have stayed the same over the two surveys (Q3, Fig. 2-1d). For this, we used generalized dissimilarity model (GDM) (Ferrier et al., 2007), an extension of generalized linear models that models pairwise dissimilarity across plots as a function of environmental and/or spatial distance. We fit separate GDM models to each time period, i.e., to the historical and modern communities separately. In addition to using the 5 climate variables (MAT, MAP, GDD, PAS, and CMD), we also used geographical distance between sites as an additional predictor variables.

We assessed changes in overstory and understory separately as we expect them to shift and change at different rates. We used the vegan package (Oskanen et al. 2022) to calculate beta-diversity across time and space (Q1 &2). We examined temporal beta-diversity (i.e., whether communities have changed overtime; Q1) further, and used the betapart package (Balsega et al. 2023) to decompose these changes to effects of nestedness and turnover, and the TBI function in the adespatial package (Dray et al. 2023) to examine the relative importance of gains vs. loses. Finally, to examine the relationships between climate variables and community turnover across space (Q3), we used the gdm package (Fitzpatrick et al. 2022). All analyses were conducted in RStudio (R Core Team, 2022).

2.4 RESULTS

2.4.1 *Changes in montane forest communities across time*

Both tree and understory communities have changed over time – temporal-beta diversity (change in community composition over time) is significantly different from zero (mean beta-diversity = 0.25, $t = 27.197$, $p < 0.01$ for tree and mean = 0.56, $t = 81.158$, p-value < 0.001 for understory). Overall, loss of species was significantly different from gain of species ($p < 0.05$ for both community types, Fig S1) indicating that plots are losing more species than they are gaining. This loss of plot level species richness is more widespread for understory communities where only 3 sites have gained species (Fig. 2-2e). Decomposing the processing behind temporal beta-diversity into its nestedness (loss or gain of species) and turnover (replacement of species) components shows differing patterns in tree and understory communities. In tree communities, beta-diversity is primarily driven by nestedness due to loss of species across time, with fewer sites changing due to turnover, or both turnover and nestedness (Fig. 2-1b-d). However, for the understory community, the contributing process driving temporal beta-diversity is a combination of changes in nestedness and turnover (Fig. 2-2f-h).

Modern communities are also becoming more heterogenous and more novel. Overstory communities are more heterogenous (V = 15800, p-value < 0.001, Fig. 2-3 a,c) and are more novel (V = 13089, p-value < 0.001) relative to the historic baseline (Fig. 2-4 a,c). Along the same lines, current understory communities are also becoming more heterogenous (V = 0, p-value < 0.001, Fig. 2-3 b,d) and more novel (V = 0, p-value < 0.001; Fig. 2-3 b,d) and to a greater degree than overstory communities. These changes in biotic similarity and novelty are accompanied by reductions in occurrences of most species (Fig S2).

2.4.2 *Influence of environmental conditions on changes in plant communities*

The relationship between community and climate across space (within a single time period) was quantified using gdm and in general shows that climate does explain variation some patterns of community composition across space, but not all. Climate (MAT, MAP, GDD and PAS) explains 17.33 % and 27.96% of the variation in the historical and the modern survey data (as measured using deviance explained from the gdm analysis). The shape of the relationship between community turnover and climate differed in the two time periods (for instance, PAS which is the most influential variable for both time periods, Fig. 2-7) as did the order of importance of variables (Fig. 2-5). Like tree communities, understory community-climate relationship also varies across survey periods (Fig. 2-5). These models explain 21.06% and 14.17% of the variation in historical and resurvey understory communities respectively.

2.5 DISCUSSION

Using historical forest community composition as a baseline, we explored whether communities in a montane coniferous forest have changed and reshuffled over the span of ~ 40 years, and found that both tree and understory communities have changed in the last 40 years. Specifically, tree and understory communities are more differentiated today (differ more from each other than communities did in the past). Additionally, both tree and understory communities today, include combinations of species that were less likely to occur together in the past (i.e. increased novelty), with greater novelty in the understory than overstory communities. Finally, we found that community-climate relationships differed between the two survey periods, suggesting a changing relationship between community structure and the environment. We discuss these results, their implications, and caveats to our study below.

2.5.1 *Overstory and understory communities have changed over time, but differently*

Inherent differences in rates at which overstory and understory species respond to rapid climate change may explain our findings and implies the potential for even greater novelty in the future. In our study, we found that tree communities lagged behind understory communities in community shifts, with some plots exhibiting no change over time in overstory community composition (Fig. 2-2). This is not surprising, since these long-lived slowly maturing conifers may demonstrate a significant degree of demographic inertia in the face of changing climates. For example, recruitment limitation at the leading edge because of long maturity times and extinction lags at the trailing edges due to long lifespans and increased time to mortality (HilleRisLambers et al., 2015; Kroiss & HilleRisLambers, 2015) are likely to drive the slower turnover we saw in overstory communities. Although understory species in our systems are also perennial and may face dispersal limitation, and may additionally be shielded from climate change due to the buffering effects of canopy cover (De Frenne et al., 2019, 2021), our finding that the understory community is changing at a faster rate that the overstory community suggests recruitment limitation and long-lived adults are less common. In the absence of a large disturbance (like fire), we believe these differences between overstory and understory in their rates of community change will likely be maintained in the near future.

2.5.2 *Communities are becoming more novel and more differentiated*

The effects of recent climate change on the community composition in these montane forest communities led to novel communities (relative to past communities, Fig. 2-3) and increased dissimilarity (across communities in the same time period, Fig. 2-4) due to complex combination of local dynamics that we did not expect. First, the regional species pool across the two surveys was very similar (80 % overlap with 15 species in historical and 19 species in modern for tree species; 96 % overlap with 91 species in historical and 89 species in modern for tree species), which means that most changes occurred due to local additions and extinctions, rather than the whole-scale introduction of new species or the entire loss of species from the park. Additionally, community shifts in both the overstory and understory were accompanied by decreases in local plot species richness (on average by 14.01 species in the understory, 0.59 species in the overstory Fig S1), implying that local extirpations outweighed local additions. In total, this suggests that community novelty in recent communities arose because species that were added to communities were less likely to occur with ‘resident’ species in historical communities. At the same time, we suspect a greater community dissimilarity occurred in more recent times, because species most likely to be lost from communities were actually more common than those retained (in contrast to our assumptions).

How unique are these changes to community composition? This is a difficult question to answer, because few studies have simultaneously focused on the emergence of novelty and biotic homogenization. However, these increases in dissimilarity across recent communities contrasts with (Fig. 2-3) previous studies that have largely found widespread homogenization in communities in response to recent climate change (Aguirre-Gutiérrez et al., 2020; Savage & Vellend, 2015; Zwiener et al., 2018). One reason for this might be that most studies showing biotic homogenization found gains in local richness, primarily of common species that was sometimes accompanied by loss of rare species (Finderup Nielsen et al., 2019; Zwiener et al., 2018). Consistent with this idea is that the very few studies that found increased biotic dissimilarity, as we did, also observed a loss in species richness in this communities (Menéndez-Guerrero et al., 2020; Vale et al., 2021). Our results, along with conceptual models of biotic homogenization (Olden & Poff, 2003; Rolls et al., 2023) indicate that a decrease in plot level species richness can result in increasing differentiation and novelty over time if the species lost are shared across plots in space.

In all, we believe that the changes in community composition we saw, both temporally and spatially, have the potential to disrupt biotic interactions, potentially feeding back to generate further changes in community composition and even in ecosystem functioning. For example, the redistribution of species in ways that leads to a reassembly of communities, like we found, could lead to increases in generalized rather than specialized interactions (Lurgi et al., 2012) and can alter competition either due change in intensity of competition or loss/gain of competitors (Alexander et al., 2015; Lancaster et al., 2017). Although it is not entirely clear how an increase in community dissimilarity (implying greater functional trait distribution across the entire landscape) accompanied by local loss of species richness would affect ecosystem functioning; biotic differentiation tends to increase multifunctionality of ecosystems (van der Plas et al., 2016) while loss of common species can deteriorate ecosystem function (Winfree et al., 2015). Regardless of their ultimate effects, the ongoing impacts of climate change on community composition, interactions between those species, and ecosystem function could be even greater in regions facing multiple environmental changes, including climate change. For instance interactive effects of land-use change have already linked to greater rates of species range shifts (Guo et al., 2018) and changes in temporal-beta diversity (Marta et al., 2021).

2.5.3 *Community-climate relationships are not consistent across survey periods*

We found that the relationship between climate and community turnover (i.e., community dissimilarity) differed in historical and resurvey communities (Fig. 2-5), suggesting that there might be an increasing mismatch between climate and community composition. Lags in plant community responses to climate change can be due dispersal, establishment, and/or extinction lags (Alexander et al., 2015; HilleRisLambers et al., 2015) leading to disequilibrium between the plant community and the abiotic conditions observed. These disequilibrium vegetation dynamics have been observed in postglacial range expansion of temperate vegetation which took place over multiple centuries and resulting in considerable lags in biotic responses to this climate change (Svenning & Sandel, 2013). Studies of contemporary plant communities have also found lags in community-level responses to contemporary climate change in forested systems, including in montane areas (Bertrand et al., 2011; De Frenne et al., 2013; Duque et al., 2015; Rosenblad et al., 2023; Savage & Vellend, 2015) where we might have expected fewer lags due to lower climate velocities.

What might contribute to these apparent lags in community responses to changing climates, resulting in differing climate-community relationships? There are two main possibilities, which have very different implications for our understanding of the implications of climate change for communities. One possibility is that life history characteristics leading to demographic inertia, including a long generation time and limited dispersal, constrains the ability of organisms to keep up with climate change, resulting in changes in the relationship between community structure and climate. This mechanism implies a delayed vulnerability, which may eventually have negative impacts on ecosystem functions associated with diversity. Alternatively, macroclimate-based assessments of climate and climate change may overestimate the amount of change we might expect in plant communities (Maclean & Early, 2023), if microclimate buffering limits the actual amount of climate change experienced by many communities, implying potential resilience (as long as buffering holds). Of course, both mechanisms can operate at the same time. Regardless of the implications of a delayed vulnerability vs. an underappreciated resilience for community change, these disequilibrium vegetation dynamics can certainly reduce the predictive power of our models (Felton et al., 2022; Fitzpatrick et al., 2018), contribute to climatic debt (Bertrand et al., 2016), and imply the need for further studies of range shift rates and local microclimate change.

2.5.4 *Caveats and future studies*

While the ability to compare contemporary plant communities to a historical baseline allowed us to explicitly examine changes in community compositions over time, this also introduced an important caveat to our study – the comparability of the historical and the resurvey communities. First, since our surveys were not conducted in permanent plots, it is possible that the resurvey captured “pseudoturnover” due to errors in relocation of plots (Vellend et al., 2013). However, we expect this to be a source of noise rather than a systematic error. Moreover, we were unable to replicate survey methods between the historical and the resurvey raising the possibility that changes in community composition are a result of differences in sampling protocols. We accounted for this in our analysis by examining species presence-absence rather than abundances and limiting our species pool to either species that were identified in both surveys, and species that experienced large changes in occurrences.

While climate is an important driver of biodiversity patterns, is not the only factor determining community composition. For instance, range limits of conifer species in the PNW were explained by climate variables well, but only for upper range limits, suggesting a potential role for biotic factors at lower range limits (A. K. Ettinger et al., 2011). Competition can also influence the impact of climate change on tree growth (Ford et al., 2017) and range determination (Lyu & Alexander, 2022). Other abiotic factors like topography and soil characteristics are also known to influence community composition and alter the impacts of climate change on communities (Classen et al., 2015; Dearborn & Danby, 2017; Maclean et al., 2015; Putten et al., 2016). Disturbance is another factor that has been important in altering community responses to climate change in forests (Brice et al., 2019; Danneyrolles et al., 2019; Stevens et al., 2015; Tanner et al., 2022). Even in studies of temporal beta-diversity, factors like disturbance and land use practices were additional important determinants of change in beta-diversity and had interactions with change in climatic factors (Brice et al., 2019; Marta et al., 2021). In Cascade Range itself, disturbances like fires can accelerate upward range shift of plant species (Wilson et al. *In prep*), and gap dynamics and the resultant light availability in the understory can alter rates of change in understory communities (De Frenne et al., 2015; Valladares et al., 2016). As such, future studies of changes in community composition over time could improve explanatory power by explicitly accounting for additional variables known be important for determining organismal and community composition across space and time.

2.6 CONCLUSIONS

We demonstrate that forest plant communities are already shifting in response to climate change, exhibiting greater differentiation and the emergence of novel communities over the last 40 years. Despite these changes, plant communities appear to be in disequilibrium with current climate, suggesting lagged responses. Other drivers of community composition (soil, topography, disturbance) and factors that lead to lags in organismal response to change (demographic inertia and microclimatic buffering) are likely modulating climate change-community change relationships. Overall, these changes in community composition present new challenges to conservation and management and will require better monitoring of both climate and community change (to better predict and understand changes) combined with proactive management and restoration, and a consideration of how these changes alter socio-ecological systems (Hobbs et al., 2009; Mori et al., 2017; Seastedt et al., 2008).

2.7 REFERENCES

Afkhami, M. E., McIntyre, P. J., & Strauss, S. Y. (2014). Mutualist-mediated effects on species' range limits across large geographic scales. *Ecology Letters*, *17*(10), 1265–1273. https://doi.org/10.1111/ele.12332

Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S. L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T. R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemińska, K., Phillips, O. L., & Oliveras, I. (2020). Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. *Nature Communications*, *11*(1), 3346. https://doi.org/10.1038/s41467-020-16973-4

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, *24*(2), 563–579. https://doi.org/10.1111/gcb.13976

Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*(7570), 515–518. https://doi.org/10.1038/nature14952

Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., & Chunco, A. J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, *14*(7), 677–689. https://doi.org/10.1111/j.1461-0248.2011.01620.x

Baiser, B., Olden, J. D., Record, S., Lockwood, J. L., & McKinney, M. L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1748), 4772–4777. https://doi.org/10.1098/rspb.2012.1651

Baselga A, Orme D, Villeger S, De Bortoli J, Leprieur F, Logez M, Martinez-Santalla S, Martin-Devasa R, Gomez-Rodriguez C, Crujeiras R (2023). _betapart: Partitioning Beta Diversity into Turnover and Nestedness Components_. R package version 1.6, <https://CRAN.R-project.org/package=betapart>.

Benning, J. W., & Moeller, D. A. (2021). Microbes, mutualism, and range margins: testing the fitness consequences of soil microbial communities across and beyond a native plant's range. *New Phytologist*, *229*(5), 2886–2900. https://doi.org/10.1111/nph.17102

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., & Gégout, J.-C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517–520. https://doi.org/10.1038/nature10548

Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., de Ruffray, P., Gégout, J.-C., & Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nature Communications*, *7*(1), 12643. https://doi.org/10.1038/ncomms12643

Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I. H., Winter, M., Bjorkman, A. D., Bowler, D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J., Isbell, F., Jones, H. P., Navarro, L. M., … Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, *366*(6463), 339–345. https://doi.org/10.1126/science.aaw1620

Brice, M., Cazelles, K., Legendre, P., & Fortin, M. (2019). Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. *Global Ecology and Biogeography*, *28*(11), 1668–1681. https://doi.org/10.1111/geb.12971

Brown, C. D., & Vellend, M. (2014). Non-climatic constraints on upper elevational plant range expansion under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1794), 20141779. https://doi.org/10.1098/rspb.2014.1779

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences*, *111*(2), 723–727. https://doi.org/10.1073/pnas.1315800111

Chandregowda, M. H., Tjoelker, M. G., Pendall, E., Zhang, H., Churchill, A. C., & Power, S. A. (2022). Root trait shifts towards an avoidance strategy promote productivity and recovery in <scp> C $_3$ </scp> and <scp> C $_4$ </scp> pasture grasses under drought. *Functional Ecology*, *36*(7), 1754–1771. https://doi.org/10.1111/1365-2435.14085

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Classen, A. T., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M. A., Moorhead, L. C., & Patterson, C. M. (2015). Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*, *6*(8), art130. https://doi.org/10.1890/ES15-00217.1

Cleland, E. E., Allen, J. M., Crimmins, T. M., Dunne, J. A., Pau, S., Travers, S. E., Zavaleta, E. S., & Wolkovich, E. M. (2012). Phenological tracking enables positive species responses to climate change. *Ecology*, *93*(8), 1765–1771. https://doi.org/10.1890/11-1912.1

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., & Mynsberge, A. R. (2011). Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum Elevations. *Science*, *331*(6015), 324–327. https://doi.org/10.1126/science.1199040

Danneyrolles, V., Dupuis, S., Fortin, G., Leroyer, M., de Römer, A., Terrail, R., Vellend, M., Boucher, Y., Laflamme, J., Bergeron, Y., & Arseneault, D. (2019). Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. *Nature Communications*, *10*(1), 1265. https://doi.org/10.1038/s41467-019-09265-z

Davis, M. B., & Shaw, R. G. (2001). Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science*, *292*(5517), 673–679. https://doi.org/10.1126/science.292.5517.673

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., … Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297. https://doi.org/10.1111/GCB.15569

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, *110*(46), 18561–18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., & Verheyen, K. (2015). Light accelerates plant responses to warming. *Nature Plants*, *1*(9), 15110. https://doi.org/10.1038/nplants.2015.110

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution 2019 3:5*, *3*(5), 744–749. https://doi.org/10.1038/S41559-019-0842-1

Dearborn, K. D., & Danby, R. K. (2017). Aspect and slope influence plant community composition more than elevation across forest-tundra ecotones in subarctic Canada. *Journal of Vegetation Science*, *28*(3), 595–604. https://doi.org/10.1111/jvs.12521

Dobrowski, S. Z., Abatzoglou, J., Swanson, A. K., Greenberg, J. A., Mynsberge, A. R., Holden, Z. A., & Schwartz, M. K. (2013). The climate velocity of the contiguous United States during the 20th century. *Global Change Biology*, *19*(1), 241–251. https://doi.org/10.1111/gcb.12026

Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guénard G, Jombart T, Larocque G, Legendre P, Madi N, Wagner HH (2023). _adespatial: Multivariate Multiscale Spatial Analysis_. R package version 0.3-21, <https://CRAN.R-project.org/package=adespatial>.

Duque, A., Stevenson, P. R., & Feeley, K. J. (2015). Thermophilization of adult and juvenile tree communities in the northern tropical Andes. *Proceedings of the National Academy of Sciences*, *112*(34), 10744–10749. https://doi.org/10.1073/pnas.1506570112

Ettinger, A., & HilleRisLambers, J. (2017). Competition and facilitation may lead to asymmetric range shift dynamics with climate change. *Global Change Biology*, *23*(9), 3921–3933. https://doi.org/10.1111/gcb.13649

Ettinger, A. K., Chamberlain, C. J., Morales-Castilla, I., Buonaiuto, D. M., Flynn, D. F. B., Savas, T., Samaha, J. A., & Wolkovich, E. M. (2020). Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change*, *10*(12), 1137–1142. https://doi.org/10.1038/s41558-020-00917-3

Ettinger, A. K., Ford, K. R., & HilleRisLambers, J. (2011). Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, *92*(6), 1323–1331. https://doi.org/10.1890/10-1639.1

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., Knott, J. A., & Oswalt, C. M. (2017). Divergence of species responses to climate change. *Science Advances*, *3*(5). https://doi.org/10.1126/sciadv.1603055

Felton, A. J., Shriver, R. K., Stemkovski, M., Bradford, J. B., Suding, K. N., & Adler, P. B. (2022). Climate disequilibrium dominates uncertainty in long-term projections of primary productivity. *Ecology Letters*, *25*(12), 2688–2698. https://doi.org/10.1111/ele.14132

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*(3), 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x

Feurdean, A., Willis, K. J., Parr, C. L., Tanţău, I., & Fărcaş, S. (2010). Post-glacial patterns in vegetation dynamics in Romania: homogenization or differentiation? *Journal of Biogeography*, *37*(11), 2197–2208. https://doi.org/10.1111/j.1365-2699.2010.02370.x

Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M., & Bruun, H. H. (2019). More is less: net gain in species richness, but biotic homogenization over 140 years. *Ecology Letters*, *22*(10), 1650–1657. https://doi.org/10.1111/ele.13361

Fitzpatrick, M. C., Blois, J. L., Williams, J. W., Nieto-Lugilde, D., Maguire, K. C., & Lorenz, D. J. (2018). How will climate novelty influence ecological forecasts? Using the Quaternary to assess future reliability. *Global Change Biology*, *24*(8), 3575–3586. https://doi.org/10.1111/gcb.14138

Fitzpatrick M, Mokany K, Manion G, Nieto-Lugilde D, Ferrier S (2022). _gdm: Generalized Dissimilarity Modeling_. R package version 1.5.0-9.1, <https://CRAN.R-project.org/package=gdm>.

Ford, K. R., Breckheimer, I. K., Franklin, J. F., Freund, J. A., Kroiss, S. J., Larson, A. J., Theobald, E. J., & HilleRisLambers, J. (2017). Competition alters tree growth responses to climate at individual and stand scales. *Canadian Journal of Forest Research*, *47*(1), 53–62. https://doi.org/10.1139/cjfr-2016-0188

Franklin, J. F., Moir, W. H., Hemstrom, M. A., Greene, S. E., & Smith, B. G. (1988). *The Forest Communities of Mount Rainier National Park*. U.S. Department of the Interior, National Park Service.

Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018). Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, *27*(11), 1268–1276. https://doi.org/10.1111/geb.12774

Gao, S., Liang, E., Liu, R., Babst, F., Camarero, J. J., Fu, Y. H., Piao, S., Rossi, S., Shen, M., Wang, T., & Peñuelas, J. (2022). An earlier start of the thermal growing season enhances tree growth in cold humid areas but not in dry areas. *Nature Ecology & Evolution*, *6*(4), 397–404. https://doi.org/10.1038/s41559-022-01668-4

Garcia, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple Dimensions of Climate Change and Their Implications for Biodiversity. *Science*, *344*(6183). https://doi.org/10.1126/science.1247579

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M. R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., … Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, *2*(2), 111–115. https://doi.org/10.1038/nclimate1329

Gougherty, A. V., Keller, S. R., & Fitzpatrick, M. C. (2021). Maladaptation, migration and extirpation fuel climate change risk in a forest tree species. *Nature Climate Change*, *11*(2), 166–171. https://doi.org/10.1038/s41558-020-00968-6

Grimm, N. B., Chapin, F. S., Bierwagen, B., Gonzalez, P., Groffman, P. M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P. A., Schimel, J., & Williamson, C. E. (2013). The impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the Environment*, *11*(9), 474–482. https://doi.org/10.1890/120282

Guo, F., Lenoir, J., & Bonebrake, T. C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, *9*(1), 1315. https://doi.org/10.1038/s41467-018-03786-9

HilleRisLambers, J., Anderegg, L. D. L., Breckheimer, I., Burns, K. M., Ettinger, A. K., Franklin, J. F., Freund, J. A., Ford, K. R., & Krolss, S. J. (2015). Implications of Climate

Change for Turnover in Forest Composition. *Northwest Science*, *89*(3), 201–218. https://doi.org/10.3955/046.089.0304

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*(11), 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Jackson, S. T., & Overpeck, J. T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, *26*(S4), 194–220. https://doi.org/10.1017/S0094837300026932

Keenan, T. F., Gray, J., Friedl, M. A., Toomey, M., Bohrer, G., Hollinger, D. Y., Munger, J. W., O'Keefe, J., Schmid, H. P., Wing, I. S., Yang, B., & Richardson, A. D. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change*, *4*(7), 598–604. https://doi.org/10.1038/nclimate2253

Kroiss, S. J., & HilleRisLambers, J. (2015). Recruitment limitation of long-lived conifers: implications for climate change responses. *Ecology*, *96*(5), 1286–1297. https://doi.org/10.1890/14-0595.1

Lancaster, L. T., Morrison, G., & Fitt, R. N. (2017). Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160046. https://doi.org/10.1098/rstb.2016.0046

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J.-C. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*. https://doi.org/10.1111/j.1600-0587.2010.06279.x

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Lôbo, D., Leão, T., Melo, F. P. L., Santos, A. M. M., & Tabarelli, M. (2011). Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions*, *17*(2), 287–296. https://doi.org/10.1111/j.1472-4642.2010.00739.x

Lurgi, M., López, B. C., & Montoya, J. M. (2012). Novel communities from climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1605), 2913–2922. https://doi.org/10.1098/rstb.2012.0238

Lyu, S., & Alexander, J. M. (2022). Competition contributes to both warm and cool range edges. *Nature Communications*, *13*(1), 2502. https://doi.org/10.1038/s41467-022-30013-3

Maclean, I. M. D., & Early, R. (2023). Macroclimate data overestimate range shifts of plants in response to climate change. *Nature Climate Change*, *13*(5), 484–490. https://doi.org/10.1038/s41558-023-01650-3

Maclean, I. M. D., Hopkins, J. J., Bennie, J., Lawson, C. R., & Wilson, R. J. (2015). Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography*, *24*(11), 1340–1350. https://doi.org/10.1111/geb.12359

Marta, S., Brunetti, M., Manenti, R., Provenzale, A., & Ficetola, G. F. (2021). Climate and land-use changes drive biodiversity turnover in arthropod assemblages over 150 years. *Nature Ecology & Evolution*, *5*(9), 1291–1300. https://doi.org/10.1038/s41559-021-01513-0

Menéndez-Guerrero, P. A., Green, D. M., & Davies, T. J. (2020). Climate change and the future restructuring of Neotropical anuran biodiversity. *Ecography*, *43*(2), 222–235. https://doi.org/10.1111/ecog.04510

Metz, J., Lampei, C., Bäumler, L., Bocherens, H., Dittberner, H., Henneberg, L., Meaux, J., & Tielbörger, K. (2020). Rapid adaptive evolution to drought in a subset of plant traits in a large-scale climate change experiment. *Ecology Letters*, *23*(11), 1643–1653. https://doi.org/10.1111/ele.13596

Mori, A. S., Lertzman, K. P., & Gustafsson, L. (2017). Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology*, *54*(1), 12–27. https://doi.org/10.1111/1365-2664.12669

Moritz, C., & Agudo, R. (2013). The Future of Species Under Climate Change: Resilience or Decline? *Science*, *341*(6145), 504–508. https://doi.org/10.1126/science.1237190

Olden, J. D., & Poff, N. L. (2003). Toward a Mechanistic Understanding and Prediction of Biotic Homogenization. *The American Naturalist*, *162*(4), 442–460. https://doi.org/10.1086/378212

Ordonez, A. (2013). Realized climatic niche of North American plant taxa lagged behind climate during the end of the Pleistocene. *American Journal of Botany*, *100*(7), 1255–1265. https://doi.org/10.3732/ajb.1300043

Ordonez, A., & Williams, J. W. (2013a). Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters*, *16*(6), 773–781. https://doi.org/10.1111/ele.12110

Ordonez, A., & Williams, J. W. (2013b). Projected climate reshuffling based on multivariate climate-availability, climate-analog, and climate-velocity analyses: implications for community disaggregation. *Climatic Change*, *119*(3–4), 659–675. https://doi.org/10.1007/s10584-013-0752-1

Ordonez, A., Williams, J. W., & Svenning, J. C. (2016a). Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change 2016 6:12*, *6*(12), 1104–1109. https://doi.org/10.1038/nclimate3127

Ordonez, A., Williams, J. W., & Svenning, J.-C. (2016b). Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change*, *6*(12), 1104–1109. https://doi.org/10.1038/nclimate3127

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022). _vegan: Community Ecology Package_. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332). https://doi.org/10.1126/science.aai9214

Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, *25*(6), 1922–1940. https://doi.org/10.1111/GCB.14619

Pörtner, H.-O., Scholes, R. J., Arneth, A., Barnes, D. K. A., Burrows, M. T., Diamond, S. E., Duarte, C. M., Kiessling, W., Leadley, P., Managi, S., McElwee, P., Midgley, G., Ngo, H. T., Obura, D., Pascual, U., Sankaran, M., Shin, Y. J., & Val, A. L. (2023). Overcoming the coupled climate and biodiversity crises and their societal impacts. *Science*, *380*(6642). https://doi.org/10.1126/science.abl4881

Putten, W. H., Bradford, M. A., Pernilla Brinkman, E., Voorde, T. F. J., & Veen, G. F. (2016). Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology*, *30*(7), 1109–1121. https://doi.org/10.1111/1365-2435.12657

Rapacciuolo, G., Maher, S. P., Schneider, A. C., Hammond, T. T., Jabis, M. D., Walsh, R. E., Iknayan, K. J., Walden, G. K., Oldfather, M. F., Ackerly, D. D., & Beissinger, S. R. (2014). Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology*, *20*(9), 2841–2855. https://doi.org/10.1111/gcb.12638

Rolls, R. J., Deane, D. C., Johnson, S. E., Heino, J., Anderson, M. J., & Ellingsen, K. E. (2023). Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews*. https://doi.org/10.1111/brv.12958

Rosenblad, K. C., Baer, K. C., & Ackerly, D. D. (2023). Climate change, tree demography, and thermophilization in western US forests. *Proceedings of the National Academy of Sciences*, *120*(18). https://doi.org/10.1073/pnas.2301754120

Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E., & Dullinger, S. (2018). Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences*, *115*(8), 1848–1853. https://doi.org/10.1073/pnas.1713936115

Savage, J., & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography*, *38*(6), 546–555. https://doi.org/10.1111/ecog.01131

Seastedt, T. R., Hobbs, R. J., & Suding, K. N. (2008). Management of novel ecosystems: are novel approaches required? *Frontiers in Ecology and the Environment*, *6*(10), 547–553. https://doi.org/10.1890/070046

Sethi, M. L., Theobald, E. J., Breckheimer, I., & Hille Ris Lambers, J. (2020). Early snowmelt and warmer, drier summers shrink postflowering transition times in subalpine wildflowers. *Ecology*, *101*(12). https://doi.org/10.1002/ecy.3171

Song, Y., Sterck, F., Sass-Klaassen, U., Li, C., & Poorter, L. (2022). Growth resilience of conifer species decreases with early, long-lasting and intense droughts but cannot be explained by hydraulic traits. *Journal of Ecology*, *110*(9), 2088–2104. https://doi.org/10.1111/1365-2745.13931

Steinbauer, K., Lamprecht, A., Winkler, M., Di Cecco, V., Fasching, V., Ghosn, D., Maringer, A., Remoundou, I., Suen, M., Stanisci, A., Venn, S., & Pauli, H. (2022). Recent changes in high-mountain plant community functional composition in contrasting climate regimes. *Science of The Total Environment*, *829*, 154541. https://doi.org/10.1016/j.scitotenv.2022.154541

Stevens, J. T., Safford, H. D., Harrison, S., & Latimer, A. M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, *103*(5), 1253–1263. https://doi.org/10.1111/1365-2745.12426

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266–1286. https://doi.org/10.3732/ajb.1200469

Tanner, E. V. J., Bellingham, P. J., Healey, J. R., & Feeley, K. J. (2022). Hurricane disturbance accelerated the thermophilization of a Jamaican montane forest. *Ecography*, *2022*(9). https://doi.org/10.1111/ecog.06100

Theobald, E. J., Breckheimer, I., & HilleRisLambers, J. (2017). Climate drives phenological reassembly of a mountain wildflower meadow community. *Ecology*, *98*(11), 2799–2812. https://doi.org/10.1002/ecy.1996

Turner, M. G., Calder, W. J., Cumming, G. S., Hughes, T. P., Jentsch, A., LaDeau, S. L., Lenton, T. M., Shuman, B. N., Turetsky, M. R., Ratajczak, Z., Williams, J. W., Williams, A. P., & Carpenter, S. R. (2020). Climate change, ecosystems and abrupt change: science priorities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190105. https://doi.org/10.1098/rstb.2019.0105

Vale, C. G., Arenas, F., Barreiro, R., & Piñeiro-Corbeira, C. (2021). Understanding the local drivers of beta-diversity patterns under climate change: The case of seaweed communities in Galicia, North West of the Iberian Peninsula. *Diversity and Distributions*, *27*(9), 1696–1705. https://doi.org/10.1111/ddi.13361

Valladares, F., Laanisto, L., Niinemets, Ü., & Zavala, M. A. (2016). Shedding light on shade: ecological perspectives of understorey plant life. *Plant Ecology & Diversity*, *9*(3), 237–251. https://doi.org/10.1080/17550874.2016.1210262

van der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., … Fischer, M. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences*, *113*(13), 3557–3562. https://doi.org/10.1073/pnas.1517903113

Vellend, M., Brown, C. D., Kharouba, H. M., McCune, J. L., & Myers-Smith, I. H. (2013). Historical ecology: Using unconventional data sources to test for effects of global environmental change. *American Journal of Botany*, *100*(7), 1294–1305. https://doi.org/10.3732/ajb.1200503

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLOS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, *5*(9), 475–482. https://doi.org/10.1890/070037

Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences*, *104*(14), 5738–5742. https://doi.org/10.1073/pnas.0606292104

Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*(7), 626–635. https://doi.org/10.1111/ele.12424

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Zwiener, V. P., Lira-Noriega, A., Grady, C. J., Padial, A. A., & Vitule, J. R. S. (2018). Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. *Global Ecology and Biogeography*, *27*(3), 298–309. https://doi.org/10.1111/geb.12695

2.8 FIGURES

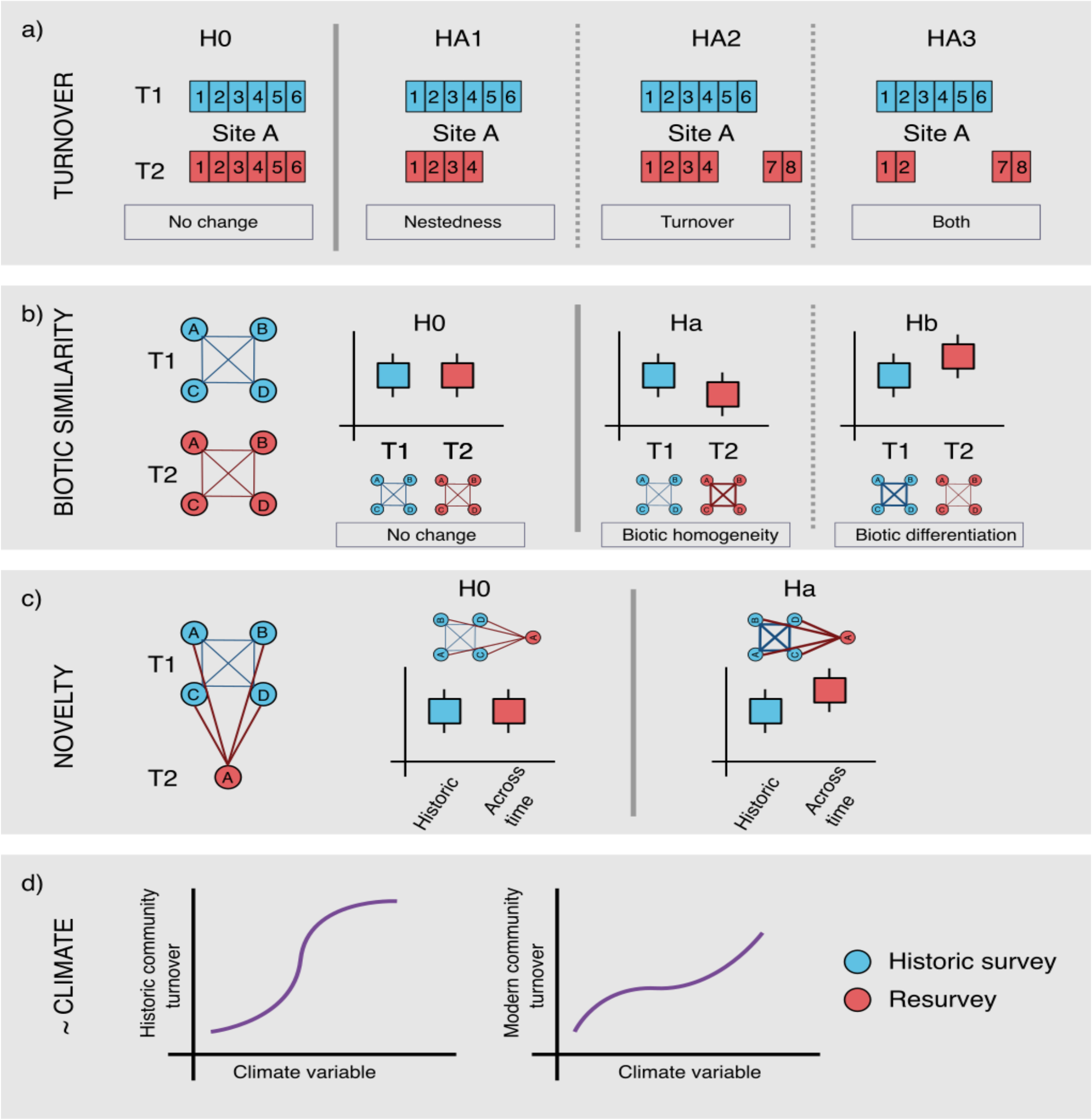


Figure 2-1. Community composition shifts was measured using three metrics between two time periods (T1: Historic and T2: Modern). a) Assessment of temporal beta-diversity could show no change in community composition between T1 and T2 (H0), change in only nestedness (loss or gain of species Panel A - HA1), change in only turnover (species replacement, Panel A - HA2) or change in both components (Panel A - HA3). b) Biotic similarity of communities across space could result in a more homogenous community (Panel B - Ha) or a more heterogenous community (Panel B - Hb) depending in the dissimilarity between plots in the same time period (indicated in the figure by the thickness of the lines with thicker lines showing more similarity).

c) Novelty in modern communities relative to communities in historic surveys were measured as dissimilarity across time and we hypothesize that modern communities will be more novel (Panel C - Ha). Finally, we expect d) the relationship between communities and climate to be different in the two survey periods.

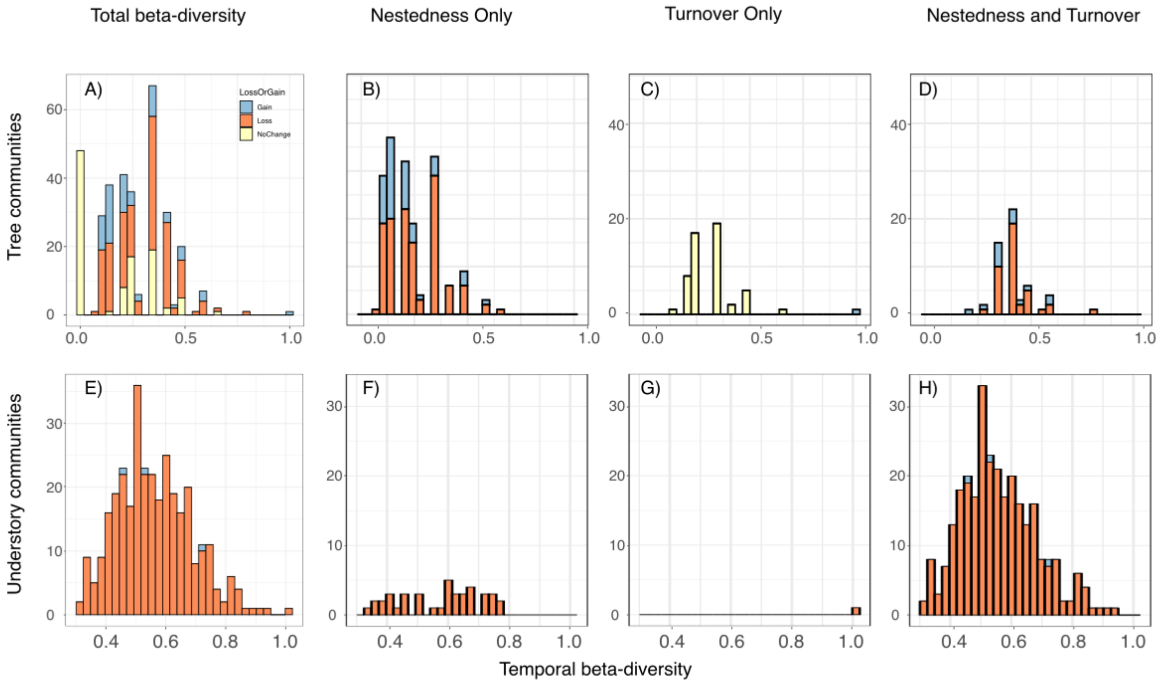


Figure 2-2. Histogram of all observed changes to community composition, per site, over time. We computed temporal beta-diversity as the dissimilarity between the community composition of a site between historical survey and resurvey for both A-D) tree and E-H) understory communities. For each temporal beta-diversity computation, we decomposed overall beta-diversity into its turnover (replacement), nestedness (loss or gain of species). Here we also plot sites that were driven only by nestedness (B,F), only by turnover(C,G) or combined (both turnover and replacement; D,H) effects.

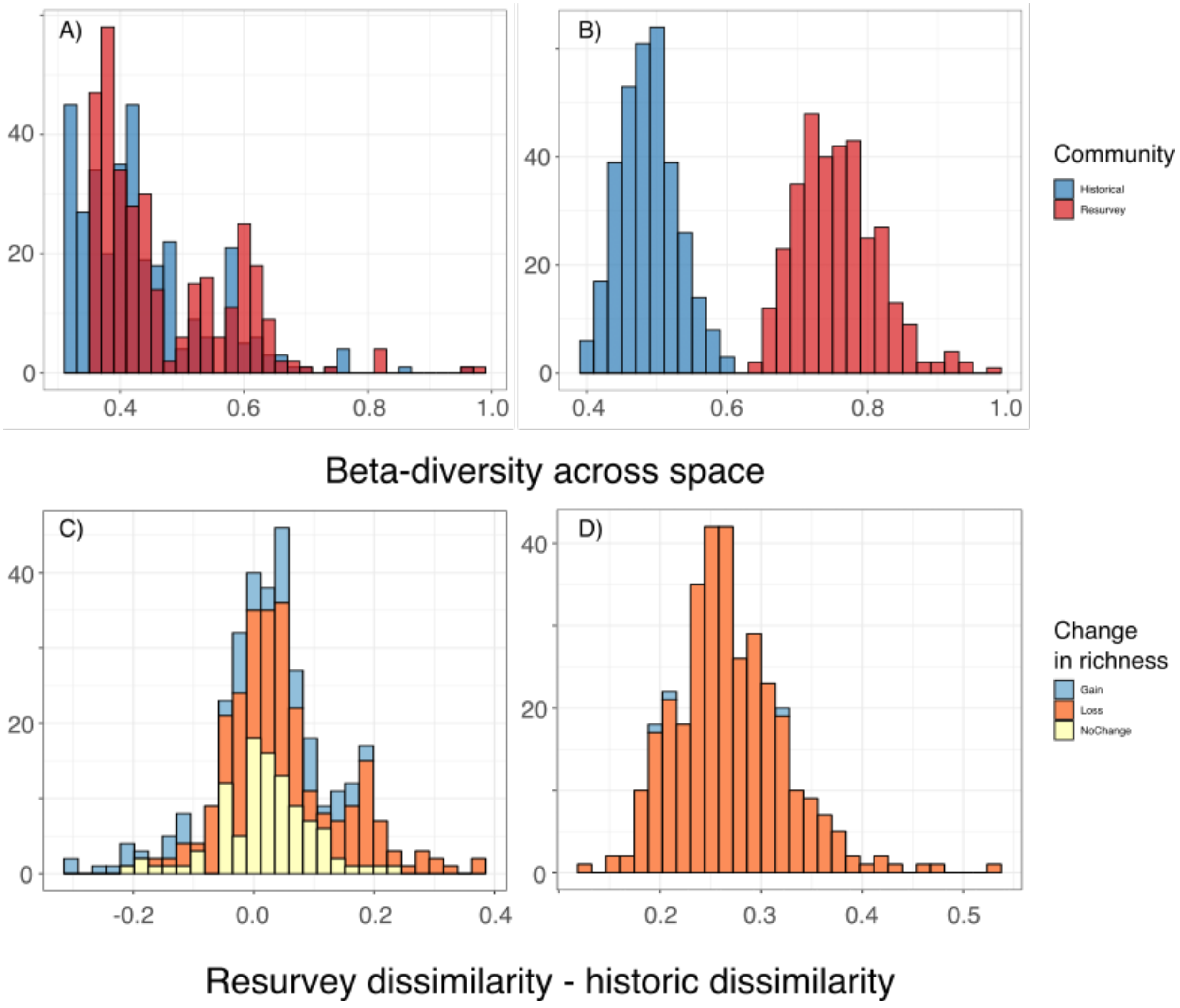


Figure 2-3. Changes in dissimilarity of communities across space. We compared the dissimilarity of historical communities (blue) and resurvey communities (red) for a) tree and b) understory communities. We also assessed whether the difference in average dissimilarity (resurvey dissimilarity – historical dissimilarity) for c) tree and d) understory communities such that positive values indicate an increase in dissimilarity (i.e., heterogeneity) while negative values indicate increasing similarity (i.e., homogeneity).

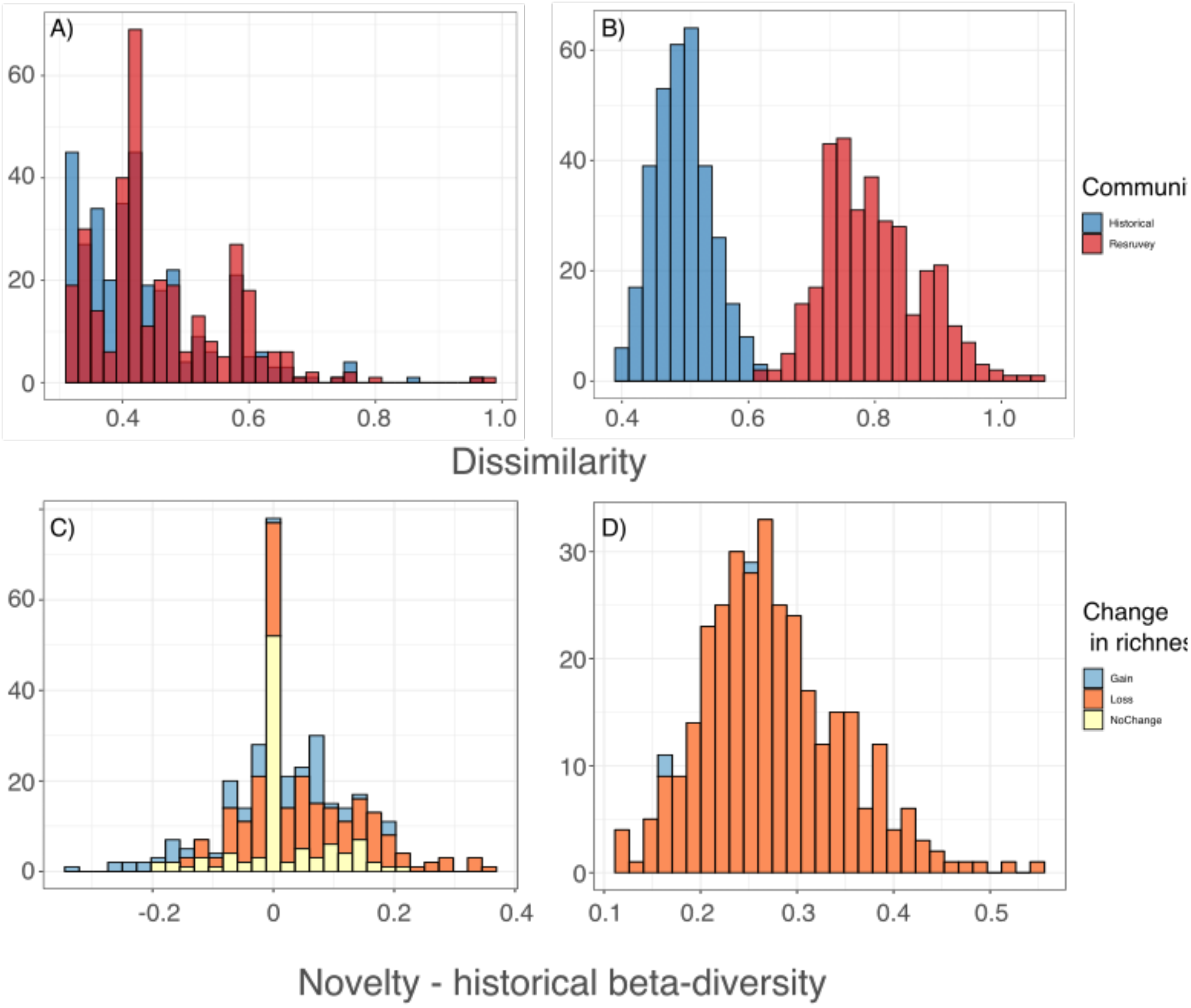


Figure 2-4. Novelty in communities was assessed as the average dissimilarity between a site in resurvey communities to all sites in historical survey communities. We compared the dissimilarity of historical communities (blue) and the novelty in resurvey communities (red) for a) tree and b) understory communities. We also assessed whether the difference in average dissimilarity (resurvey novelty – historical dissimilarity) for c) tree and d) understory communities such that positive values indicate an increase in novelty.

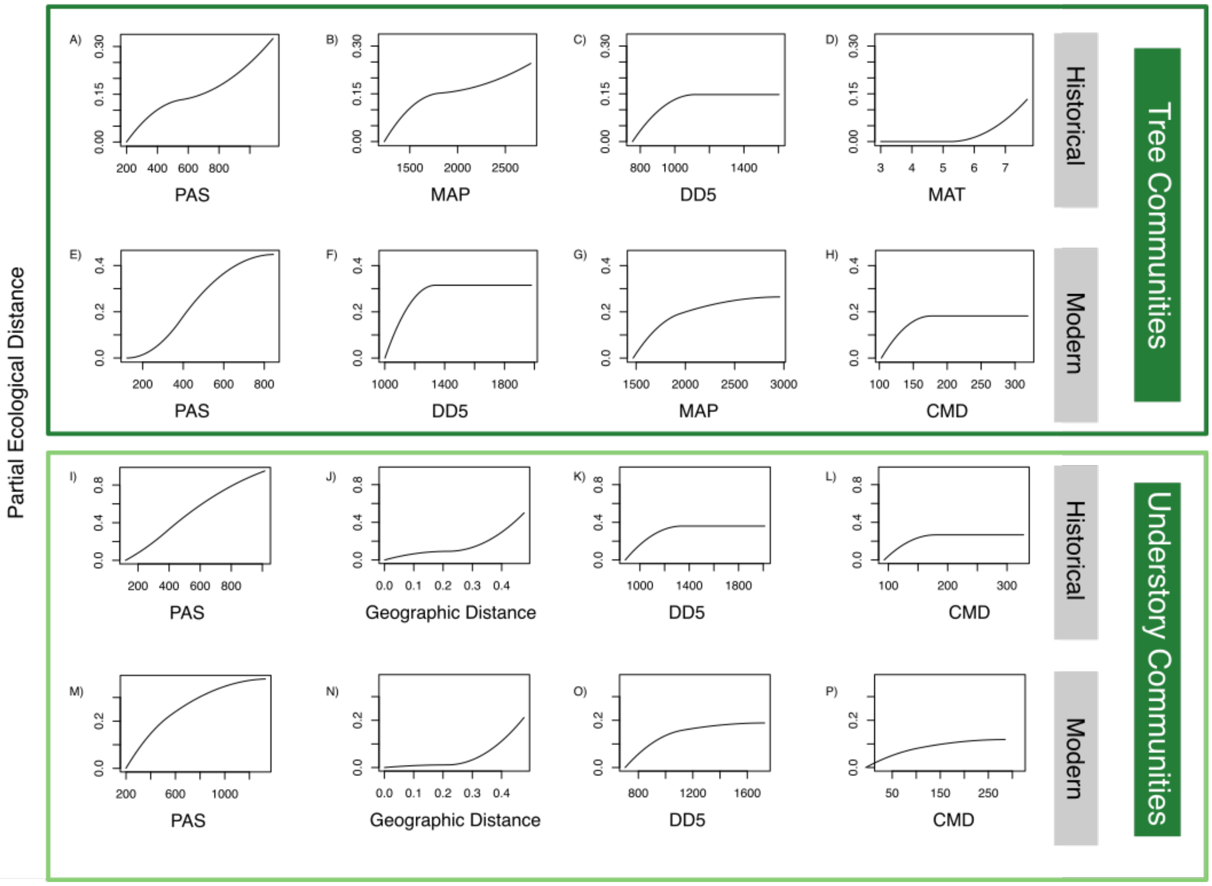


Figure 2-5. Relationships between community turnover across space and climate variables for tree communities in historical survey (A-D) and resurvey communities (E-H) and understory communities in historical survey (I-L) and resurvey (M-P). For each plot, the y axis represents the partial ecological distance, the x-axis shows one climate variable, and the relationship is represented by an I-spline. Variables are arranged in order of importance for each community-survey combination.

2.9 SUPPLEMENTARY INFORMATION

Figure S1. B-C plot showing losses or gains of species in each plot. Each symbol represents a plot with gains shown in squares and losses in circles for A) understory and B) tree communities across time.

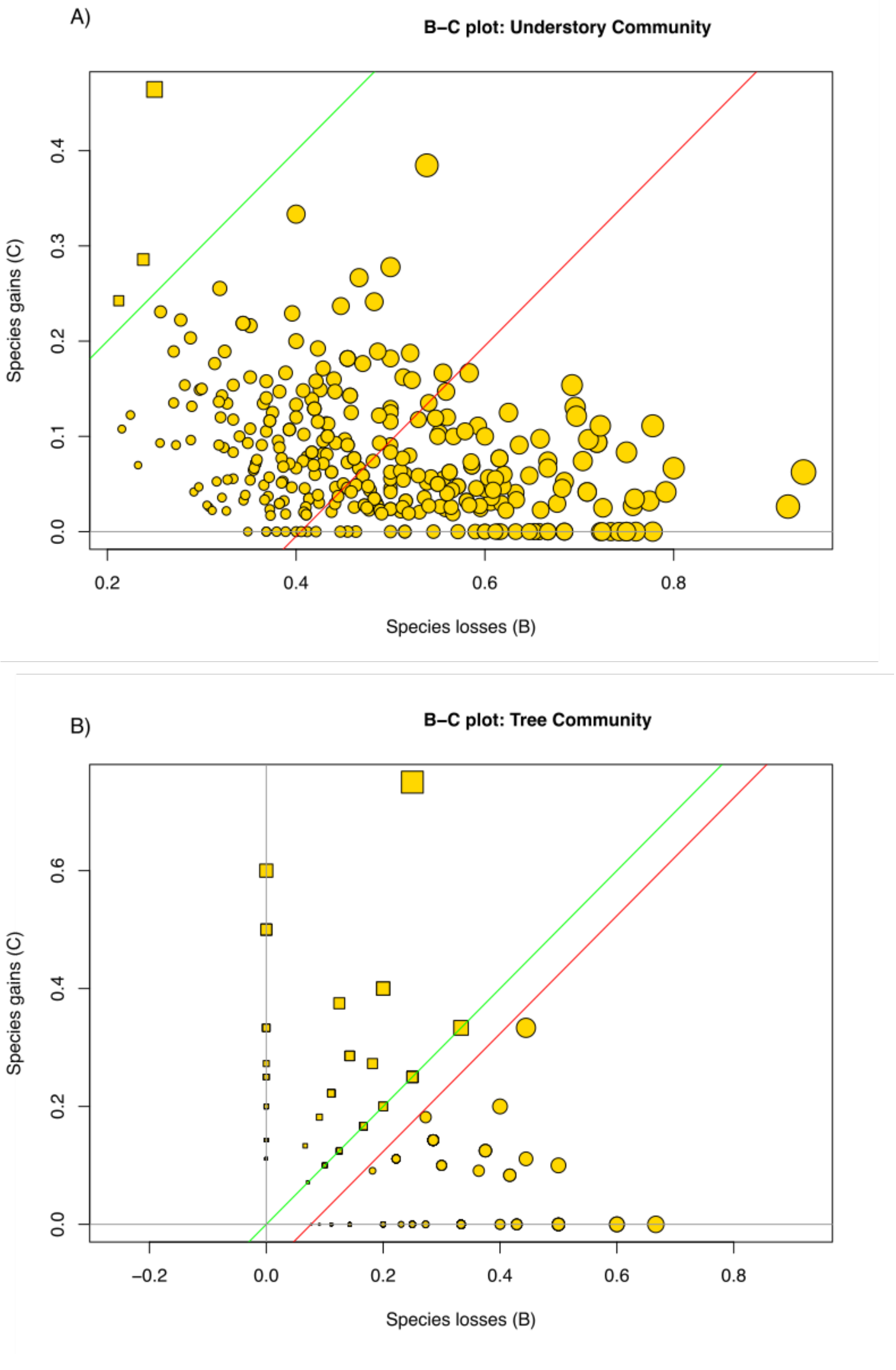
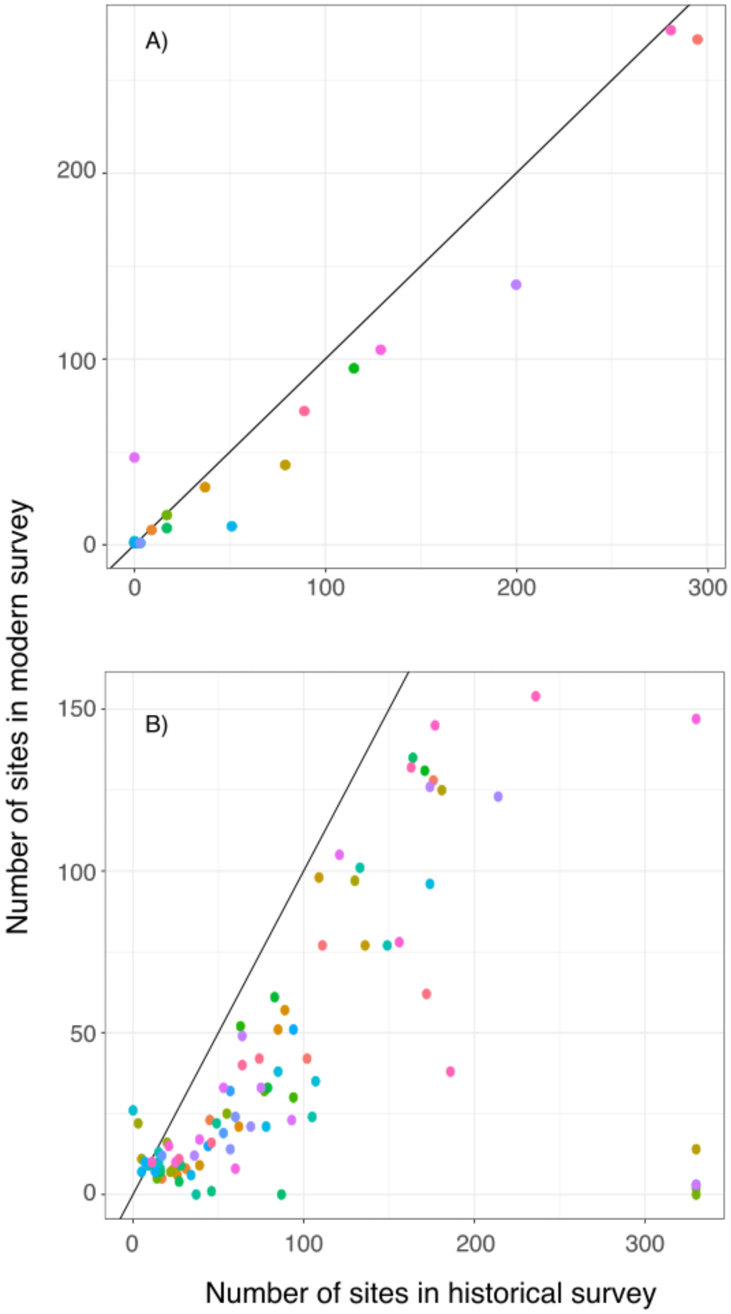


Figure S2. Occurrences of each species (number of sites each species was found in) for the historical and the modern surveys for A) tree and B) understory communities. Each species is represented by a different color and the black line shows the 1:1 line. If the data points are below the 1:1 line, it means that the species was found in fewer sites in the modern survey compared to the historical survey.



Chapter 3. APPLYING CLIMATE CHANGE REFUGIA TO FOREST MANAGEMENT AND OLD GROWTH RESTORATION

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3.1 ABSTRACT

Recent studies highlight the potential of climate change refugia (CCR) to support the persistence of biodiversity in regions that may otherwise become unsuitable with climate change. However, a key challenge in using CCR for climate resilient management lies in how CCR may intersect with existing forest management strategies, and subsequently influence how landscapes buffer species from negative impacts of warming climate. We address this challenge in temperate coastal forests of the Pacific Northwestern United States, where declines in the extent of late-successional forests have prompted efforts to restore old-growth forest structure. One common approach for doing so involves selectively thinning forest stands to enhance structural complexity. However, dense canopy is a key forest feature moderating understory microclimate and potentially buffering organisms from climate change impacts, raising the possibility that approaches for managing forests for old-growth structure may reduce the extent and number of CCR. We used remotely-sensed vegetation indices to identify CCR in an experimental forest with control and thinned (restoration) treatments, and explored the influence of biophysical variables on buffering capacity. We found that remotely sensed vegetation indices commonly used to identify CCR were associated with understory temperature and plant community composition, and thus captured aspects of landscape buffering that might instill climate

resilience and be of interest to management. We then examined the interaction between current restoration strategies and CCR, and found that selective thinning for promoting old-growth structure had only very minor, if any, effects on climatic buffering. In all, our study demonstrates that forest management approaches aimed at restoring old-growth structure through targeted thinning do not greatly decrease buffering capacity, despite a known link between dense canopy and CCR. More broadly, this study illustrates the value of using remote sensing approaches to identify CCR, facilitating the integration of climate change adaptation with other forest management approaches.

3.2 INTRODUCTION

The negative effects of climate change on biodiversity are challenging conservation managers to develop management strategies that bolster ecological resilience to climate change. Traditional solutions such as creating preserves or restoring habitats to past conditions may not be enough, especially if the impacts of climate change and climate change adaptation are not explicitly included in management plans. Recent research has highlighted the value and promise of including climate change refugia (CCR) in management planning to improve climate change resilience. CCR are regions of the landscape that remain relatively buffered from contemporary climate change, thus allowing for the persistence of biodiversity (Morelli et al., 2016). Mapping CCR may illuminate how and where organisms persist and thrive in extreme conditions (Barrows et al., 2020; Morelli et al., 2016) and managing for CCR may provide opportunities for biodiversity to respond and adapt to climate change impacts (Morelli et al., 2020).

Past research on CCR has largely been conducted in systems thought to be especially vulnerable to climate change, like disturbance-prone forests (Collins et al., 2019; Krawchuk et al., 2020; Maher et al., 2021) and coral reefs (Frade et al., 2018; Stewart et al., 2021). CCR research has not been frequently applied to ecosystems that are potentially more “resilient” to climate change (i.e., an area with high microclimatic diversity and lower human modification ensuring greater landscape diversity and connectedness such as moist coastal temperate forests in the PNW, e.g., Anderson et al., 2016) and not as prone to large-scale disturbances, such as wildfire. The lack of CCR research in these locations could be problematic, both because organisms adapted to stable environments might actually have a harder time adjusting to climate change but also because all habitats are likely to eventually be vulnerable to future climate change, given its likely magnitude (Ackerly et al., 2020; Williams et al., 2008). Moreover, ignoring ecosystems now assumed to be resilient might be unwise due to potential threshold responses to climate (Evans et al., 2017), and because it takes time to understand a system and implement conservation and management strategies (Naujokaitis-Lewis et al., 2018).

The mesic temperate forests of the Pacific Northwest (PNW), United States, comprise one ecosystem considered relatively more climate change resilient, because of relatively high landscape connectivity (Anderson et al., 2016), and lower short-term risk to drought and fire (Buotte et al., 2019). Old-growth PNW forests have been the focus of extensive management efforts to (re)create old-growth structure (Franklin & Johnson, 2012a; T. A. Spies et al., 2010, 2018), but these approaches generally ignore potential impacts of climate change. Late-successional forests, including old-growth forests in the PNW, provide extensive carbon storage above-and below-ground (Luyssaert et al., 2008; Zhou et al., 2006), and research has documented their capacity for microclimatic buffering (Frey, Hadley, & Betts, 2016). The increased vulnerability of these coniferous forests to climate change over time (McDowell & Allen, 2015; Seidl et al., 2017) makes management and conservation all the more critical in these (so far) resilient forests.

Although review and synthetic papers have outlined the conditions under which CCR might play a role in conservation under climate change (Morelli et al., 2020), few empirical studies have interrogated how current management practices and goals might work alongside CCR as a tool for conservation. This missing link hinders the conversion of CCR from useful to usable science. Currently, declines in old-growth (Lindenmayer et al., 2012) and late successional forests (Davis et al., 2015) have prompted managers in many forested regions to focus on forest restoration (Spies et al., 2010), including attempts to speed up succession and promote the development of late-successional forest characteristics in secondary forests (Case *et al*. In review).

One method used to achieve this goal involves managing stand density by selectively thinning forests (stand-thinning) (Bauhus et al., 2009; Carey, 2003; Franklin & Johnson, 2012b). Decreasing tree density has the potential to reduce impacts from disturbances like drought (D'Amato et al., 2013; Sohn et al., 2016), and can enhance structural complexity (Chamberlain et al., 2021) while providing a method of biomass production with neutral to positive impacts on biodiversity (Verschuyl et al., 2011). Experimental studies have shown that thinning can lead to increased growth of adult and young trees (Sullivan et al. 2006), seedling regeneration, and understory cover (Ares et al., 2010). However, as canopy cover is associated with microclimate buffering (de Frenne et al., 2019; Frey, Hadley, & Betts, 2016), and can moderate biodiversity response to climate change (de Frenne et al., 2013; Dietz et al., 2020; Zellweger et al., 2020), stand-thinning could have unintended consequences on CCR within forests. Forest thinning can also lead to increased vapor pressure deficit (Rambo & North, 2009) as denser canopy can moderate canopy vapor pressure deficit (von Arx et al., 2013). Thus, these management and restoration techniques, which rely on stand thinning, may affect forest resilience to climate change through potential impacts on climate buffering.

In this study we examined how common approaches to restoring old-growth forest habitats interact with the location and extent of CCR, potentially impacting our ability to preserve CCR for climate change adaptation. Specifically, we asked whether forests that are managed for restoration using stand-thinning have lost or reduced buffering capacity. This is of particular interest as negative interactions between density-reduction and loss of canopy cover could hamper efforts to apply CCR in some managed forests. We used both on-the-ground and remote-sensed observational data in a mesic temperate coastal forest in Willapa Bay, WA, USA to explore this issue, asking the following questions:

1) What environmental characteristics are associated with CCR in a coastal mixed-conifer forest?
2) Are CCR related to forest understory abiotic (temperature) and biotic (plant community composition) characteristics?
3) How do current forest restoration methods, specifically stand-thinning (30% removal), impact buffering capacity?

3.3 MATERIALS AND METHODS

3.3.1 *Study region*

We focused our study on the forested regions in Ellsworth Creek Preserve (hereafter, “Ellsworth”) and Willapa National Wildlife Refuge (Willapa Hills region, southwestern Washington, USA) co-managed by The Nature Conservancy (TNC) and Willapa National Wildlife Refuge (WNWR; **Fig. 3-1**). The regional climate consists of generally cool wet winters (6 °C, 1202.9 mm) and warm dry summers (14.3 °C, 153.4 mm) with mean annual temperature of 10.1 °C as well as an average annual precipitation of 2845.0 mm according to 1981-2010 climate normal based on data from the nearby Long Beach Experiment Station (Menne et al., 2009).

Managed by TNC, Ellsworth is a 33 km^2 coastal forest that encompasses a majority of the Ellsworth Creek watershed. Although there are patches of old-growth stands containing western red-cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menzesii*) and western hemlock (*Tsuga heterophylla*), a large part of the preserve consists of younger and denser forests that were, until recently, managed primarily for timber production. By 2001, only 7% of the old-growth stands in the Ellsworth basin remained standing and greater than 16% of the basin has been logged twice (Churchill et al., 2007). As part of the Ellsworth Creek Adaptive Management Study, TNC implemented a watershed scale experiment to a 20.4 km^2 area within the Ellsworth Creek watershed with the goal of accelerating the development of old-growth habitat. TNC applied sub-basin scale restoration treatments in 2009-2013 across eight sub-basins, including three controls (no restoration actions taken, hereafter “Control”), two passive restoration (no forest management action taken except full recontouring and decompaction (Apodaca et al., 2018) of old logging roads to help restore drainage patterns, hereafter “Decommissioned Roads”), and three thinned (forest stands were thinned by ~ 30% and roads maintained, hereafter “Thinned”) sub-basins (**Fig. 3-1**). While these basin designations were maintained for the most part, some roads (**Fig. S1, Table S1**) in the Thinned and Control basins were also decommissioned due to instability of roads and operational constraints.

3.3.2 *Vegetation indices*

We used Normalized Difference Vegetation Index (NDVI) and Normalized Difference Moisture Index (NDMI) to identify CCRs. These vegetation indices, derived from spectral data obtained from LANDSAT5, 7, and 8 (30m X 30m spatial resolution). Both NDVI and NDMI are widely used and represent vegetation density and plant health, and vegetation moisture content respectively. We used all available satellite imagery acquired during summer months (June-September) between 1999 and 2021 and calculated NDVI and NDMI for each cell in each image as ratios between different wavelengths (NDVI = (NIR-Red)/(NIR + Red); NDMI = (NIR - SWIR)/(NIR + SWIR)).

3.3.3 *Environmental data*

We examined a combination of climatic, topographic, and edaphic variables (**Table S2**). Temperature and precipitation associated climate variables were obtained from ClimateNA (Wang et al., 2016), a software package that downscales PRISM data with Delta-downscaling to 90 m using geographically weighted regression. These variables consisted of accumulated annual degree days above 5°C (DD5), climate moisture deficit (CMD), mean annual precipitation (MAP), mean annual precipitation as snow (MAPS), beginning of frost-free period (BPF) and temperature seasonality (TD). Annual potential solar radiation (RAD), estimated actual (with cloud) solar radiation (90m resolution) and log transformed distance from surface water (DIS) were computed using Geographic Resources Analysis Support System (GRASS GIS) (Scharmer et al., 2000). Edaphic variables (90-m spatial resolution) included in the analyses were soil probability of bedrock (BDR), and soil organic carbon content (CAR), surface soil PH in H_2O (PH), and percent sand in surface soil (SND) from SoilGrids (Hengl et al., 2017). Topographic variables (30-m spatial resolution) used in this study include Slope, Aspect, Roughness, Topographic position index (TPI), Topographic Roughness index (TRI), Topographic heat-load index (THI) and Topographic wetness index (TWI. These variables were computed from underlying digital terrain models from LIDAR data collected in 2007 (Washington State Department of Natural Resources (WSDNR), 2020) in R using the lidR (Roussel et al., 2020; Roussel & Auty, 2022) , spatialEco (J. Evans & Murphy, 2021), raster (Hijmans & van Etten, 2012) and dynatopmodel (Metcalfe et al., 2015) packages. In addition to these gridded environmental data, we also collected temperature every 2 hours using HOBO Pendant® loggers at 20 sites (5 in each of the resurveyed sub-basins; **Fig. 3-1**) from September

2020 to September 2021 (Pradhan et al., 2023).

3.3.4 *Forest characteristics data*

The vegetation in all eight sub-basins was surveyed in permanent monitoring plots (17.8 m radius circular plots) prior to implementation of the restoration treatments (2006-2007). A subset of these plots was resurveyed in 2020 (60 sites in two Control and two Thinned sub-basins; **Fig. 3-1**). Within each plot, diameter at breast height (DBH) for all trees with DBH > 14.48 cm was measured, and four subplots (2.5 m radius at 9 m from plot center) were established where seedling tally (height between 14.99cm and 137.16 cm), sapling tally (trees with height >= 137.16 cm and < 14.48 cm DBH), and percent cover for all species in the understory (including seedlings that are < 11.43 cm) were assessed. Plot-level plant community composition (species presence-absence) was derived by combining tree, seedling, sapling, and understory species occurrence information such that detected species were marked as "present" and un-detected were marked as "absent". While a lack of detection isn't necessarily a true absence, our field survey methods are relatively robust to detectability issues. Age for all forested stands were determined using standard dendrochronological methods (Stokes & Smiley, 1996).

3.3.5 *Identifying Climate Change Refugia (CCR)*

We defined CCR as locations where organisms are likely to experience more stable environmental conditions relative to the surrounding landscape, even when the regional climate fluctuates (**Fig. 3-2**). CCR can result from a greater buffering capacity due to the combination of

1) the topo-edaphic characteristics of the landscape and how they interact with and alter regional climate at a local level (abiotic) and 2) the density of overstory vegetation (e.g. canopy cover). We identified CCRs from the responses of focal organisms (trees) to differences in climate stability, assuming that tree performance would be high and less variable in CCRs. We consider CCR at the scale of 30 meters, but of course, CCR can be much larger or much smaller depending on the scale of the organism and methodological approach. Specifically, we used vegetation indices (Vis) derived from remote-sensing to allow us to quantify variation in performance via greenness, which allowed us to gain insight into CCRs across broader spatial and temporal scales than our on-the-ground data collection area.

We calculated the coefficient of variation (ratio of the standard deviation to the mean of the vegetation indices) of summer NDVI ($NDVI_{CV}$) and NDMI ($NDMI_{CV}$) between 1999 and 2021. We opted to use coefficient of variation as our measure of stability as it accounts for the mean and thus makes comparisons between data series with different means possible. Cells (measuring 30m x 30m) were designated CCR if the coefficient of variation fell within the lowest 25th percentile (following the methods in Cartwright 2018, but taking a less conservative portion of the area as CCR). This allowed us to convert the continuous $NDVI_{CV}$ and $NDMI_{CV}$ values into presence vs. absence of CCR (hereafter CCR_{NDVI} and CCR_{NDMI}).

To assess what environmental variables influence CCR presence and absence, we focused on the eight experimental sub-basins. We used Boosted Regression Trees (BRT) (Elith et al., 2008) to identify environmental variables that had the greatest predictive abilities. Before proceeding with BRT, we first removed variables that were highly correlated based on a random sample of 2000 cells. Elevation and the six macroclimate variables (BFP, CMD, MAP, MAPS, TD and DD5) were all highly correlated with one another (> 0.75 Pearson's R), so we retained

MAP and DD5 based on a Principle Component Analysis (using vegan (Oksanen et al., 2022), **Fig S2**). Roughness, TRI and Slope were also highly correlated with one another and here we retained Slope. Using these variables, we fit BRT models (100 iterations) for presence absence of CCR based on NDVI (learning rate = 0.005, bag fraction = 0.65, tree complexity = 8) and NDMI (learning rate = 0.005 bag fraction = 0.5, tree complexity = 8). Model parameters were selected based on a search of parameter space to ensure that the final models had 1000-5000 trees, high AUC-ROC and low predictive deviance (based on a separate testing dataset). For each iteration, we randomly sampled 2000 cells from the experimental basins and assigned 1500 cells as our training data and 500 cells as our testing dataset.

3.3.6 *Relationship between CCR and forest characteristics*

We examined the extent to which CCR are associated with variation in both abiotic and biotic aspects of these forests. First, we assessed whether variation in NDVI and NDMI reflects forest floor buffering capacity, as measured by temperature on the ground. We calculated $NDVI_{CV}$ and $NDMI_{CV}$ for June-September of 2021. We then compared these coefficients of variation to the coefficient of variation of daily mean, maximum, and minimum temperatures collected on-the-ground at 20 sites during the same time period (**Fig. 3-1**) using ordinary least squares regressions in R. Next, we examined associations between CCRs and biotic aspects of these forests using vegetation surveys of forest stands at Ellsworth. To assess whether CCRs explained variation in forest characteristics beyond the variation explained by experimental treatment (i.e., whether the plots were in the Control or Thinned treatments) and age of the stand, we conducted Canonical Correspondence Analysis (CCA) due to the multivariate nature of our data. CCAs are a type of constrained ordinations where community composition (relative understory cover and species presence-absence) is constrained to be a function of the explanatory variables (stand age, treatment status, and our two CCR measures: $NDVI_{CV}$ and $NDMI_{CV}$). While there are many multivariate techniques available, we chose to use CCA because results from gradient analyses revealed that species in our dataset can be assumed to vary in a non-linear and unimodal fashion along the environmental gradient. These unimodal responses are better described by CCA than other comparable multivariate approaches. We performed separate CCAs for the pre-treatment (conducted in 2006 and 2007) and post-treatment (conducted in 2020) surveys.

3.3.7 *Impacts of stand-thinning on CCR*

To check for impacts of stand-thinning on CCR, we assessed whether any changes in the coefficient of variation in pre- and post-treatment NDVI and NDMI were different depending on the experimental treatment (i.e., whether the stands were Thinned or Control). For this, we first calculated the coefficient of variation in NDVI and NDMI for the pre-treatment (1999 to 2008) and post-treatment (2013-2021) time periods, and then calculated the difference in variation (post-thinning coefficient of variation - pre-thinning coefficient of variation; hereafter "change in $NDVI_{CV}$" and "change in $NDMI_{CV}$", respectively) for all the basins within the Ellsworth Creek Preserve experiment. Exploratory analyses with Moran's I demonstrated that there was significant spatial autocorrelation in our CCR metrics (the coefficient of variation of vegetation indices). To take this spatial autocorrelation into account, we fit spatial simultaneous autoregressive error models using the spatialreg and spdep packages (R. Bivand, 2022; R. Bivand et al., 2013, 2021; R. S. Bivand & Wong, 2018). Spatial simultaneous autoregressive error models extend an ordinary least squares model by including an additional error term to incorporate the spatial autocorrelation structure between a spatial unit and all other spatial units within a specified neighborhood. We used difference in variation (change in $NDVI_{CV}$ or change in $NDMI_{CV}$) as our response variables, and treatment status (Thinned, Decommissioned Roads, or Control), stand age, and their interaction as explanatory variables in these models. To create the neighborhood objects, we used an upper distance bound of 45 m, i.e., any sites closer than 45 m were considered neighbors. We selected this distance as it had the lowest minimum residual spatial autocorrelation across ten different distances we tested, ranging from 30m to 1500m.

3.4 RESULTS

3.4.1 *Identifying CCR and their relationship with environmental factors*

During the time period assessed in this study (1999-2020), the coefficient of variation for NDVI and NDMI demonstrated spatial variation, with similarities in patterns for both $NDVI_{CV}$ and $NDMI_{CV}$ (**Fig. 3-3**). Although CCR were identified throughout the experimental area, they were more common in the central and southern basins. The BRTs explained 72.7 % ± 0.4% of the deviance in CCR_{NDVI} and 74.0% ± 0.4% of the deviance for CCR_{NDMI} over 100 iterations (**Table 3-1**). All models were retained for interpretation as their predictive performance was considered acceptable (AUC-ROC > 0.75; **Table 3-1**). Although the relative influence of environmental variables on CCR presence-absence was different for CCR_{NDVI} and CCR_{NDMI}, the identities of the most influential environmental variables were consistent: Stand age, Log transformed distance from surface water (DIS), annual potential solar radiation (SOL), and soil organic carbon (CAR)(**Fig. 3-4**). Examining the partial dependence plots of the top 6 variables for each of the CCR provides insight into the relationship between CCR presence-absence and environmental variables. Stand age was one of the most important variables and had a non-linear relationship with both CCR_{NDVI} and CCR_{NDMI} such that CCR were least prevalent in young stands and had higher prevalence in older stands (although there was a slight decline and then a slight in medium aged stands (~50 years)) (**Figs. S3** and **S4**). CCR also tend to occur in areas that are further from surface water, have higher potential solar radiation and lower soil carbon (**Figs. S3** and **S4**).

3.4.2 *Relationship of CCR and forest characteristics*

We found that the coefficient of variation in the vegetation indices, stand age and treatment status together significantly influenced forest characteristics measured on the ground. All constraining variables explained 13.58 % ($p = 0.001$) and 11.01% ($p = 0.001$) variation in relative understory cover in surveys conducted before (2006-2007) and after (2020) treatment, respectively (**Fig. 3-5 a and b**). In both cases, stand age was the most important and significant constraining variable ($F = 5.7674$ $p = 0.001$ for pre-treatment and $F = 3.1015$, $p = 0.001$ for post-treatment surveys). Apart from stand age, treatment status was only marginally significant ($F = 1.5365$, $p = 0.063$) for the post-treatment and not significant ($F = 0.9057$, $p = 0.544$) for the pre-treatment survey. Neither $NDVI_{CV}$ or $NDMI_{CV}$ significantly contributed to the ordinations for either survey, indicating that they are not as important for quantifying understory abundance compared to stand age and treatment status.

For species presence-absence (species in the overstory and understory), the constraining variables explained 14.64% ($p = 0.001$) and 11.37% ($p = 0.001$) of the total variation for the pre-treatment and the post-treatment surveys, respectively (**Fig. 3-5 c and d**). Similar to understory abundance, stand age was a significant constraining variable for both pre-treatment ($F = 4.5513$, p = 0.001) and post-treatment (F = 3.0099, p = 0.001) surveys. In addition to stand age, treatment status was also an important constraining variable (F = 1.6068, p = 0.004 for pre-treatment and F = 1.5402, p = 0.006 for post-treatment surveys). In contrast to understory abundance, variation of NDVI and NDMI significantly contributed to the ordination of presence-absence of species, suggesting that they explain additional variation in species presence-absence beyond variation explained by stand age and treatment status. $NDVI_{CV}$ was significant for pre-treatment surveys (F=1.8826, p=0.002) but not for post-treatment surveys (F = 1.1258, p = 0.292), while $NDMI_{CV}$ was significant for both pre- (F = 1.3925, p = 0.048) and post-treatment surveys (F=1.4285, p = 0.045). These differences in importance for $NDVI_{CV}$ and $NDMI_{CV}$ for understory abundance show that while variation derived from these two indices have broadly **(Fig. 3-3)** similar patterns, they are still spatially distinct. Finally, in terms of the abiotic forest characteristics, $NDVI_{CV}$ was positively correlated with variation in summer minimum ($r^2 = 0.22$, p-value < 0.05) and maximum ($r^2 = 0.28$, p-value < 0.05) temperatures (**Fig. 3-6**). We did not find a statistically significant relationship between temperature and $NDMI_{CV}$.

3.4.3 *Impact of stand-thinning on CCR*

Overall, the spatial simultaneous autoregressive error models for change in $NDVI_{CV}$ explained 86.0 % of the variation in the data (based on Nagelkerke pseudo-R-squared) and showed that stand age and experimental treatment were important predictors. Thinning treatment was not a significant predictor of change in $NDVI_{CV}$ or $NDMI_{CV}$. In other words, changes in the variation of vegetation indices in Thinned stands were not statistically different from changes in Control stands (**Table 3-2**). Additionally, both post-treatment and post-treatment $NDVI_{CV}$ and $NDMI_{CV}$ **(Fig. 3-7)** were higher for older stands and lower for stands that had decommissioned roads (**Table 3-2**). The spatial simultaneous autoregressive error models for change in $NDMI_{CV}$ explained much lower variation in the data (Nagelkerke pseudo-$r^2 = 0.103$, **Table 3-2**).

3.5 DISCUSSION

We illustrate an approach for identifying CCR and assessing how current management practices interact with CCR – providing insight into incorporating climate change adaptation into existing forest management. Most importantly, stand-thinning (as a restoration technique) did not appear to reduce the buffering capacity of these forests, as measured using the variation in NDVI and NDMI. The most influential macroclimatic and topo-edaphic variables for predicting CCR presence/absence were stand age, distance to water, presence of bedrock and soil carbon content. We found that stand age was important in describing CCR locations, variation in plant community composition, and change in the coefficient of variation of vegetation indices. Finally, our remotely-sensed measures of buffering capacity were also associated with both plant community composition and understory temperature, indicating that theses metrics of CCR are correlated with local, ground-based measurements. Below we discuss these results and their implications in more detail.

3.5.1 *Restoration thinning does not reduce buffering capacity*

Our finding, that restoration thinning did not reduce buffering capacity, may be surprising given a documented link between canopy cover and buffering capacity (Betts et al., 2018; Zellweger et al., 2020). Indeed, many previous studies have found that canopy cover stabilizes understory microclimate by lowering average and maximum temperatures and keeping minimum temperatures more stable (de Frenne et al., 2021; Ewers & Banks-Leite, 2013; von Arx et al., 2013). However, most of these previous studies compared areas with trees to areas without trees; our study differs by examining effects of more subtle changes in canopy cover, as induced by management, on microclimate. Our findings suggest that reducing stand density by approximately 30% left behind enough canopy to preserve its buffering capacity, or canopy cover recovered quickly enough over ~ 10 years after the treatments were conducted at least in younger stands.

Disentangling the impacts of trade-offs between different aspects of canopy complexity (like canopy cover vs. vertical complexity) in future studies could provide more insight into how thinning treatments can be applied without compromising buffering capacity. Our study examined effects of variable density thinning, where some areas are left alone while others are thinned more intensively (creating gaps), and it is possible that different thinning treatments applied in other management contexts could more strongly affect buffering capacity. For example, in our study area, although thinning treatments reduced canopy cover, they also increased outer canopy vertical complexity (canopy rumple index,; Chamberlain et al., 2021) a critical component of canopy complexity and structural diversity.

Interestingly, stands where roads were decommissioned had increased buffering capacity after the roads were de-compacted and recontoured. These results, while unexpected, suggest that there may be additional advantages to road decommissioning in managed forests – specifically, by increasing the buffering capacity and therefore climate resilience of these habitats. One potential reason could be the positive long-term impacts of road decommissioning on hydrological and geomorphological processes (T. A. Spies et al., 2018; Switalski et al., 2004). Additionally, wind is a key source of disturbance and vegetation damage at Ellsworth

(Davis et al., 2015) and decommissioning roads likely reduces wind infiltration further into these stands thereby stabilizing vegetation greenness and moisture in our study system.

3.5.2 *Stand age has complex relationships with CCR*

Across all our analyses, stand age was one of the most important and consistent factors that influenced CCR (both their location and the impacts of restoration thinning on them). For example, we found that CCR presence was lowest in young stands (**Fig. S3 and 4**), which aligns with our expectations. Other studies have found that higher structural heterogeneity in older, rather than younger, forests is linked to more microclimate buffering capacity (Betts et al., 2018; de Frenne et al., 2019) and older forests tend to have more stable productivity (He et al., 2012). However, recent studies comparing the resilience of mature vs younger forests to climate change impacts show evidence of lower resilience in older forest canopies (Liu et al., 2021). Additionally, while we have stands ranging from 11 to 150 years at Ellsworth, these forests are younger than many of the structurally complex old-growth forests in which other canopy - microclimate buffering studies were conducted (**Fig. S5**). Thus, while our findings align with the expectation of a greater presence of CCR in older forests, they should still be interpreted cautiously, as forests in the region do not achieve full structural complexity until 150 or 200 years (Franklin et al., 2002; T. Spies & Franklin, 1988), a successional state we could not include for our study area. This uneven distribution of ages inhibits our ability to fully understand whether older forests are more likely to harbor CCR.

We also want to highlight the influence that successional stages might have on assessments of vegetation response to climatic stability/variability as successional changes leading to more stable vegetation indices as stands mature and canopy gaps fill up. Previous studies have documented positive trends in NDVI that align with successional transitions from vegetation types and late-successional self-thinning (Fiore et al., 2020) and postfire recovery (Vanderhoof et al., 2021). In our study system, younger stands generally experienced an increase in NDVI and NDMI in the earlier years followed by a plateau, although this pattern was also present in some of the more mature stands (**Fig. S6 and S7**). It is possible that an increased baseline NDVI and NDMI, as caused by succession in younger stands, could have resulted in decreased NDVI / NDMI CVs in the post-treatment period (less variation because stands are closer to maximal NDVI). We suggest that future efforts in identifying CCR in systems at different successional stages that use a remote sensing approach (as we did) should take successional trajectories in NDVI and NDMI into account.

3.5.3 *Satellite-based CCR are related to on-the ground biotic and abiotic phenomenon*

Our study provides strong support for identifying CCR using remote-sensing based measurements of forest stability, by using on the ground measurements of forest microclimate and plant community composition. Few studies, regardless of the approach they used to quantify CCR, have examined the relevance of these CCR to on-the-ground biotic and abiotic metrics (Barrows et al., 2020). Our finding that variation in on-the-ground forest temperatures were positively correlated with buffering capacity (based on NDVI, **Fig. 3-6**), at least within a single year, lends support to the use of these indices. A second line of support for our methodology and identification of CCR comes from forest community composition patterns - we found that variation in NDVI and NDMI were relevant in explaining forest community composition (**Fig. 3-5**), suggesting that CCR do influence forest communities.

Despite similarity in the ability of the two vegetation indices to identify CCR, there were some differences in their spatial patterns. NDVI is the normalized difference between the near infrared and red bands and represents a proxy for vegetation greenness while NDMI is the normalized difference between near infrared and shortwave infrared bands and has been used as a proxy for vegetation moisture, particularly in drought prone areas. As these two metrics represent fundamentally different (and potentially complementary) vegetation properties, they have different patterns across space. Thus, while examining vegetation indices can give us an idea of the stability of climatic conditions (and thus buffering capacity), whether we focus on NDVI or NDMI might depend on the environmental characteristics that are considered most important and most limiting. For instance, if the trend of increasing climatic water deficit in the PNW (Abatzoglou et al., 2014) continues, NDMI-based assessments of CCR might become more useful even in these moist and relatively drought resistant forests.

3.5.4 *Caveats and future directions*

CCR identified in our study are hypothesized areas that are *likely* to offer organisms refuge from global climate change by providing localized areas buffered from strong temperature and / or moisture extremes; they are not a guarantee. Two key questions will impact the effectiveness of CCR – 1) do our CCR capture the climatic factors that are most relevant to organisms at Ellsworth?, and 2) do CCR buffer organisms from climate change? We discuss these caveats below.

First, to assess whether CCR capture understory microclimate, we used temperature data collected in a single year to assess the relationship between variation in NDVI and NDMI with understory temperature. It is not clear whether these within year patterns will be consistent across years, especially at longer timescales. A logical next step would be to assess patterns of stability for multiple years, i.e., to check whether there is temporal variation in microclimate stability. Moreover, we only used one aspect of climate, understory temperature measurements, to connect microclimate to CCR based on remote sensing. While different aspects of temperature (like means, maximums, minimums and variability) likely influence plant community composition (Frey, Hadley, & Betts, 2016; Zellweger et al., 2020), other microclimatic factors such as soil moisture and light availability also do (Andrus et al., 2018; de Pauw et al., 2022) and should also be examined for correspondence across remote-sensed and on the ground measurement. The importance of examining multiple microclimatic factors is also highlighted by the fact that there was no significant relationship between $NDMI_{CV}$ and variation in temperature minimums and maximums; since NDMI is a measure of vegetation moisture, comparing variation in NDMI to a metric of moisture (like soil moisture or relative humidity) might be more appropriate in future studies. In all, we believe that the multi-faceted effects of restoration treatments like thinning on different aspects of microclimate buffering are likely to have complex effects on organisms of interest, and therefore deserve further investigation.

Second, the efficacy of CCR identified using our methods likely differ through time and by organism. The forests we studied were predominantly in early successional stages (<25 years), with fewer sites in later successional stages (very few >100 years old). As such, we are unable to compare the buffering capacity of these younger stands to more mature stands within our study area (~149 yrs) or even old growth forests that are known to have an insulating effect on understory microclimate (Frey, Hadley, Johnson, et al., 2016; Wolf et al., 2021). Refining our understanding of the nature of buffering capacity and canopy complexity and density, such as temporal changes in buffering capacity with successional changes and comparison of buffering capacity of late-successional and old-growth forests to early successional forests, will help fine tune the application of climate-smart restoration. Another important extension of this study would be to assess whether organisms that occur within these forests are indeed buffered from impacts of climate change as this can depend on the resource requirements and traits of the organisms of interest (Troia et al., 2019).

3.6 CONCLUSIONS

Our results suggest that restoring forests to accelerate the development of old growth habitat using stand-thinning and road decommissioning can be done synergistically with preserving and promoting landscape buffering capacity (CCRs). This implies that although thinning stands for restoration does reduce canopy cover, this management approach, if conducted carefully, does not necessarily reduce buffering capacity and climate change resilience (Magruder et al., 2013; Wells et al., 2022). Coordinating management with CCR identification, for example prior to the implementation of thinning treatments, could provide a positive synergy between these approaches. For instance, restoration thinning in these forests is based on variable density thinning where certain portions of the stands are left alone and not thinned (i.e., skips); as such, these skips could be prioritized in locations with greater buffering capacity (CCR) to ensure this capacity is protected from thinning. Overall, we demonstrate the importance of assessing the trade-offs between distinct management goals and demonstrate a method of assessing these tradeoffs that could be applied to other lands where managers are interested in incorporating climate-smart management into already existing management frameworks.

3.7 ACKNOWLEDGEMENTS

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3.8 REFERENCES

Abatzoglou, J. T., Rupp, D. E., & Mote, P. W. (2014). Seasonal Climate Variability and Change in the Pacific Northwest of the United States. *Journal of Climate*, *27*(5), 2125–2142. https://doi.org/10.1175/JCLI-D-13-00218.1

Ackerly, D. D., Kling, M. M., Clark, M. L., Papper, P., Oldfather, M. F., Flint, A. L., & Flint, L. E. (2020). Topoclimates, refugia, and biotic responses to climate change. *Frontiers in Ecology and the Environment*, *18*(5), 288–297. https://doi.org/10.1002/FEE.2204

Anderson, M.G., Barnett, A., Clark, M., Prince, J., Olivero Sheldon, A. and Vickery B. 2016. Resilient and Connected Landscapes for Terrestrial Conservation. The Nature Conservancy, Eastern Conservation Science, Eastern Regional Office. Boston, MA.

Andrus, R. A., Harvey, B. J., Rodman, K. C., Hart, S. J., & Veblen, T. T. (2018). Moisture availability limits subalpine tree establishment. *Ecology*, *99*(3), 567–575. https://doi.org/10.1002/ECY.2134

Apodaca, M., Tippie, M., Verde, A. M., Barandino, V., Jones, B., & Rios, J. (2018). *Guidelines for Storing and Decommissioning Roads*. USDA Forest Service, National Technology and Development Program.

Ares, A., Neill, A. R., & Puettmann, K. J. (2010). Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. *Forest Ecology and Management*, *260*(7), 1104–1113. https://doi.org/10.1016/J.FORECO.2010.06.023

Barrows, C. W., Ramirez, A. R., Sweet, L. C., Morelli, T. L., Millar, C. I., Frakes, N., Rodgers, J., & Mahalovich, M. F. (2020). Validating climate-change refugia: empirical bottom-up approaches to support management actions. *Frontiers in Ecology and the Environment*, *18*(5), 298–306. https://doi.org/10.1002/FEE.2205

Bauhus, J., Puettmann, K., & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management*, *258*(4), 525–537. https://doi.org/10.1016/J.FORECO.2009.01.053

Betts, M. G., Phalan, B., Frey, S. J. K., Rousseau, J. S., & Yang, Z. (2018). Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions*, *24*(4), 439–447. https://doi.org/10.1111/DDI.12688

Bivand, R. (2022). R Packages for Analyzing Spatial Data: A Comparative Case Study with Areal Data. *Geographical Analysis*, *54*(3), 488–518. https://doi.org/10.1111/GEAN.12319

Bivand, R., Hauke, J., & Kossowski, T. (2013). Computing the jacobian in gaussian spatial autoregressive models: An illustrated comparison of available methods. *Geographical Analysis*, *45*(2), 150–179. https://doi.org/10.1111/GEAN.12008

Bivand, R., Millo, G., & Piras, G. (2021). A review of software for spatial econometrics in r. *Mathematics*, *9*(11). https://doi.org/10.3390/MATH9111276

Bivand, R. S., & Wong, D. W. S. (2018). Comparing implementations of global and local indicators of spatial association. *Test*, *27*(3), 716–748. https://doi.org/10.1007/S11749-018-0599-X

Buotte, P. C., Levis, S., Law, B. E., Hudiburg, T. W., Rupp, D. E., & Kent, J. J. (2019). Near-future forest vulnerability to drought and fire varies across the western United States. *Global Change Biology*, *25*(1), 290–303. https://doi.org/10.1111/GCB.14490

Carey, A. B. (2003). Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. *Forestry: An*

International Journal of Forest Research, *76*(2), 127–136. https://doi.org/10.1093/FORESTRY/76.2.127

Case, M. J., Ettinger, A. K., & Pradhan, K. In review. Quantifying the effects of forest restoration on old-growth characteristics, with implications for wildlife habitat and climate change resilience in the coastal Pacific Northwest (USA). Conservation Science & Practices

Chamberlain, C. P., Kane, V. R., & Case, M. J. (2021). Accelerating the development of structural complexity: lidar analysis supports restoration as a tool in coastal Pacific Northwest forests. *Forest Ecology and Management*, *500*, 119641. https://doi.org/10.1016/J.FORECO.2021.119641

Churchill, D., Larson, A., Cedar, K., Rolph, D., & Kollasch, T. (2007). *SOUTH WILLAPA BAY CONSERVATION AREA: FOREST LANDSCAPE RESTORATION PLAN*.

Collins, L., Bennett, A. F., Leonard, S. W. J., & Penman, T. D. (2019). Wildfire refugia in forests: Severe fire weather and drought mute the influence of topography and fuel age. *Global Change Biology*, *25*(11), 3829–3843. https://doi.org/10.1111/GCB.14735

D'Amato, A. W., Bradford, J. B., Fraver, S., & Palik, B. J. (2013). Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*, *23*(8), 1735–1742. https://doi.org/10.1890/13-0677.1

Davis, L., Kollasch, T., Smith, K. M., & Boston, K. (2015). South Willapa Bay Conservation Area, Washington, United States of America. In *Forest Plans of North America* (pp. 225–233). Elsevier. https://doi.org/10.1016/B978-0-12-799936-4.00026-6

de Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., de Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., … Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297. https://doi.org/10.1111/GCB.15569

de Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellen, M., Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(46), 18561–18565. https://doi.org/10.1073/PNAS.1311190110

de Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution 2019 3:5*, *3*(5), 744–749. https://doi.org/10.1038/S41559-019-0842-1

de Pauw, K., Sanczuk, P., Meeussen, C., Depauw, L., de Lombaerde, E., Govaert, S., Vanneste, T., Brunet, J., Cousins, S. A. O., Gasperini, C., Hedwall, P. O., Iacopetti, G., Lenoir, J., Plue, J., Selvi, F., Spicher, F., Uria-Diez, J., Verheyen, K., Vangansbeke, P., & de Frenne, P. (2022). Forest understorey communities respond strongly to light in interaction with forest structure, but not to microclimate warming. *New Phytologist*, *233*(1), 219–235. https://doi.org/10.1111/NPH.17803

Dietz, L., Collet, C., Dupouey, J. L., Lacombe, E., Laurent, L., & Gégout, J. C. (2020). Windstorm-induced canopy openings accelerate temperate forest adaptation to global warming. *Global Ecology and Biogeography*, *29*(11), 2067–2077. https://doi.org/10.1111/GEB.13177

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813. https://doi.org/10.1111/J.1365-2656.2008.01390.X

Evans, J., & Murphy, M. (2021). *spatialEco*. R Package Version 1.3-6. https://github.com/jeffreyevans/spatialEco

Evans, P. M., Newton, A. C., Cantarello, E., Martin, P., Sanderson, N., Jones, D. L., Barsoum, N., Cottrell, J. E., A'Hara, S. W., & Fuller, L. (2017). Thresholds of biodiversity and ecosystem function in a forest ecosystem undergoing dieback. *Scientific Reports 2017 7:1*, *7*(1), 1–9. https://doi.org/10.1038/S41598-017-06082-6

Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. *PLOS ONE*, *8*(3), e58093. https://doi.org/10.1371/JOURNAL.PONE.0058093

Fiore, N. M., Goulden, M. L., Czimczik, C. I., Pedron, S. A., & Tayo, M. A. (2020). Do recent NDVI trends demonstrate boreal forest decline in Alaska? *Environmental Research Letters*, *15*(9), 095007. https://doi.org/10.1088/1748-9326/AB9C4C

Frade, P. R., Bongaerts, P., Englebert, N., Rogers, A., Gonzalez-Rivero, M., & Hoegh-Guldberg, O. (2018). Deep reefs of the Great Barrier Reef offer limited thermal refuge during mass coral bleaching. *Nature Communications 2018 9:1*, *9*(1), 1–8. https://doi.org/10.1038/s41467-018-05741-0

Franklin, J. F., & Johnson, K. N. (2012a). A Restoration Framework for Federal Forests in the Pacific Northwest. *Journal of Forestry*, *110*(8), 429–439. https://doi.org/10.5849/JOF.10-006

Franklin, J. F., & Johnson, K. N. (2012b). A Restoration Framework for Federal Forests in the Pacific Northwest. *Journal of Forestry*, *110*(8), 429–439. https://doi.org/10.5849/JOF.10-006

Franklin, J. F., Spies, T. A., Pelt, R. van, Carey, A. B., Thornburgh, D. A., Berg, D. R., Lindenmayer, D. B., Harmon, M. E., Keeton, W. S., Shaw, D. C., Bible, K., & Chen, J. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, *155*(1–3), 399–423. https://doi.org/10.1016/S0378-1127(01)00575-8

Frey, S. J. K., Hadley, A. S., & Betts, M. G. (2016). Microclimate predicts within-season distribution dynamics of montane forest birds. *Diversity and Distributions*, *22*(9), 944–959. https://doi.org/10.1111/DDI.12456

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4). https://doi.org/10.1126/SCIADV.1501392/SUPPL_FILE/1501392_SM.PDF

He, L., Chen, J. M., Pan, Y., Birdsey, R., & Kattge, J. (2012). Relationships between net primary productivity and forest stand age in U.S. forests. *Global Biogeochemical Cycles*, *26*(3). https://doi.org/10.1029/2010GB003942

Hengl, T., de Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE*, *12*(2), e0169748. https://doi.org/10.1371/JOURNAL.PONE.0169748

Hijmans, R., & van Etten, J. (2012). raster: Geographic analysis and modeling with raster data. In *R package version 2.0-12.* http://CRAN.R-project.org/package=raster

Krawchuk, M. A., Meigs, G. W., Cartwright, J. M., Coop, J. D., Davis, R., Holz, A., Kolden, C., & Meddens, A. J. H. (2020). Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. *Frontiers in Ecology and the Environment*, *18*(5), 235–244. https://doi.org/10.1002/FEE.2190

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2012). Ecology: Global decline in large old trees. *Science*, *338*(6112), 1305–1306. https://doi.org/10.1126/SCIENCE.1231070/ASSET/B7E2C823-D690-4564-99F3-32AC578F9958/ASSETS/GRAPHIC/338_1305_F1.JPEG

Liu, F., Liu, H., Xu, C., Shi, L., Zhu, X., Qi, Y., & He, W. (2021). Old-growth forests show low canopy resilience to droughts at the southern edge of the taiga. *Global Change Biology*, *27*(11), 2392–2402. https://doi.org/10.1111/GCB.15605

Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., Ciais, P., & Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature 2008 455:7210*, *455*(7210), 213–215. https://doi.org/10.1038/NATURE07276

Magruder, M., Chhin, S., Palik, B., & Bradford, J. B. (2013). Thinning increases climatic resilience of red pine. *Canadian Journal of Forest Research*, *43*(9), 878–889. https://doi.org/10.1139/cjfr-2013-0088

Maher, C. T., Millar, C. I., Affleck, D. L. R., Keane, R. E., Sala, A., Tobalske, C., Larson, A. J., & Nelson, C. R. (2021). Alpine treeline ecotones are potential refugia for a montane pine species threatened by bark beetle outbreaks. *Ecological Applications*, *31*(3), e2274. https://doi.org/10.1002/EAP.2274

McDowell, N. G., & Allen, C. D. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change 2015 5:7*, *5*(7), 669–672. https://doi.org/10.1038/NCLIMATE2641

Menne, M. J., Williams, C. N., & Vose, R. S. (2009). The U.S. Historical Climatology Network Monthly Temperature Data, Version 2. *Bulletin of the American Meteorological Society*, *90*(7), 993–1008. https://doi.org/10.1175/2008BAMS2613.1

Metcalfe, P., Beven, K., & Freer, J. (2015). Dynamic TOPMODEL: A new implementation in R and its sensitivity to time and space steps. *Environmental Modelling & Software*, *72*, 155–172. https://doi.org/10.1016/J.ENVSOFT.2015.06.010

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*(5), 228–234. https://doi.org/10.1002/FEE.2189

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/JOURNAL.PONE.0159909

Naujokaitis-Lewis, I., Pomara, L. Y., & Zuckerberg, B. (2018). Delaying conservation actions matters for species vulnerable to climate change. *Journal of Applied Ecology*, *55*(6), 2843–2853. https://doi.org/10.1111/1365-2664.13241

Pradhan, K., Ettinger, A., Case, M., & HilleRisLambers, J. (2023). Data from: Assessing climate change refugia in forests managed for restoration. In *Dryad, Dataset*.

Rambo, T. R., & North, M. P. (2009). Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. *Forest Ecology and Management*, *257*(2), 435–442. https://doi.org/10.1016/J.FORECO.2008.09.029

Roussel, J. R., Auty, D., Coops, N. C., Tompalski, P., Goodbody, T. R. H., Meador, A. S., Bourdon, J. F., de Boissieu, F., & Achim, A. (2020). lidR: An R package for analysis of Airborne Laser Scanning (ALS) data. *Remote Sensing of Environment*, *251*, 112061. https://doi.org/10.1016/J.RSE.2020.112061

Scharmer, K., Greif, J., Aguiar, R., Albuisson, M., Beyer, H. G., Borisenkov, E. P., Bourges, B., Czeplak, G., Lund, H., Joukoff, A., Scharmer, K., Page, J. K., Terzenbach, U., & Wald, L. (2000). *The European solar radiation atlas, Vol. 2: Database and exploitation software* (K. Scharmer & J.-J. Greif, Eds.). Les Presses de l'École des Mines.

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change 2017 7:6*, *7*(6), 395–402. https://doi.org/10.1038/NCLIMATE3303

Sohn, J. A., Saha, S., & Bauhus, J. (2016). Potential of forest thinning to mitigate drought stress: A meta-analysis. *Forest Ecology and Management*, *380*, 261–273. https://doi.org/10.1016/J.FORECO.2016.07.046

Spies, T. A., Giesen, T. W., Swanson, F. J., Franklin, J. F., Lach, D., & Johnson, K. N. (2010). Climate change adaptation strategies for federal forests of the Pacific Northwest, USA: Ecological, policy, and socio-economic perspectives. *Landscape Ecology*, *25*(8), 1185–1199. https://doi.org/10.1007/S10980-010-9483-0/TABLES/1

Spies, T. A., Stine, P. A., Gravenmier, R. A., Long, J. W., & Reilly, M. J. (2018). Synthesis of science to inform land management within the Northwest Forest Plan area. *Gen. Tech. Rep. PNW-GTR-966. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 1020 p. 3 Vol.*, *966*. https://doi.org/10.2737/PNW-GTR-966

Spies, T., & Franklin, J. (1988). Old Growth and Forest Dynamics in the Douglas-Fir Region of Western Oregon and Washington. *Natural Areas Journal.*, *8*(3), 190–201.

Stewart, H. A., Kline, D. I., Chapman, L. J., Altieri, A. H., Kline, D. I., Chapman, L. J., Altieri, A. H., & C Peters, D. P. (2021). Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. *Ecosphere*, *12*(3), e03413. https://doi.org/10.1002/ECS2.3413

Stokes, M. A., & Smiley, T. L. (1996). *An Introduction to Tree-ring Dating*. The University of Arizona Press.

Switalski, T., Bissonette, J., … T. D.-F. in E., & 2004, undefined. (2004). Benefits and impacts of road removal. *Wiley Online Library*. https://doi.org/10.1890/1540-9295(2004)002[0021:BAIORR]2.0.CO;2

Troia, M. J., Kaz, A. L., Niemeyer, J. C., & Giam, X. (2019). Species traits and reduced habitat suitability limit efficacy of climate change refugia in streams. *Nature Ecology & Evolution 2019 3:9*, *3*(9), 1321–1330. https://doi.org/10.1038/s41559-019-0970-7

Vanderhoof, M. K., Hawbaker, T. J., Ku, A., Merriam, K., Berryman, E., Cattau, M., Vanderhoof, M. K., Hawbaker, T. J., Ku, A., Merriam, K., Berryman, E., & Cattau, M. 2021. (2021). Tracking rates of postfire conifer regeneration vs. deciduous vegetation recovery across the western United States. *Ecological Applications*, *31*(2), e02237. https://doi.org/10.1002/EAP.2237

Verschuyl, J., Riffell, S., Miller, D., & Wigley, T. B. (2011). Biodiversity response to intensive biomass production from forest thinning in North American forests – A meta-analysis. *Forest Ecology and Management*, *261*(2), 221–232. https://doi.org/10.1016/J.FORECO.2010.10.010

von Arx, G., Graf Pannatier, E., Thimonier, A., & Rebetez, M. (2013). Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *Journal of Ecology*, *101*(5), 1201–1213. https://doi.org/10.1111/1365-2745.12121

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLOS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Washington State Department of Natural Resources (WSDNR). (2020). *Washington Lidar Portal. Available online: https://lidarportal.dnr.wa.gov/#47.40950:-122.03613:7.*

Wells, G. J., Ryan, C. M., Artur, L., Ribeiro, N., Bowers, S., Hargreaves, P., Fernando, J., Farao, A., & Fisher, J. A. (2022). Tree harvesting is not the same as deforestation. *Nature Climate Change 2022 12:4*, *12*(4), 307–309. https://doi.org/10.1038/s41558-022-01326-4

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *PLOS Biology*, *6*(12), e325. https://doi.org/10.1371/JOURNAL.PBIO.0060325

Wolf, C., Bell, D. M., Kim, H., Nelson, M. P., Schulze, M., & Betts, M. G. (2021). Temporal consistency of undercanopy thermal refugia in old-growth forest. *Agricultural and Forest Meteorology*, *307*, 108520. https://doi.org/10.1016/J.AGRFORMET.2021.108520

Zellweger, F., de Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Zhou, G., Liu, S., Li, Z., Zhang, D., Tang, X., Zhou, C., Yan, J., & Mo, J. (2006). Old-growth forests can accumulate carbon in soils. *Science*, *314*(5804), 1417. https://doi.org/10.1126/SCIENCE.1130168

3.9 TABLES

Table 3-1. Model parameters and results from Boosted Regression Trees. Higher AUC-ROC values indicate better predictive performance. Cross-validation values are obtained from cross-validation during model building on the training dataset (1500 sites). Prediction values are based on 500 independent sites.

	$\mathrm{CCR}_{\mathrm{NDVI}}$	**$\mathrm{CCR}_{\mathrm{NDMI}}$**
Self AUC-ROC	0.988± 0.001	0.989± 0.001
Percent deviance explained	63.2% ± 0.5%	64.8 % ± 0.5%
Cross-validation AUC-ROC	0.847 ± 0.001	0.859 ± 0.001
Cross-validation percent deviance explained	27.74% ± 0.2%	30.6 % ± 0.002%
Prediction correlation	0.556 ± 0.004	0.590 ± 0.003
Prediction AUC-ROC	0.846± 0.002	0.862± 0.002

Table 3-2. Model results from Spatial Error Model to assess the influence of stand age, treatment type, and their interaction on the change in coefficient of variation of vegetation indices (NDVI and NDMI) pre- and post- thinning. All pixels within experimental stands were used in the analyses with a neighborhood distance of 45m. Statistically significant predictors ($p < 0.05$) are greyed out in the table for easier visualization.

Vegetation indices	Parameters	Estimate	Std. Error	z-value	Pr(>|z|)
Change in $NDVI_{CV}$	Intercept	-3.921	0.404	-9.700	< 2.2e-16
	Stand age	0.016	0.004	3.797	0.0001
	Treatment (Thinning)	0.160	0.557	0.288	0.7734
	Treatment (Decommisioned roads)	-1.062	0.454	-2.338	0.0194
	Stand age X Thinning	0.003	0.008	0.458	0.6472
	Stand age X Decommisioned roads	0.009	0.005	1.765	0.0775
Change in $NDMI_{CV}$	Intercept	-19.706	5.365	-3.674	0.0002
	Stand age	0.254	0.110	2.308	0.0210
	Treatment (Thinning)	-13.770	9.213	-1.495	0.1350
	Treatment (Decommisioned roads)	-38.899	7.351	-5.291	0.0000
	Stand age X Thinning	0.323	0.175	1.843	0.0654
	Stand age X Decommisioned roads	0.255	0.131	1.947	0.0516

3.10 FIGURES

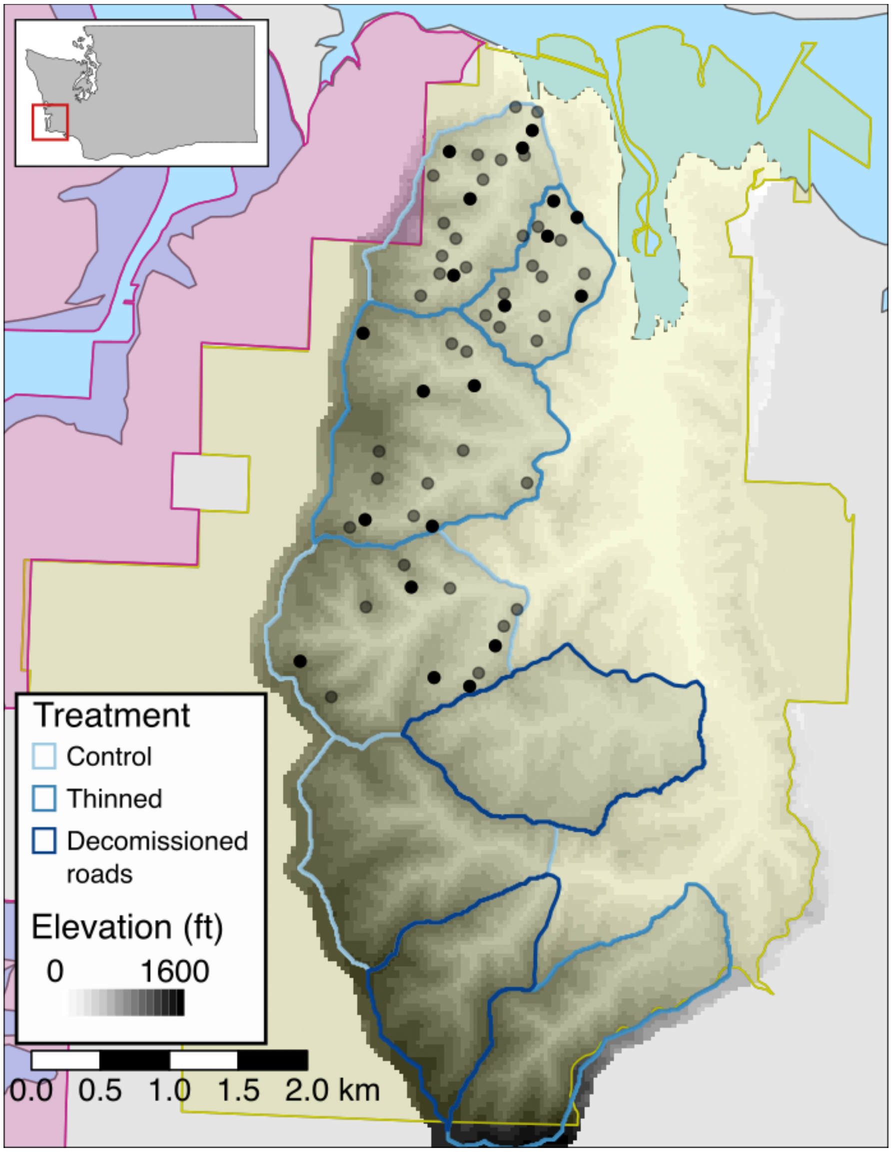

Figure 3-1. Study site, Willapa Bay, Washington, USA. Area of interest includes forested regions within Willapa National Wildlife Refuge (in violet) and Ellsworth Creek Preserve (in yellow). Elevation of the Ellsworth Creek watershed is shown in grayscale. Dots (grey and black) indicate sites where vegetation surveys were conducted in 2020 and 2006. Black dots indicate sites where we collected temperature data in 2020-2021. Experimental basins are also separated into control (no treatment), decommissioned roads (where previous logging roads were decommissioned) and thinned (where stands were thinned by ~ 30%). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

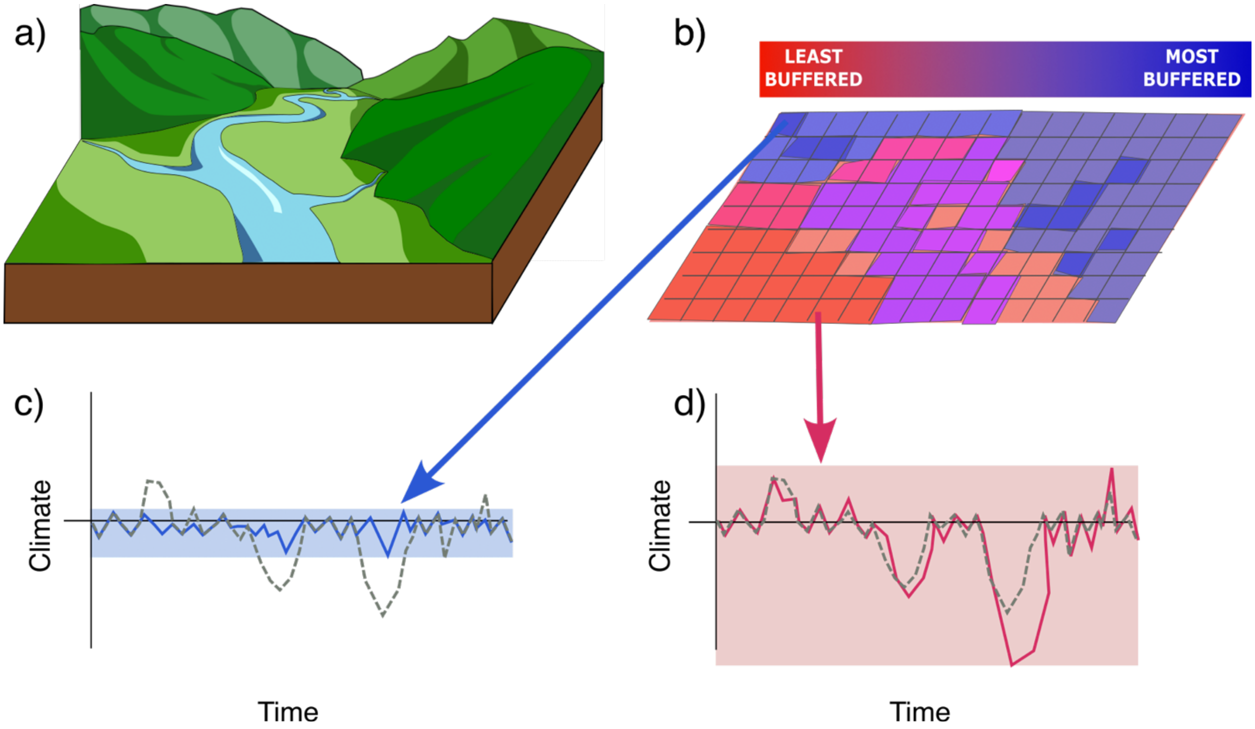

Figure 3-2. We used variability in vegetation response to understand climate buffering capacity. This conceptual figure shows a) a hypothetical landscape of interest where the buffering capacity across this landscape is visualized as b) a raster with more buffered areas represented in blue and less buffered areas represented in red. As climate fluctuates across time (dashed grey lines), c) areas that are relatively more buffered (blue) have lower variability across time and are decoupled from the regional climate. On the other hand, d) areas that are less buffered (red) will be more responsive to regional climatic fluctuations and thus have larger variability across time

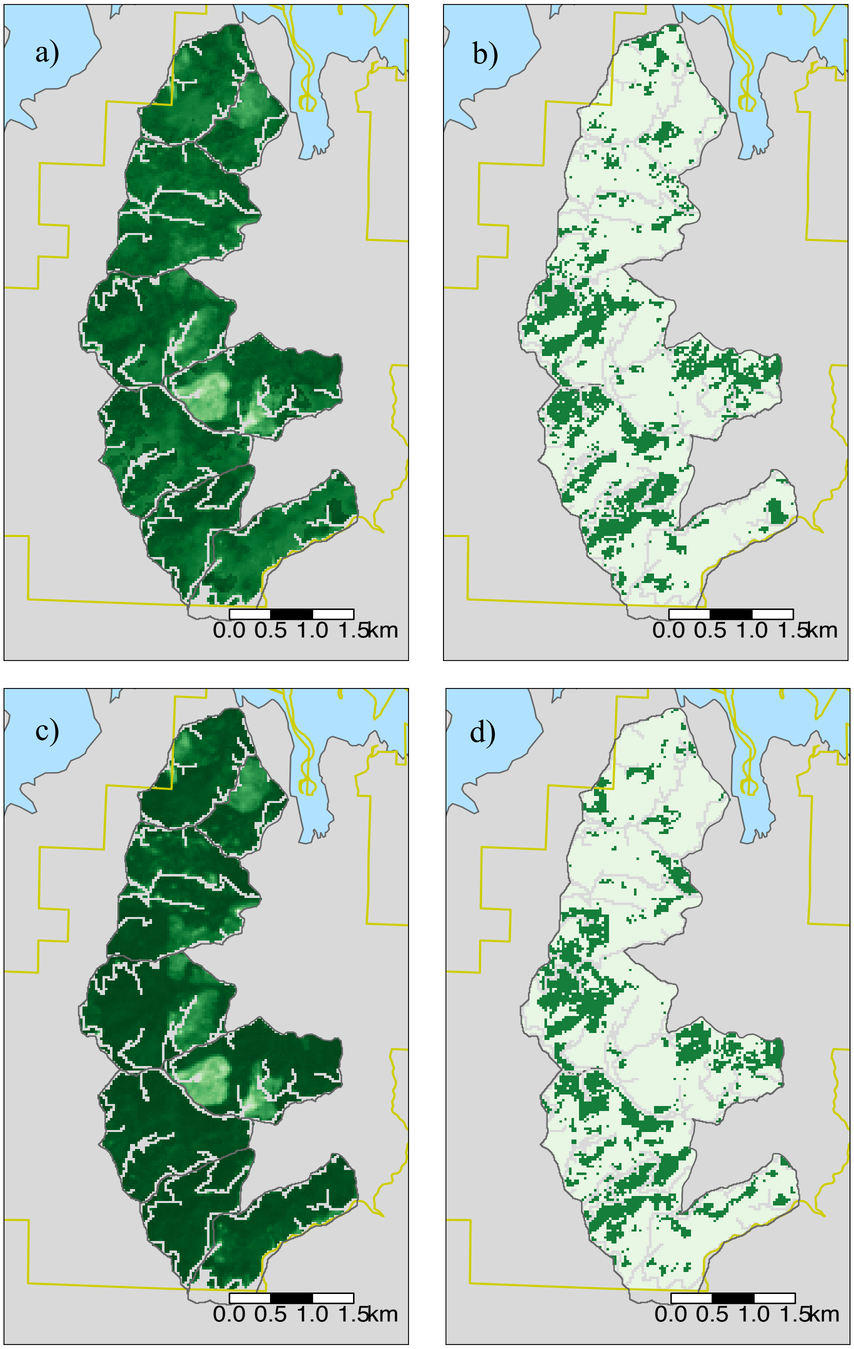

Figure 3-3. Variation of vegetation indices in experimental sub-basins within Ellsworth Creek Preserve. Based on summer (June-September) data from 1999-2021, darker greens indicate less variation in a) variation in vegetation greenness (NDVI_{CV}) and c) variation in vegetation moisture (NDMI_{CV}). This was converted into presence absence with dark greens representing presences and light green showing absences for climate change refugia based on b) vegetation greenness (CCR_{NDVI}) and d) vegetation moisture (CCR_{NDMI})

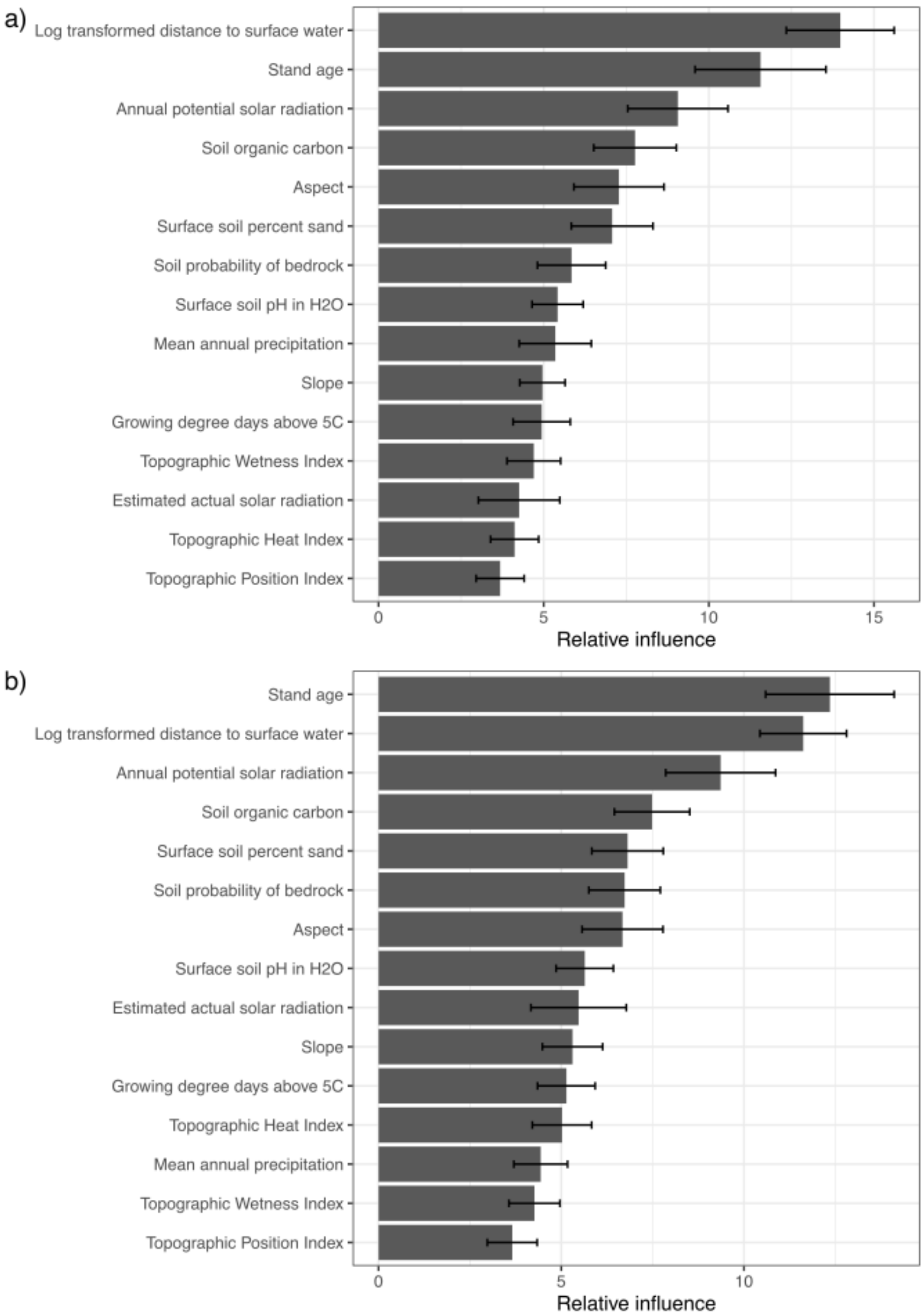

Figure 3-4. Relative importance of variables used in boosted regression tree for climate change refugia based on a) vegetation greenness (CCR_{NDVI}) and b) vegetation moisture (CCR_{NDMI}) averaged over 100 iterations using 1500 random cells for model fitting. Higher values indicate larger influence on the presence of climate change refugia and the relative importance of all variables add up to 100. Error bars represent standard error

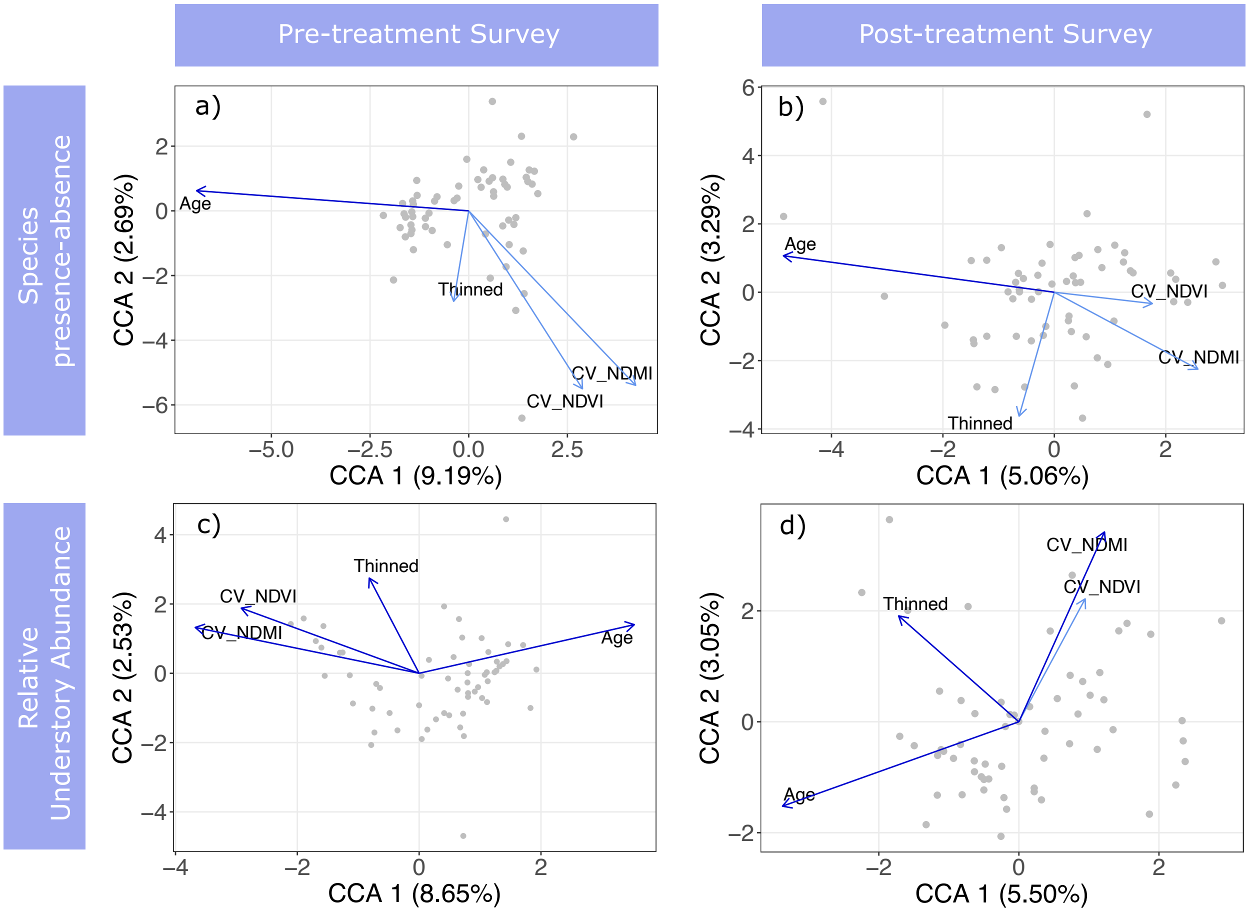

Figure 3-5. Canonical correspondence analysis ordination plots for forest characteristics for a-b) overstory and understory species presence-absence and c-d) relative understory abundance. The relative associations of constraining variables to one another are similar for pre-treatment vegetation (a,c) and post-treatment vegetation (b,d) which are shown with blue arrows (dark blue arrows $p < 0.05$ while light blue are not significant) where longer arrows indicate greater contribution to the ordination. Note here that CCA1 is significant for all ordinations, but CCA2 is not significant for pre-treatment surveys.

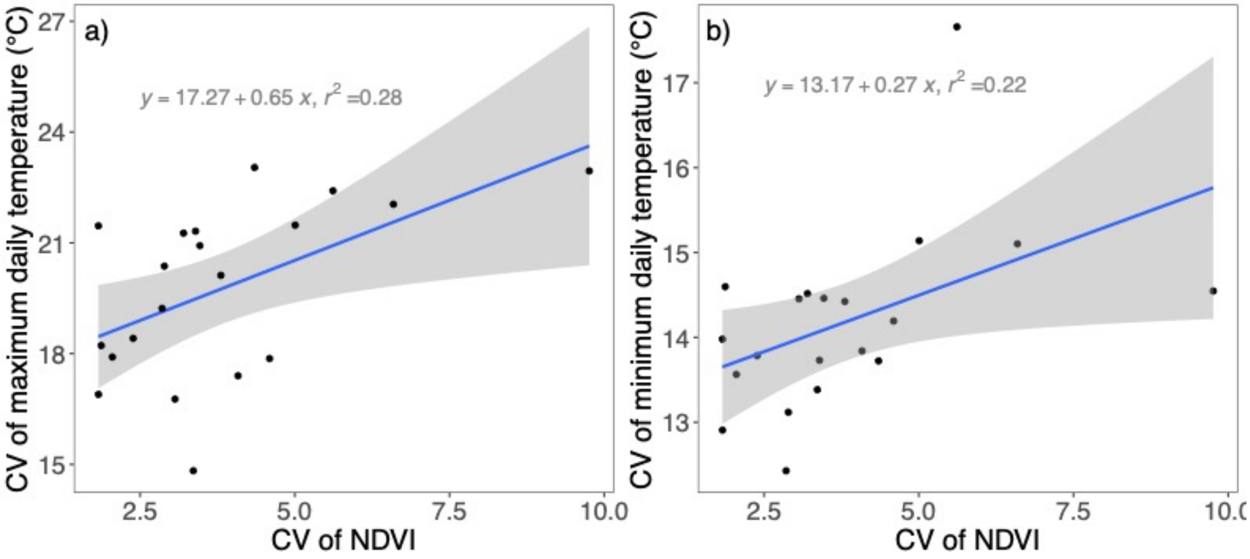

Figure 3-6. Relationship between variation in forest floor temperatures and variation in vegetation greenness ($NDVI_{CV}$) shows a positive correlation for a) minimum daily temperatures and b) maximum daily temperatures. Data were collected from 20 sites spread out across four experimental sub-basins in Ellsworth Creek Preserve.

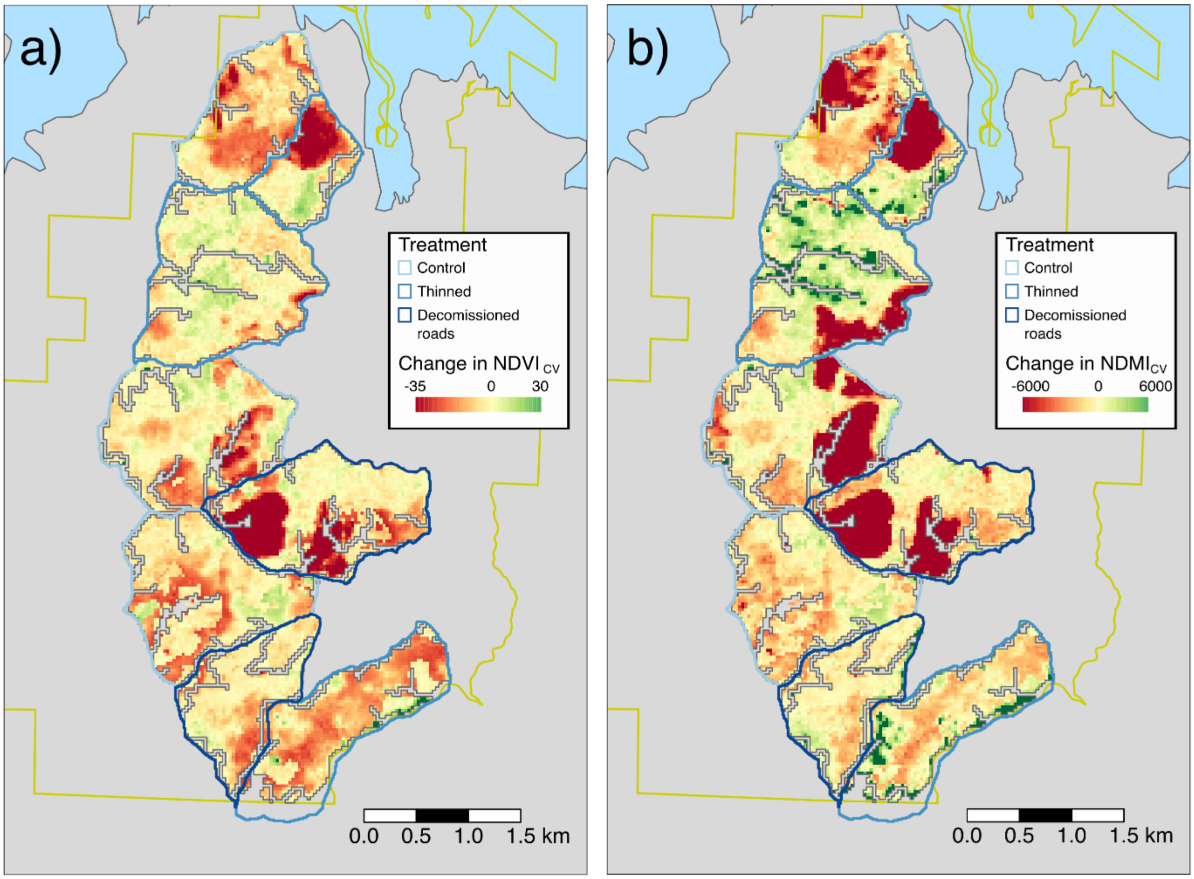

Figure 3-7. Change in variation of vegetation indices from pre-treatment to the post-treatment time period. Higher values of change (greens) show an increase in variation while lower values (reds) show decreased variation after treatment.

3.11 SUPPLEMENTARY MATERIAL

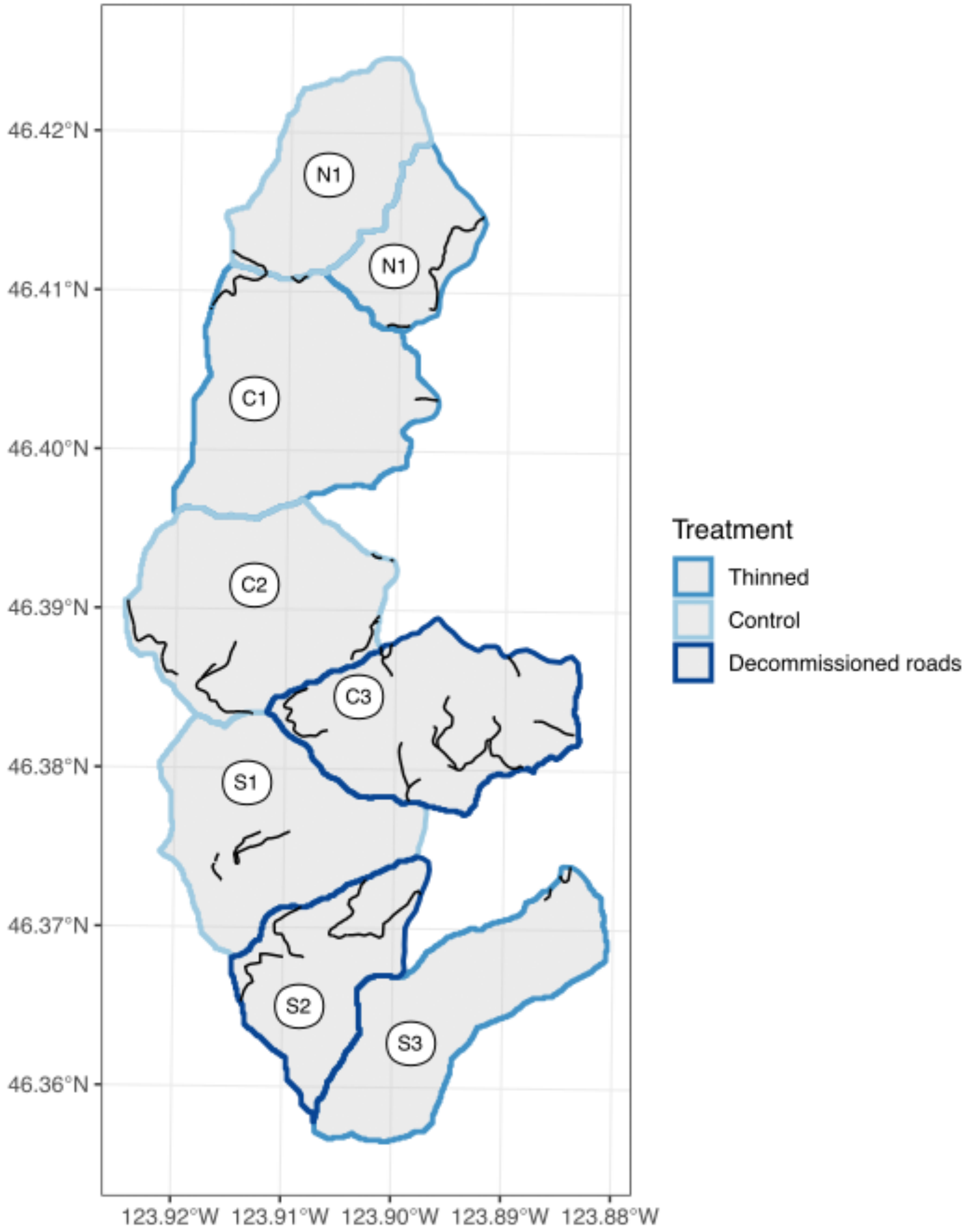

Figure S1. Ellsworth Experimental set up. The Ellsworth creek watershed was divided into subbasins as shown in the figure with 3 in thinned,3 in control and 2 in decommissioned roads subbasins. Black lines show roads that were decommissioned.

Table S1. Total length of roads decommissioned in different treatment

Treatment	Basin	Length of road decommissioned/area of basin (m^{-1})
Control	N1	0.000255
	C2	0.00119
	S1	0.000574
Thinned	N2	0.00155
	C1	0.0004
	S3	0.000181
Decommissioned roads	C3	0.00213
	S2	0.00216

Table S2. Description of variables used in Boosted Regression Tree analysis. Variables that were retained and used in the final analysis are presented in black while variables that were initially considered but removed from the final analysis are shown in grey.

Variables	Description	Spatial resolution (m)	Data source and derivation
DD5	**Accumulated annual degree days above 5°C**. Growing degree days.	90	Derived from (Wang et al., 2016)and downscaled using delta-downscaling using geographically weighted regression
TD	**Temperature seasonality**. Change in temperature over the course of a year	90	Derived from (Wang et al., 2016)and downscaled using delta-downscaling using geographically weighted regression
CMD	**Climate moisture deficit**	90	Derived from (Wang et al., 2016)and downscaled using delta-downscaling using geographically weighted regression
MAP	**Mean annual precipitation** in mm.	90	Derived from (Wang et al., 2016)and downscaled using delta-downscaling using geographically weighted regression
MAPS	**Mean annual precipitation as snow.** Average of annual precipitation as snow in mm between August in the previous year to July in the current year.	90	Derived from (Wang et al., 2016)and downscaled using delta-downscaling using geographically weighted regression
BPF	**Beginning of frost-free period**	90	Derived from (Wang et al., 2016)and downscaled using delta-downscaling using geographically weighted regression
RAD	**Annual potential solar radiation**	90	Calculated in GRASS GIS module r.sun
MRA	**Estimated actual (with cloud) solar radiation**	90	PTP_SOL * (PCL_MAN * 0.5)
DIS	**Log transformed distance from surface water**	90	Distance calculation from GRASS GIS module r.grow.distance
BDR	**Soil probability of bedrock**	90	Downscaled from (Hengl et al., 2017)using bilinear interpolation and gap filling
CAR	**Soil organic carbon content**	90	Downscaled from (Hengl et al., 2017) using bilinear interpolation and gap filling
PH	**Surface soil PH in H2O**	90	Downscaled from (Hengl et al., 2017) using bilinear interpolation and gap filling
SND	**Percent sand in surface soil**	90	Downscaled from (Hengl et al., 2017) using bilinear interpolation and gap filling

Slope	**Slope.** Steepness of the cell.	90	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the terrain() function from raster package (Hijmans & van Etten, 2012)in R
Aspect	**Aspect.** The compass direction of the cell.	90	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the terrain() function from raster package (Hijmans & van Etten, 2012) in R
Roughness	**Roughness.** Difference between the maximum and the minimum value of a cell and its 8 surrounding cells.	90	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the terrain() function from raster package (Hijmans & van Etten, 2012) in R
TPI	**Topographic Position Index**. Elevation of a cell relative to the surrounding pixels (over a specific radius, r). TPI indicates whether a cell is in a cove, a ridge or in between. $TPI = elevation_0 - \overline{elevation}$ $\overline{elevation} = \frac{1}{n_r} \sum i \in r^{elevation_i}$	30	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the tpi() function from spatialEco package (Evans & Murphy, 2021) in R
THI	**Topographic heat-load index**. THI indicates whether an area is topographically shaded or topographically exposed. For locations in the northern hemisphere, $THI = -1.467 + (1.582 \times \cos(l) \times \cos(slope)) + (-1.5 \times \cos(folded\ aspect) \times \sin(slope) \times \sin(l)) + (-0.262 \times \sin(l) \times \sin(slope)) + (0.607 \times \sin(folded\ aspect) \times \sin(slope))$ $where\ l\ is\ the\ \lvert ymin(extent) \rvert * 0.017453293, and$ $folded\ aspect = \lvert (3.141593 - abs(Aspect - 3.926991) \rvert \rvert$	30	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the hli() function from spatialEco (Evans & Murphy, 2021) package in R
TRI	**Topographic Ruggedness Index**. The mean of the absolute differences between the value of a cell and the value of its 8 surrounding cells. For an n X n window, $TRI_{(n)} = \frac{\sum_{i=-N}^{N} \sum_{j=-N}^{N} \lvert z_{ij} - z_{00} \rvert}{(n^2-1)}$	30	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the terrain() function from raster package (Hijmans & van Etten, 2012) in R

	$where\ N = \frac{(n-1)}{2}$		
TWI	**Topographic Wetness Index.** TWI is a steady state wetness index that determines the hydrological flow at a certain location as determined by upslope areas draining through that location and the local slope. $TWI = \ ln\left(\frac{a}{tan(b)}\right)$ $where\ a = \ local\ upslope\ area,$ $b = local\ slope\ in\ radians$	30	Derived from LIDAR data (Washington State Department of Natural Resources (WSDNR), 2020) using the upslope.area() function from dynatopmodel package (Metcalfe et al., 2015)in R
CV_{NDVI}	**Coefficient of Variation of Normalized Difference Vegetation Index.** NDVI was calculated using the following formula $NDVI = \frac{NIR-Red}{NIR+Red}$ $where\ NIR = near\ infra\ red$ $CV_{NDVI} = \frac{\sigma_{NDVI}}{\mu_{NDVI}}$	30	Derived from Landsat 5,7, and 8
CV_{NDMI}	**Coefficient of Variation of Normalized Difference Moisture Index.** NDMI was calculated using the following formula $NDMI = \frac{NIR-SWIR}{NIR+SWIR}$ $where\ NIR = near\ infrared\ and\ SWIR$ $= short$ $- wave\ infrared$ $CV_{NDMI} = \frac{\sigma_{NDMI}}{\mu_{NDMI}}$	30	Derived from Landsat 5,7, and 8
Stand Age	**Stand age in 2019** calculated for each stand measured at the stand level on site	n/a	Using standard dendrochronological methods from Stokes and Smiley 1968

Evans, J., & Murphy, M. (2021). *spatialEco*. R Package Version 1.3-6. https://github.com/jeffreyevans/spatialEco

Hengl, T., de Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M. N., Geng, X., Bauer-Marschallinger, B., Guevara, M. A., Vargas, R., MacMillan, R. A., Batjes, N. H., Leenaars, J. G. B., Ribeiro, E., Wheeler, I., Mantel, S., & Kempen, B. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE*, *12*(2), e0169748. https://doi.org/10.1371/JOURNAL.PONE.0169748

Hijmans, R., & van Etten, J. (2012). raster: Geographic analysis and modeling with raster data. In *R package version 2.0-12.* http://CRAN.R-project.org/package=raster

Metcalfe, P., Beven, K., & Freer, J. (2015). Dynamic TOPMODEL: A new implementation in R and its sensitivity to time and space steps. *Environmental Modelling & Software*, *72*, 155–172. https://doi.org/10.1016/J.ENVSOFT.2015.06.010

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America. *PLOS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Washington State Department of Natural Resources (WSDNR). (2020). *Washington Lidar Portal. Available online: https://lidarportal.dnr.wa.gov/#47.40950:-122.03613:7.*

Figure S2. Principle component analysis of environmental variables. This analysis was used along with correlations among variables to select predictors for Boosted Regression Tree Analysis. Here variables shown are shown for a subset of 2000 cells from across the experimental basins**.** PCM_CMD = climate moisture deficit; PCM_BFP = beginning of frost free period; PTP_ELV = Elevation; PCM_PAS = mean annual precipitation as snow; PCM_TD = temperature seasonality; PCM_MAP = mean annual precipitation; PCM_DD5 = accumulated annual degree days above 5°C

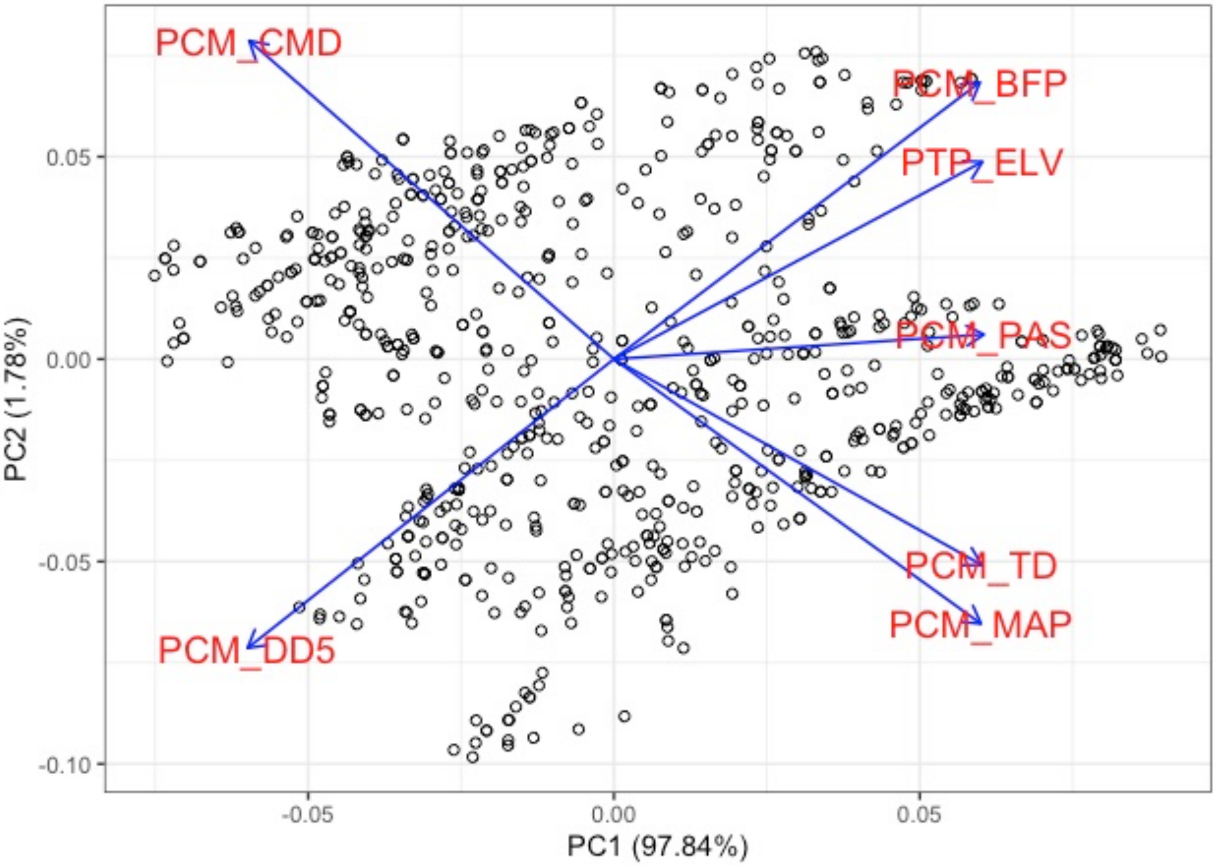

Figure S3. Partial dependence plots of predictor variable from Boosted Regression Tree of $NDVI_{CV}$ presence-absence. Density (pink) above each plot represents the distribution of data and vertical lines show the 5th and 95th percentile.
Age = Stand age, Aspect = Aspect, BDR = soil probability of bedrock, CAR = soil organic carbon, DD5 = accumulated degree days above 5C, DIS = log transformed distance to surface water, MAP = Mean annual precipitation, MRA = Estimate actual (with cloud) solar radiation, PHO = surface soil pH in H2O, Slope = slope, SND = surface soil percent sand, SOL = Annual potential solar radiation, THI = Topographic heat load index, TPI = topographic position index, TWI = Topographic wetness index,

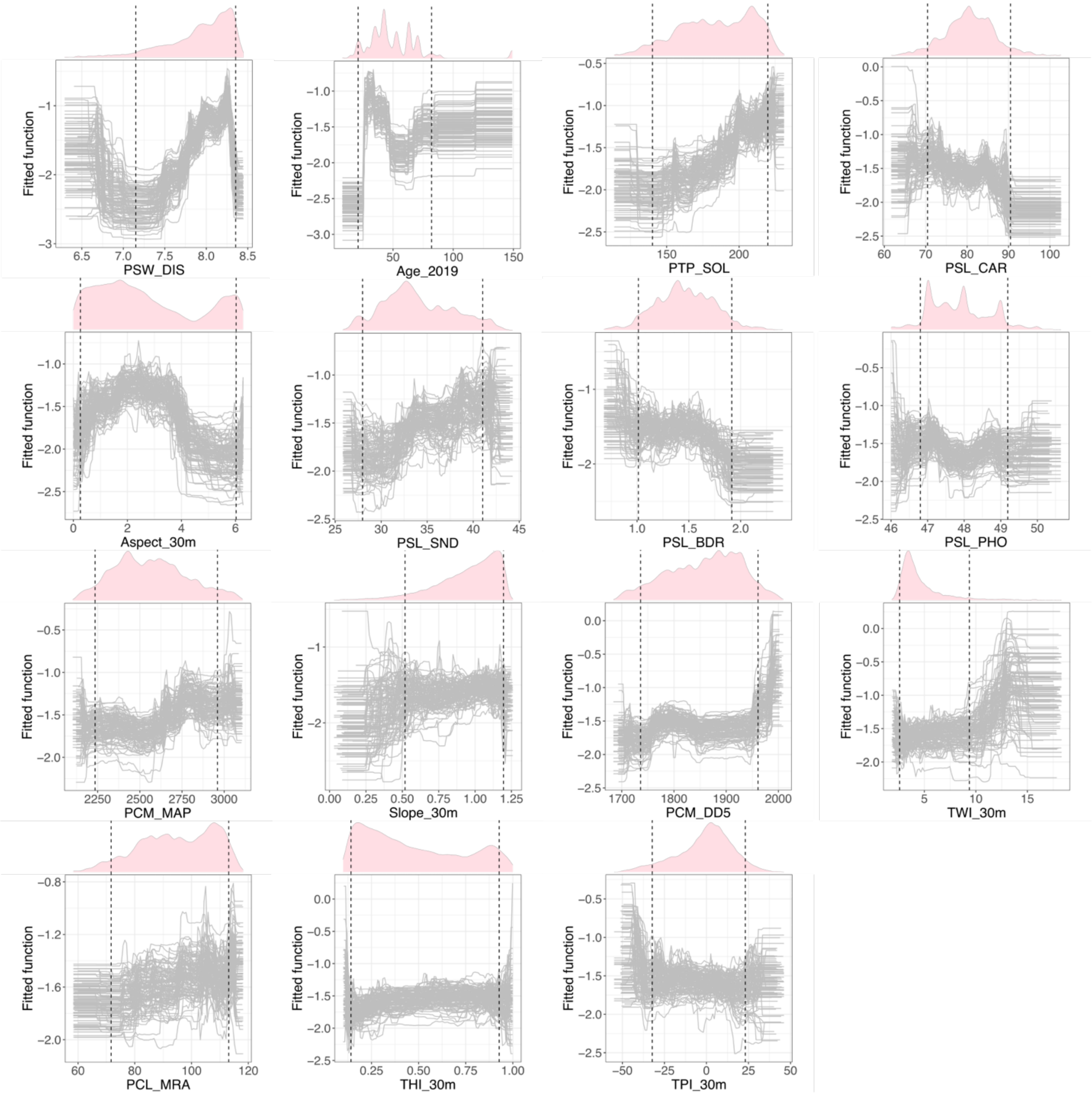

Figure S4. Partial dependence plots of predictor variable from Boosted Regression Tree of $NDMI_{CV}$ presence-absence. Density (pink) above each plot represents the distribution of data and vertical lines show the 5th and 95th percentile.
Age = Stand age, Aspect = Aspect, BDR = soil probability of bedrock, CAR = soil organic carbon, DD5 = accumulated degree days above 5C, DIS = log transformed distance to surface water, MAP = Mean annual precipitation, MRA = Estimate actual (with cloud) solar radiation, PHO = surface soil pH in H2O, Slope = slope, SND = surface soil percent sand, SOL = Annual potential solar radiation, THI = Topographic heat load index, TPI = topographic position index, TWI = Topographic wetness index

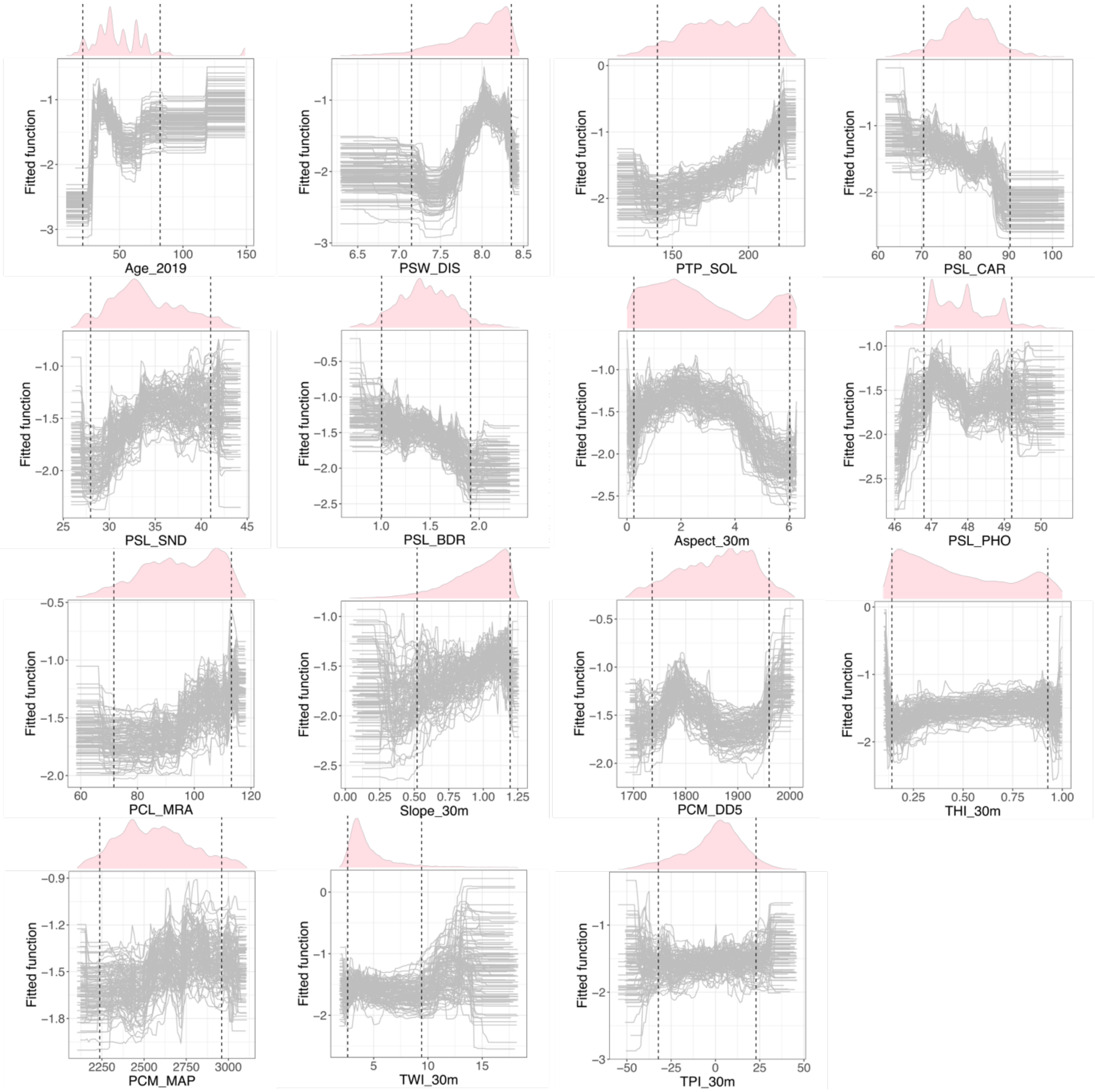

Figure S5. Distribution of stand ages in Ellsworth. Stand ages were computed for 2019.

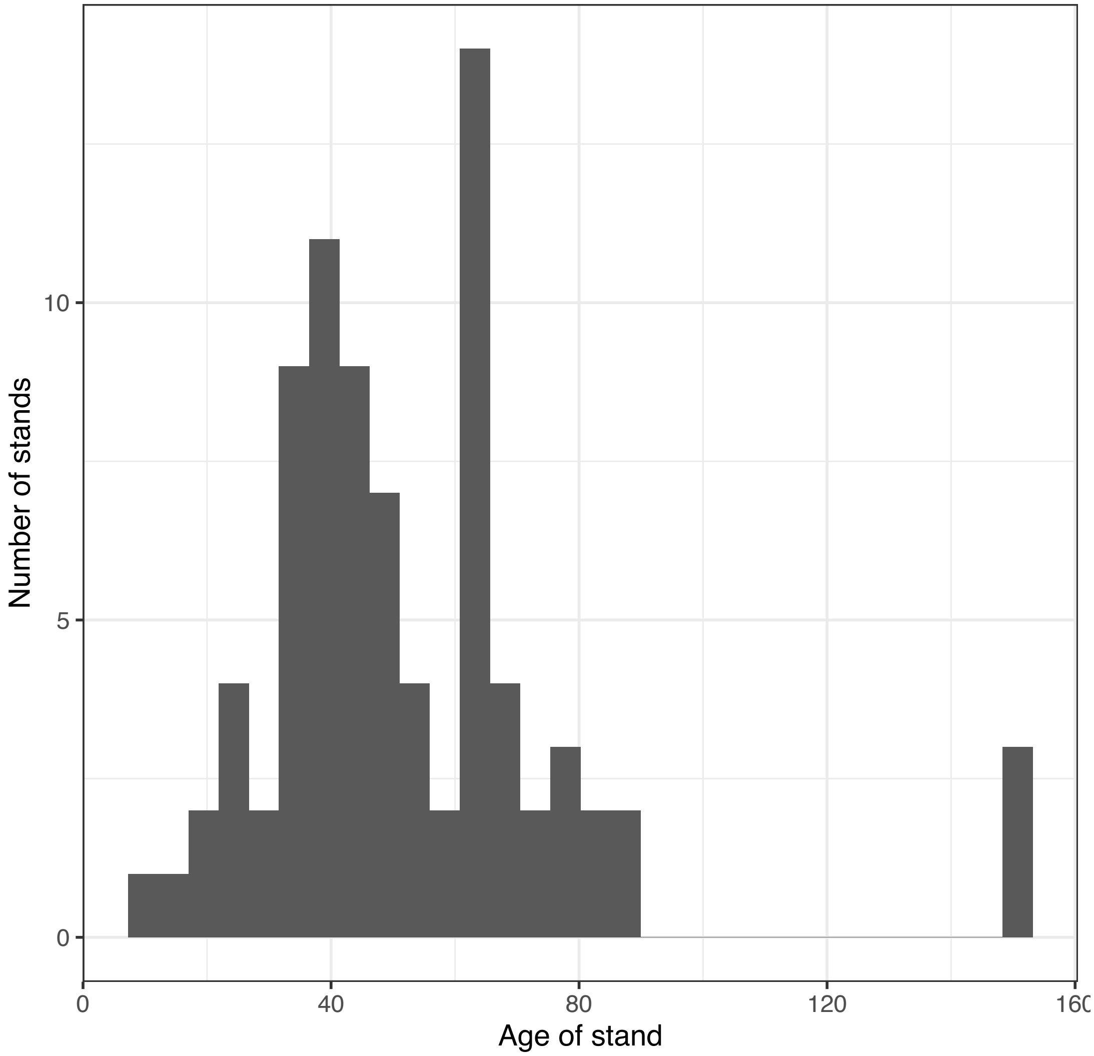

Figure S6. Patterns of mean NDVI across study period. Each facet represents a stand of a specific age group with each line representing a single pixel.

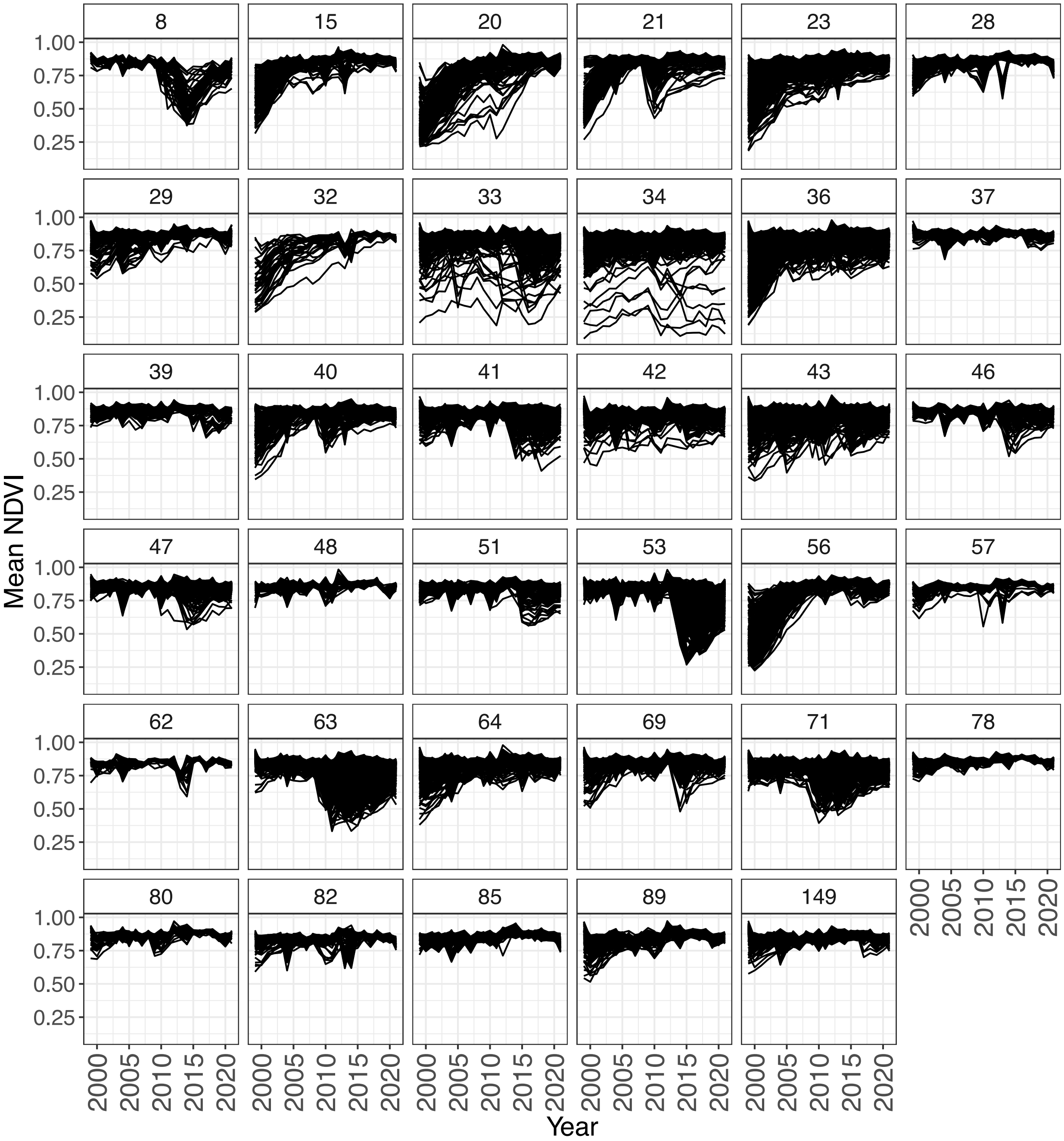

Figure S7. Patterns of mean NDMI across study period. Each facet represents a stand of a specific age group with each line representing a single pixel.

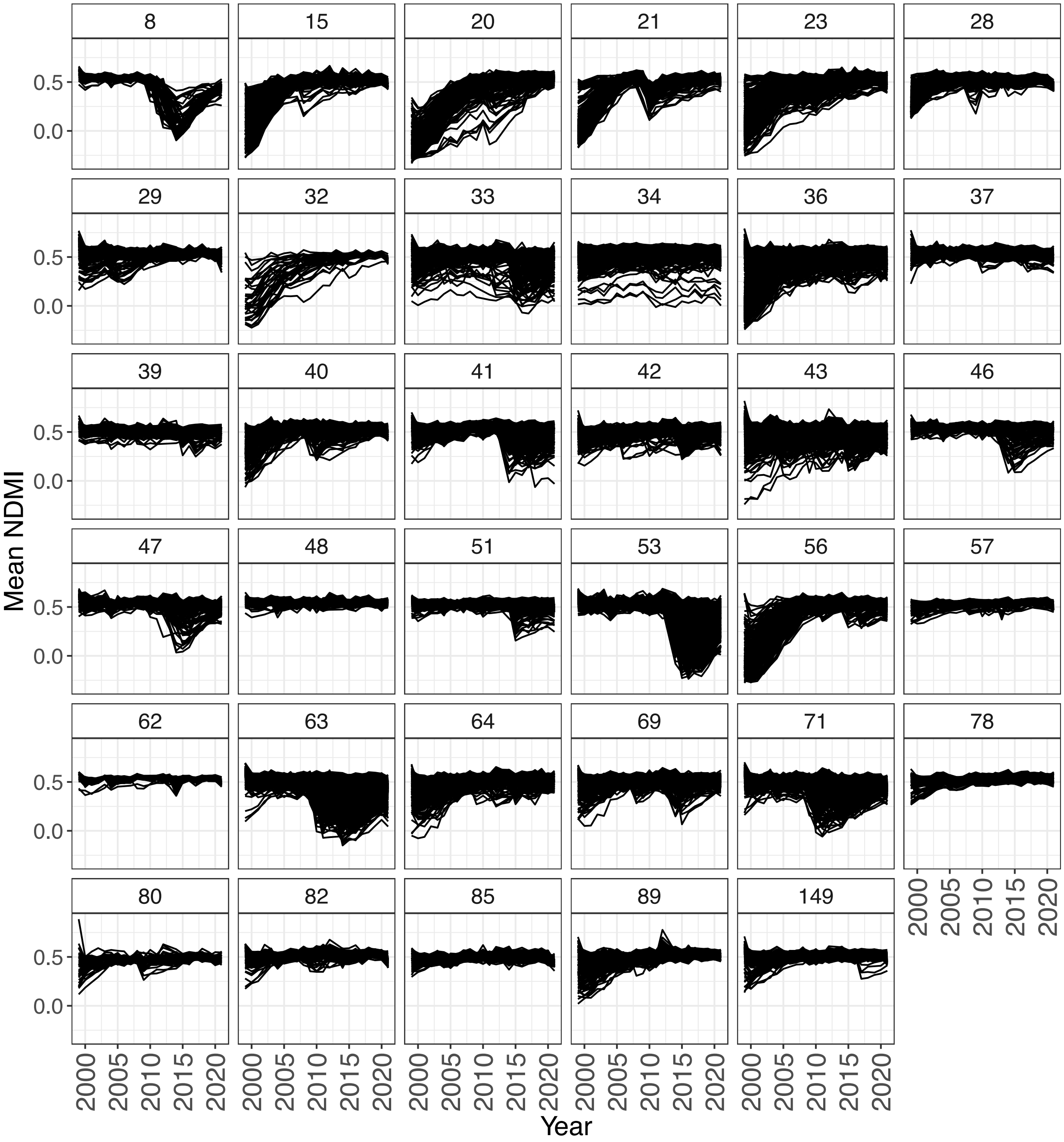

Table S3. Model results from Spatial Error Model to assess the influence of stand age, treatment type, and their interaction on the change in coefficient of variation of vegetation indices (NDVI and NDMI) pre- and post- thinning. Stands that had mixed treatments (i.e., stands in control and thinned basins with decommissioned roads) were excluded in this analysis. All pixels within remaining experimental stands were used in the analyses with a neighborhood distance of 45m. Statistically significant predictors ($p < 0.05$) are greyed out in the table for easier visualization.

Vegetation indices	Parameters	Estimate	Std. Error	z-value	Pr(>|z|)
Change in NDVI$_{CV}$	Intercept	-3.569	0.566	-6.304	02.892 e^{-10}
	Stand age	0.008	0.006	1.348	0.178
	Treatment (Thinning)	-0.137	0.663	-0.207	0.836
	Treatment (Decommisioned roads)	-1.689	0.587	-2.877	0.004
	Stand age X Thinning	0.000	0.009	0.024	0.981
	Stand age X Decommisioned roads	0.018	0.006	2.697	0.007
Change in NDMI$_{CV}$	Intercept	-16.822	8.696	-1.934	0.053
	Stand age	0.207	0.170	1.217	0.224
	Treatment (Thinning)	-20.222	12.991	-1.556	0.120
	Treatment (Decommisioned roads)	-50.734	10.764	-4.713	2.439 e^{-6}
	Stand age X Thinning	0.443	0.250	1.772	0.076
	Stand age X Decommisioned roads	0.363	0.191	1.902	0.057

CONCLUSION

Climate change is pushing already vulnerable forests towards even more reduced resilience. To counter this challenge, we must better understand how forests are changing, what the implications are, and how to combine new management approaches alongside traditional management practices. In this dissertation, I examined conifer leaf traits and forest communities in the Pacific Northwest region of the United States. In Chapter 1, our findings indicate that species turnover may be required for these coniferous forests to effectively respond to climate change and maintain ecosystem functions. Our Chapter 2 work shows that plant communities are indeed changing in response to climate change and are becoming more heterogenous (dissimilar from contemporary communities) and more novel (combinations of species that are not commonly found together). Taken together, these results are concerning as delays in community shifts and rearrangement of community composition has the potential to alter ecosystem function. However, our work in Chapter 3 provides us with a potential path forward. We found that we can manage forests for the dual goals of old-growth habitat restoration and climate change adaptation, by assessing the synergy between current management strategies and climate change refugia. Overall, this body of work demonstrates the value of examining communities in the present and the past to guide the future.