Title

Understanding How Regeneration Traits Mediate Chaparral Post-Fire Recovery and Restoration

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Understanding How Regeneration Traits Mediate Chaparral Post-Fire Recovery and Restoration

A Dissertation submitted in partial satisfaction
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in

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by

Meg Kargul

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Dedication

I dedicate this dissertation to my mom, Janice Kargul. Although no longer with us, her passion, dedication, and kindness continues to inspire me.

ABSTRACT OF THE DISSERTATION

Understanding How Regeneration Traits Mediate Chaparral Post-Fire Recovery and Restoration

by

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Doctor of Philosophy Graduate Program in Plant Biology
University of California, Riverside, March 2024
Dr. Loralee Larios, Chairperson

With increasing alterations to disturbance regimes, understanding the mechanisms that mediate community recovery is vital to prevent habitat degradation. Plant traits can link responses from individuals across multiple levels of ecological processes to predict community recovery, but this may be contingent on selecting the right trait at the right life stage and scale of environmental gradient or the diversity of traits and functional strategies. Regeneration traits (early life stage traits), which often differ from adult traits, may be more indicative of successful establishment post-disturbance, yet are not used to predict recovery and rarely used in restoration of degraded habitats. Therefore, I aimed to assess how regeneration traits mediate post-fire recovery and restoration in chaparral shrublands. I asked 1) how regeneration and adult traits differ and which are more predictive of recovery, 2) how spatial scale influences trait filtering and variation at different life stages, and 3) how regeneration trait functional strategies and restoration timing influence restoration success. To assess life stage trait differences, I collected functional traits for regenerating plants within multiple burn scars and for adults in nearby unburned areas in Southern California. To link traits to recovery, I measured community composition and survival over multiple years. To test the influence of spatial scales, I used the trait same sampling design across a regional scale elevation gradient and within different local scale aspects. To test chaparral restoration methods, I planted shrubs with different regeneration trait functional strategies (i.e., acquisitive, conservative, diverse) into burn scars at different times since fire. I found regeneration traits were more resource-acquisitive than adult traits, and the functional diversity of regeneration traits, but not adult traits, predicted recovery (Q1). Regeneration traits were more strongly filtered at the regional scale and had different drivers of trait variation compared to adults (Q2). The conservative regeneration trait functional strategy had higher survival one year post-planting, and planting sooner after fire improved restoration success (Q3). Overall, this work first highlights how regeneration traits can be used to improve community recovery predictions, and provides experimental evidence to improve post-fire restoration outcomes using a trait-based approach.

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Introduction

With increasing alterations to disturbance regimes, recovery mechanisms must be better understood to prevent habitat type conversion (D'Antonio and Vitousek 1992; Houghton et al. 2001; Park and Jenerette 2019). Disturbances regularly result in heterogeneous recovery from the mosaic of disturbance severity and environmental gradients present across a landscape (White and Jentsch 2004). This heterogeneous recovery can shift community states, variation in community response (dispersion), and recovery capacities (Pickett and White 1985; Houseman et al. 2008). With ongoing environmental change such as climate change driven hotter droughts increasing background mortality and disturbance severity (e.g., fire severity; Allen et al. 2015) and increased disturbance frequency from anthropogenic causes (e.g., increased fire frequency from human ignitions; Balch et al. 2017), this heterogeneity can result in areas vulnerable to stalled recovery and habitat conversion (Guiterman et al. 2022). Thus, predicting how communities respond to disturbances is a pressing ecological need especially in light of altered disturbance regimes and associated global climate change (Turner and Gardner 2015; Syphard et al. 2022).

Plant strategies and their corresponding traits are key to understanding how communities respond to disturbances and environmental gradients (Grime 1977; Suding et al. 2008; Mori et al. 2013). The application of functional traits - characteristics of a plant that are important in their response to the environment and their effect on ecosystem properties (e.g., specific leaf area, height, seed mass; Westoby et al. 2002) - are increasingly used to improve predictions of community responses to environmental gradients and disturbances (Díaz et al. 1999; Lavorel and Garnier 2002; McGill et al. 2006; Mouillot et al. 2013). Thus far, plant traits taken from adults have primarily been utilized to predict community response to disturbance and global climate change (for example see Frenette-Dussault et al. 2013; Kimball et al. 2016); however, plant traits at early life stages regenerating from disturbances can differ from those later in life for long-lived species (Spasojevic et al. 2014; Dayrell et al. 2018). Early life stage traits, also known as regeneration traits, can be integral to the recovery process as these traits may dictate successful establishment and survival under post-disturbance stressors (Larson and Funk 2016; Zirbel and Brudvig 2020; Arend da Silva et al. 2020). Moreover, to use any trait to predict recovery, it is integral that individual trait performance be linked to demographic processes (e.g., survival, growth), an important but often overlooked step (Cadotte et al. 2015; Laughlin et al. 2020). The long-term resilience of a system (i.e., the ability of a system to absorb a disturbance and reorganize similar structure, function, and relationships as the pre-disturbance state; Holling 1973; Elmqvist et al. 2003; Suding 2011) is further mediated by the overall diversity of functional traits and strategies (functional diversity) within the system (Elmqvist et al. 2003). Thus, incorporating regeneration traits that are linked to key demographic processes and functional diversity into our assessments of recovery is key to increasing our predictive capacity.

The inference gained from trait-based approaches is dependent on identifying the relevant scale and source of trait variation (Violle et al. 2012; Laughlin et al. 2012; Shipley et al. 2016), as predicting community recovery is a complex problem dependent on ecological processes acting at different spatial scales (Chase 2014). The spatial scale of an environmental gradient can differentially influence trait variation, such that regional scale gradients create more trait variation at the species level (i.e., interspecific variation) while local scale gradients create more trait variation at the individual level (i.e., intraspecific variation; Lajoie and Vellend 2015). However, less research has focused on disentangling how drivers of trait variation (e.g., adaptive trait variation at the species vs individual level) differ between early life stage and adult plants compared to the influence of environmentally driven trait variation. Identifying drivers of trait variation at the regeneration stage will aid in more accurate predictors of recovery, as niche requirements shift through ontogeny (Li et al. 2019). Therefore, identifying how life stage and spatial scale together drive trait variation will improve our ability to apply trait-based approaches to predicting recovery.

The increasing threat of habitat type conversions due to altered disturbance regimes and climate change has created a pressing need for restoration (Park and Jenerette 2019; Guiterman et al. 2022; Syphard et al. 2022). Underlying ecological processes can change when disturbance regimes are altered, resulting in altered recovery (Falk et al. 2022) and failed or unintended outcomes in restoration (Allen et al. 2018; Engel et al. 2019; Brambila et al. 2022). The application of trait-based approaches can be used to achieve functional and compositional restoration goals within ecosystem management (Laughlin 2014; Perring et al. 2015; Gornish et al. 2023), and the restoration of communities resilient to disturbance, defined as the ability to recover and adapt post-disturbance, may offer solutions to stalled recovery and habitat type conversions (Millar et al. 2007; Falk et al. 2022; Ren and Coffman 2023). Traits can be used to select species with functional strategies that relate to restoration goals (e.g., acquisitive strategies to promote rapid establishment, conservative strategies to promote survival in harsh environments; Funk et al. 2008), but experimentally testing functional strategy species palettes is needed to improve restoration success (Perring et al. 2015). Matching the right trait to the right environment can improve seedling success during restoration (Balazs et al. 2020). Therefore, it is important to consider that as recovery operates at the regeneration stage, regeneration traits should be leveraged in post-disturbance restoration (Zirbel and Brudvig 2020) and as resource conditions change post-disturbance, the timing of restoration may further impact the success of trait strategies and restoration outcomes (Brudvig 2011). Thus, assessing how regeneration trait-based approaches can improve planting success in different times since disturbance scenarios may improve restoration outcomes.

The post-fire setting is an ideal system for understanding mechanisms of heterogeneous recovery. Fires implicitly create spatial and temporal heterogeneity that influence community composition and recovery capacity (Christensen 1985). How a species responds to disturbances via regeneration strategies can help mediate and maintain recovery (Keeley 2018). Post-fire regeneration strategies include resprouting from stored energy or recruiting as seedlings, where species can exist on a continuum of obligate (only one strategy) to facultative (employ multiple strategies; Bond and Midgley 2001; Pausas et al. 2004). However, increasing fire frequency and prolonged drought conditions are resulting in weakened recovery and habitat type conversions, such as from shrublands to grasslands (Keeley and Brennan 2012; Syphard et al. 2019; Park and

Jenerette 2019). Shorter fire return intervals reduce recovery when seed banks are not replenished (Zedler et al. 1983), and the added stress from drought increases seedling susceptibility to mortality (Jacobsen and Pratt 2018). This reduced recovery can result in a loss of ecosystem function and services (e.g., high soil erosion risk from lack of soil stabilizing vegetation; Underwood et al. 2022), creating a pressing need for restoration. Restoration of fire-prone habitats, such as chaparral, have largely been unsuccessful (Allen et al. 2018), creating a need to study post-fire regeneration in a new way. The quantification of regeneration traits and evaluation of their function in heterogeneous post-disturbance recovery is needed to improve recovery predictions and restoration success.

Thus, the goal of this dissertation is to understand how regeneration traits mediate post-fire recovery and restoration. Within chaparral ecosystems, I ask 1) how do regeneration traits and their diversity predict post-fire recovery, 2) how does spatial scale influence trait filtering and variation at different life stages, and 3) how do regeneration trait functional strategies and restoration timing influence restoration success?

References

Allen, C. D., 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), art129. https://doi.org/10.1890/es15-00203.1

Allen, E. B., Williams, K., Beyers, J. L., Phillips, M., Ma, S., & D'Antonio, C. M. (2018). Chaparral Restoration. In E. C. Underwood, H. D. Safford, N. A. Molinari, & J. E. Keeley (Eds.), *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives* (pp. 347–384). Springer International Publishing. https://doi.org/10.1007/978-3-319-68303-4_13

Arend da Silva, I., Guido, A., & Müller, S. C. (2020). Predicting plant performance for the ecological restoration of grasslands: the role of regenerative traits. *Restoration Ecology*, *28*(5), 1183–1191. https://doi.org/10.1111/rec.13182

Balazs, K. R., Kramer, A. T., Munson, S. M., Talkington, N., Still, S., & Butterfield, B. J. (2020). The right trait in the right place at the right time: Matching traits to environment improves restoration outcomes. *Ecological Applications: A Publication of the Ecological Society of America*, *30*(4), e02110. https://doi.org/10.1002/eap.2110

Balch, J. K., Bradley, B. A., Abatzoglou, J. T., Nagy, R. C., Fusco, E. J., & Mahood, A. L. (2017). Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(11), 2946–2951. https://doi.org/10.1073/pnas.1617394114

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution*, *16*(1), 45–51. https://doi.org/10.1016/s0169-5347(00)02033-4

Brambila, A., Reed, P. B., Bridgham, S. D., Roy, B. A., Johnson, B. R., Pfeifer-Meister, L., & Hallett, L. M. (2022). Disturbance: a double-edged sword for restoration in a changing climate. *Restoration Ecology*, *31*(1). https://doi.org/10.1111/rec.13675

Brudvig, L. A. (2011). The restoration of biodiversity: where has research been and where does it need to go? *American Journal of Botany*, *98*(3), 549–558. https://doi.org/10.3732/ajb.1000285

Cadotte, M. W., Arnillas, C. A., Livingstone, S. W., & Yasui, S.-L. E. (2015). Predicting communities from functional traits. *Trends in Ecology & Evolution*, *30*(9), 510–511. https://doi.org/10.1016/j.tree.2015.07.001

Chase, J. M. (2014). Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science*, *25*, 319–322. https://onlinelibrary.wiley.com/doi/full/10.1111/jvs.12159

Christensen, N. L. (1985). Shrubland Fire Regimes and Their Evolutionary Consequences. In *The Ecology of Natural Disturbance and Patch Dynamics* (pp. 85–100). https://doi.org/10.1016/b978-0-12-554520-4.50011-3

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics, 23*(1), 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H., & Silveira, F. A. O. (2018). Ontogenetic shifts in plant ecological strategies. *Functional Ecology, 32*(12), 2730–2741. https://doi.org/10.1111/1365-2435.13221

Díaz, S., Cabido, M., & Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. *Ecological Assembly Rules: Perspectives, Advances, Retreats*, 338–362. https://books.google.com/books?hl=en&lr=&id=RIZDYJ0zKaAC&oi=fnd&pg=PA338&dq=diaz+1999+functional+implications&ots=JkEnT7CYUE&sig=AQQDj3js41g5vLcTDE_-GXuVEg0

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment, 1*(9), 488–494. https://doi.org/10.1890/1540-9295(2003)001[0488:rdecar]2.0.co;2

Engel, M. D., Williams, K., McDonald, C. J., & Beyers, J. L. (2019). The feasibility of chaparral restoration on type-converted slopes. *Proceedings of the Chaparral Restoration Workshop, California. Gen. Tech. Rep. PSW-GTR-265. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 37-49, 265*, 37–49. https://www.fs.usda.gov/treesearch/pubs/58587

Falk, D. A., van Mantgem, P. J., Keeley, J. E., Gregg, R. M., Guiterman, C. H., Tepley, A. J., JN Young, D., & Marshall, L. A. (2022). Mechanisms of forest resilience. *Forest Ecology and Management, 512*, 120129. https://doi.org/10.1016/j.foreco.2022.120129

Frenette-Dussault, C., Shipley, B., Meziane, D., & Hingrat, Y. (2013). Trait-based climate change predictions of plant community structure in arid steppes. *Journal of Ecology, 101*(2), 484–492. https://doi.org/10.1111/1365-2745.12040

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution, 23*(12), 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Gornish, E. S., Campbell, C., Svejcar, L., Munson, S. M., Vaughn, K., Spaeth, M. K., Yelenik, S. G., Wolf, A., & Mitchell, R. (2023). Functional traits are used in restoration practice: a response to Merchant et al. (2022). *Restoration Ecology, 31*(7). https://doi.org/10.1111/rec.13880

Grime. (1977). Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist, 111*(982), 1169–1194. http://www.jstor.org/stable/2460262

Guiterman, C. H., Gregg, R. M., Marshall, L. A. E., Beckmann, J. J., van Mantgem, P. J., Falk, D. A., Keeley, J. E., Caprio, A. C., Coop, J. D., Fornwalt, P. J., Haffey, C., Hagmann, R. K., Jackson, S. T., Lynch, A. M., Margolis, E. Q., Marks, C., Meyer, M. D., Safford, H., Syphard, A. D., … Stevens, J. T. (2022). Vegetation type conversion in the US Southwest: frontline observations and management responses. *Fire Ecology, 18*(1), 6. https://doi.org/10.1186/s42408-022-00131-w

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics, 4*(1), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., & Johnson, C. A. (2001). *Climate change 2001: the scientific basis*. The Press Syndicate of the University of Cambridge. http://cedadocs.ceda.ac.uk/981/8/Chapter_7.pdf

Houseman, G. R., Mittelbach, G. G., Reynolds, H. L., & Gross, K. L. (2008). Perturbations alter community convergence, divergence, and formation of multiple community states. *Ecology, 89*(8), 2172–2180. https://doi.org/10.1890/07-1228.1

Jacobsen, A. L., & Pratt, R. B. (2018). Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands. *The New Phytologist, 219*(2), 498–504. https://doi.org/10.1111/nph.15186

Keeley, J. E. (2018). Drivers of Chaparral Plant Diversity. In E. C. Underwood, H. D. Safford, N. A. Molinari, & J. E. Keeley (Eds.), *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives* (pp. 29–51). Springer International Publishing. https://doi.org/10.1007/978-3-319-68303-4_2

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia, 169*(4), 1043–1052. https://doi.org/10.1007/s00442-012-2253-8

Kimball, S., Funk, J. L., Spasojevic, M. J., Suding, K. N., Parker, S., & Goulden, M. L. (2016). Can functional traits predict plant community response to global change? *Ecosphere , 7*(12), e01602. https://doi.org/10.1002/ecs2.1602

Lajoie, G., & Vellend, M. (2015). Understanding context dependence in the contribution of intraspecific variation to community trait–environment matching. *Ecology, 96*(11), 2912–2922. https://doi.org/10.1890/15-0156.1

Larson, J. E., & Funk, J. L. (2016). Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, *104*(5), 1284–1298. https://doi.org/10.1111/1365-2745.12613

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, *17*(7), 771–784. https://doi.org/10.1111/ele.12288

Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M., & Moore, M. M. (2020). The Net Effect of Functional Traits on Fitness. *Trends in Ecology & Evolution*, *35*(11), 1037–1047. https://doi.org/10.1016/j.tree.2020.07.010

Laughlin, D. C., Joshi, C., van Bodegom, P. M., Bastow, Z. A., & Fulé, P. Z. (2012). A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*, *15*(11), 1291–1299. https://doi.org/10.1111/j.1461-0248.2012.01852.x

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

Li, Y., Bin, Y., Xu, H., Ni, Y., Zhang, R., Ye, W., & Lian, J. (2019). Understanding Community Assembly Based on Functional Traits, Ontogenetic Stages, Habitat Types and Spatial Scales in a Subtropical Forest. *Forests, Trees and Livelihoods*, *10*(12). https://doi.org/10.3390/f10121055

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications: A Publication of the Ecological Society of America*, *17*(8), 2145–2151. https://doi.org/10.1890/06-1715.1

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews of the Cambridge Philosophical Society*, *88*(2), 349–364. https://doi.org/10.1111/brv.12004

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Park, I. W., & Jenerette, G. D. (2019). Causes and feedbacks to widespread grass invasion into chaparral shrub dominated landscapes. *Landscape Ecology*, *34*(3), 459–471. https://doi.org/10.1007/s10980-019-00800-3

Pausas, J. G., Bradstock, R. A., Keith, D. A., & Keeley, J. E. (2004). Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, *85*(4), 1085–1100. https://doi.org/10.1890/02-4094

Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof, K. X., Whiteley, A. S., Valentine, L. E., & Hobbs, R. J. (2015). Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere* , *6*(8), art131. https://doi.org/10.1890/es15-00121.1

Pickett, S. T. A., & White, P. S. (1985). Chapter 21 - Patch Dynamics: A Synthesis. In S. T. A. Pickett & P. S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics* (pp. 371–384). Academic Press. https://doi.org/10.1016/B978-0-12-554520-4.50026-5

Ren, J. W. F., & Coffman, G. C. (2023). Integrating the resilience concept into ecosystem restoration. *Restoration Ecology*. https://doi.org/10.1111/rec.13907

Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, *180*(4), 923–931. https://doi.org/10.1007/s00442-016-3549-x

Spasojevic, M. J., Yablon, E. A., Oberle, B., & Myers, J. A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* , *5*(10), art129. https://doi.org/10.1890/ES14-000159.1

Suding, K. N. (2011). Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Suding, K. N., Lavorel, S., Chapin, F. S., III, Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., & Navas, M.-L. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, *14*(5), 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Syphard, A. D., Brennan, T. J., & Keeley, J. E. (2019). Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Diversity and Distributions*, *25*(1), 90–101. https://doi.org/10.1111/ddi.12827

Syphard, A. D., Brennan, T. J., Rustigian-Romsos, H., & Keeley, J. E. (2022). Fire-driven vegetation type conversion in Southern California. *Ecological Applications: A Publication of the Ecological Society of America*, *32*(6), e2626. https://doi.org/10.1002/eap.2626

Turner, M. G., & Gardner, R. H. (2015). *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer, New York, NY. https://doi.org/10.1007/978-1-4939-2794-4

Underwood, E. C., Hollander, A. D., Molinari, N. A., Larios, L., & Safford, H. D. (2022). Identifying priorities for post-fire restoration in California chaparral shrublands. *Restoration Ecology*, *30*(3). https://doi.org/10.1111/rec.13513

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. In *Trends in Ecology & Evolution* (Vol. 27, Issue 4, pp. 244–252). https://doi.org/10.1016/j.tree.2011.11.014

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics*, *33*(1), 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

White, P. S., & Jentsch, A. (2004). Disturbance, succession, and community assembly in terrestrial plant communities. In Temperton, V. M., Hobbs, R. J., Nuttle, T., & Halle, S. (Ed.), *Assembly rules and restoration ecology: bridging the gap between theory and practice* (Vol. 5, pp. 342–366). Island Press. https://books.google.com/books?hl=en&lr=&id=BQm8BwAAQBAJ&oi=fnd&pg=PA342&dq=Disturbance+succession+community+assembly+terrestrial+plant+communities+White+Jentsch&ots=JV4Jy46-Yk&sig=QCSebFHZrgY9JGjQ39WKkHVT9BA

Zedler, P. H., Gautier, C. R., & McMaster, G. S. (1983). Vegetation Change in Response to Extreme Events: The Effect of a Short Interval between Fires in California Chaparral and Coastal Scrub. *Ecology*, *64*(4), 809–818. https://doi.org/10.2307/1937204

Zirbel, C. R., & Brudvig, L. A. (2020). Trait–environment interactions affect plant establishment success during restoration. *Ecology*, *101*(3), e02971. https://doi.org/10.1002/ecy.2971

Chapter 1: The influence of regeneration traits and topography on chaparral post-fire recovery

Abstract

With increasing alterations to disturbance regimes, understanding recovery mechanisms is vital to prevent habitat degradation. Plant traits can link responses from individuals across multiple levels of ecological processes to predict community recovery, but this may be contingent on selecting the right trait at the right life stage or the diversity of traits and functional strategies. Regeneration traits (early life stage traits), which often differ from adult traits, may be more indicative of successful establishment post-disturbance. We assessed the role of regeneration traits and strategies (i.e. resprouters, seeders) mediating post-fire chaparral shrub recovery across a topographic gradient at the population and community scale in the Cleveland National Forest, California. We collected 6 leaf functional traits for regenerating and adult plants of 16 species across Northeast and Southwest aspects within and outside a wildfire burn scar. We surveyed survival and community composition within these communities during initial post-fire recovery. We found functional traits differed across life stages but not aspects, where regenerating individuals were more resource acquisitive than adults. Traits mediated population performance for seeders but not resprouters, where regeneration height mediated survival while % leaf nitrogen mediated growth. Regeneration strategies drove community recovery over time, where resprouters had higher cover than seeders in year one, but by year two, cover was similar across strategies, which was driven by the higher density and acquisitive resource-use strategy of seeders compared to resprouters. The

diversity of regeneration traits were more predictive of recovery than adult trait diversity, indicating the functional diversity of establishing plants can mediate recovery. We demonstrated how traits scale to influence post-fire recovery, and the diversity of regeneration traits is key to increasing recovery.

Introduction

Alterations to disturbance regimes are reducing ecosystem's recovery capacity, leading to more frequent habitat type conversions and a need for improved understanding of recovery mechanisms to aid conservation efforts (White 1979, Pickett and White 1985, D'Antonio and Vitousek 1992, Park and Jenerette 2019). Predicting community recovery is a complex problem dependent on multiple ecological processes acting across large temporal and spatial scales (Cowles 1899, Connell and Slatyer 1977, Walker and del Moral 2003, Chang and HilleRisLambers 2016). Plant traits have been proposed as the key to create linkages across multiple levels of ecological processes (Suding et al. 2003, Funk et al. 2017) to improve our understanding of recovery (Suding et al. 2008, Mori et al. 2013). Yet, scaling responses from a population level to community and landscape level is challenging as trait relationships with demographic processes may shift depending on the demographic process (Laughlin et al. 2020) or the life stage (Larson and Funk 2016, Larson et al. 2021). Additionally, these trait and demographic process relationships may be further mediated by underlying environmental variation (Carmona et al. 2016, Browne et al. 2023). Taken together, these relationships between traits and demographic processes at different life stages and environmental conditions can drive community composition (Westerband and Horvitz 2017, Salguero-Gómez and Laughlin

2021), impacting variation in recovering systems. Thus, improving our understanding of recovery is contingent on being able to create linkages for traits across these multiple processes.

Linking individual trait performance and demographic processes (e.g. survival, growth) is an important but often overlooked step to predict recovery (Cadotte et al. 2015, Laughlin et al. 2020). While recovery operates at the regeneration life stage where differing demographic rates (i.e. establishment, growth, and survival) impact recovery, plant traits taken from adults are primarily utilized to predict community change (for example see Frenette-Dussault et al. 2013, Kimball et al. 2016). Early life stage traits, also known as regeneration traits, can be integral to the recovery process as these traits may dictate successful establishment and survival under post-disturbance stressors (Larson et al. 2015, Larson and Funk 2016, Zirbel and Brudvig 2020, Arend da Silva et al. 2020, Garbowski et al. 2021). Moreover, the importance of specific traits to demographic processes can differ over life stages with implications for recovery. For example, under drought conditions in shrublands, one year old seedlings more resistant to xylem cavitation experienced the lowest mortality (Pratt et al. 2008), while adult plants that were more resistant to xylem cavitation experienced higher mortality (Paddock et al. 2013). The importance of specific traits to demographic processes can also differ over regeneration strategies, where systems with repeated disturbances (i.e. natural disturbance regimes) put evolutionary pressure on species to develop different regeneration strategies to respond to the disturbance. For example, in shrublands with a fire disturbance regime, species exhibit regeneration strategies of resprouting from stored energy or recruiting as seedlings (Bond and Midgley 2001, Pausas et al. 2004). These species can exist on a continuum of obligate (only one strategy) to facultative (employ multiple strategies), where each strategy has different spatial and temporal fitness and survival benefits in relation to disturbances (Pausas and Keeley 2014). Thus, incorporating regeneration traits and regeneration strategies into our assessments of recovery is key to increasing our predictive capacity.

The diversity of functional traits and strategies (functional diversity) are also integral to ecosystem recovery and promote ecological resilience, defined as the ability of a system to absorb a disturbance and reorganize similar structure, function, and relationships as the pre-disturbance state (Holling 1973, Elmqvist et al. 2003, Suding 2011). A system with a diversity of post-disturbance functional strategies (i.e. response traits) can ensure short term recovery and long term resilience as the function of any species lost to disturbance and subsequent environmental conditions might be replaced by another functionally redundant species (Elmqvist et al. 2003, Spasojevic et al. 2016). At large spatial and temporal scales, broad functional diversity in regeneration strategies has been demonstrated to promote resilience to fires in woodlands (Spasojevic et al. 2016). However, the topographic complexity of many landscapes may result in some areas being more vulnerable to loss of this functional diversity. For example, the differing solar insolation across aspects that creates strong microclimate differences (Cooper 1922, Armesto and Martínez 1978, Dobrowski et al. 2009) can also impact post-fire regeneration where seedling establishment and resprout success are lower on drier, warmer equator-facing aspects (Kutiel 1997), potentially shifting functional diversity.

Assessing the diversity-resilience relationship at the regeneration stage in heterogeneous environments may identify areas vulnerable to lower recovery and resilience.

Recovery is structured by how abiotic and biotic factors at the regeneration stage interact in the initial year of recovery. The environment can select for certain traits (i.e. trait-environment interactions) in the initial regeneration year, setting the successional trajectory for recovery (i.e. what species and functional strategies survive and can pass through subsequent biotic filters; Funk et al. 2008). The post-disturbance environment can be flooded with resources (e.g. influx of nitrogen and light availability after a wildfire) where differing environmental conditions in pre and post disturbance communities may result in trait and resource-use strategy differences (e.g. acquisitive vs conservative) found between seedlings and adults in other studies (Laughlin et al. 2017, Dayrell et al. 2018, Harrison and LaForgia 2019), giving misleading results when adult traits are used to predict processes occurring at earlier life stages (Larson et al. 2015, Henn and Damschen 2021). Biotic interactions further impact demographic rates and recovery success, such that canopy cover can facilitate (via site amelioration) or limit establishment of water and light sensitive species, either increasing or decreasing resilience, respectively. Understanding how regeneration traits are mediated by first year post-fire conditions and testing their role in improving recovery predictions can provide deeper insight into the mechanisms driving variation in recovery.

In this study, we quantified regeneration traits of woody species and used them to predict post-fire recovery in chaparral. Chaparral has historically been auto-successional, or naturally returning to pre-disturbance compositions (Hanes 1971), with clear differences in functional strategies across topographically mediated microclimates. In Southern California chaparral, Northeast (poleward) facing aspects are cool, wet higher resource habitats (Cooper 1922) typically dominated by drought avoiding, resource acquisitive obligate resprouters (Parker et al. 2016). Southwest facing aspects are hot, dry low resource habitats (Cooper 1922) typically dominated by conservative resource-use obligate and facultative seeders (Parker et al. 2016). However, increasing fire frequency and prolonged drought conditions are resulting in weakened recovery and habitat type conversions from shrublands to grasslands in recent decades (Keeley and Brennan 2012, Syphard et al. 2019, Park and Jenerette 2019). Shorter fire return intervals reduce recovery when seed banks are not replenished (Zedler et al. 1983), and the added stress from drought increases seedling susceptibility to mortality (Jacobsen and Pratt 2018). This can be exacerbated on Southwest aspects (Parker et al. 2016) resulting in patchy recovery across the landscape. Previous work on chaparral post-fire functional traits have been on adults or individuals ranging across multiple years of recovery, not solely the first year after fire (Ackerly et al. 2002, Cornwell and Ackerly 2009, Anacker et al. 2011, but see Pratt et al. 2012 testing regeneration traits in a greenhouse experiment). This can lead to inaccurate recovery predictions if key recourse-use strategies (Dayrell et al. 2018) and assembly mechanisms (Spasojevic et al. 2014) are misidentified when traits are not ontogenetically conserved. Investigating how first-year regeneration traits compare to adult traits and influence recovery after fire has not been studied in chaparral, but improved recovery predictions could greatly benefit this increasingly threatened system.

To improve the capacity to scale across different dynamics contributing to variation in recovery, we designed an observational study to evaluate the role of regeneration traits and strategies across a topographic gradient in post-fire establishment and recovery of chaparral shrubs. We asked: 1) how do functional traits differ across life stage and aspect, 2) what regeneration traits and strategies mediate demographic rates (i.e. survival, growth), 3) how do regeneration traits and strategies link to recovery over aspect and time, and 4) are regeneration traits more predictive of recovery than adult traits? We did not include reproductive data in the demographic rate question since a majority of individuals had not reached maturity, therefore we focused on the key demographic rates of survival and growth to inform recovery.

Methods

Study Location

This study was conducted in chaparral shrublands in the Cleveland National Forest, Lake Elsinore, CA (33.67169, -117.459), which experienced a wildfire in 2018 (Holy Fire). The historic annual growing season (Oct. - Aug. from 1970-2022) total precipitation at the study location is 489.58 mm and mean temperature is 15.61 °C (PRISM Climate Group 2023), characteristic of the Mediterranean climate with cool, wet winters and hot, dry summers. During the study period, total growing season precipitation was 779.63 mm in 2019, 628.11 mm in 2020, 200.75 mm in 2021, and 338.54 mm in 2022. The mean annual growing season temperature was 14.98 °C in 2019, 15.98 °C in 2020, 15.88 °C in 2021, and 13.53 °C in 2022. Study sites ranged in elevation from 1014 m - 1307 m and consisted of Cieneba sandy loam, Cieneba-Rock outcrop complex, Friant fine sandy loam, and Tollhouse-Rock outcrop complex soil geology. The vegetation community was montane mixed chaparral (*Arctostaphylos glandulosa* and *Ceanothus* spp. dominant) and chamise chaparral (*Adenostoma fasciculatum* dominant; VinZant et al. 2018).

The Holy Fire burned 9,362 hectares from August 6, 2018 through September 13, 2018 and was caused by arson. The fire burned in a patchy mosaic pattern with small unburned areas remaining on the landscape. These unburned areas were used to compare traits of adult communities, in addition to unburned areas outside of the burn scar boundary. The majority of area (i.e. 85% of hectares burned) was in the moderate to high soil burn severity categories (Nicita and Halverson 2018). This wildfire was within the normal 30-100 year fire return interval for chaparral (Hanes 1971, Van de Water and Safford 2011), as the time since the last burn ranged from 38 to 64 years in the Holy Fire burn scar and 64 to 93 years in the nearby unburned areas (Department of Forest and Fire Protection CAL FIRE - Fire Perimeter data “Firep21_2”, https://www.fire.ca.gov/what-we-do/fire-resource-assessment-program/fire-perimeters).

Trait Data Collection

To determine tradeoffs in resource-use and growth strategies across life stages, regeneration strategies, and aspects, we measured a suite of traits that are indicative of resource-use strategies. We measured specific leaf area (SLA), leaf area (LA), leaf dry matter content (LDMC), % Nitrogen (N) content, and discrimination of $\delta^{13}C$, following standard functional trait protocols (Cornelissen et al. 2003). These traits were selected as SLA and LDMC are associated with a plant’s ability to acquire and use resources, while LA is associated with leaf energy and water balance while coping with temperature, drought, and nutrient stressors (Perez-Harguindeguy et al. 2013), and % N is indicative of photosynthetic capacity (Evans 1989). Discrimination of $\delta^{13}C$ is used as an indicator of intrinsic water use efficiency (iWUE) reflecting the efficiency of carbon gain through photosynthesis relative to water transpired (Farquhar et al. 1989). These traits are also associated with the leaf economic spectrum (Reich 2014) which captures key tradeoffs in acquisitive (high SLA, high LA, low LDMC, high % N, high discrimination of $\delta^{13}C$/low iWUE) vs conservative (low SLA, low LA, high LDMC, low % N, low discrimination of $\delta^{13}C$/high iWUE) resource-use strategies. For regenerating plants, we also measured height which is an indicator of competitive ability for light (Westoby et al. 2002).

We collected leaf functional traits from 5-17 individuals for each of 16 dominant regenerating species within the burn scar (regeneration traits) and for adult species in nearby unburned areas (adult traits) across Northeast (NE) and Southwest (SW) aspects (Table S1.1 collection coordinates, Table S1.2 species trait means). All regeneration traits were collected on less than one year old seedlings and aboveground biomass of resprouters (leaves collected at the end of the first growing season). Trait collections were done during scouting for community composition sites, thus some traits were collected at locations other than the composition sites. Regeneration strategy was recorded for each species as either seeder or resprouter, where facultative species were assigned based on their recruitment in the field (i.e. *Adenostoma fasciculatum* resprouter, *Adenostoma fasciculatum* seeder) in burned areas, but not in the unburned areas since it was not possible to tell if facultative species present originated as resprouters or seeders during the last disturbance.

After collection in the field, leaves were re-hydrated overnight in dark conditions to reach saturated wet weight. The following day, excess moisture was wiped off the saturated leaves, weighed to measure wet weight, then scanned to measure leaf area (ImageJ, https:// imagej.nih.gov/ij/). Leaves were dried at 60 °C for a minimum of 72 h then weighed to measure dry weight. These data were used to calculate SLA as fresh LA (cm^2) divided by dry weight (g) and LDMC as dry weight (mg) divided by wet weight (g). For isotope analysis, leaf tissue was ground at UC Riverside for a total of 3 replicates per species, aspect, and life stage and strategy comprised of leaves from 1-5 individuals. Leaf δ^{13}C and % N content were measured at the University of Wyoming Stable Isotope Facility (http://www.uwyo.edu/sif/) where samples were analyzed for δ^{13}C and % N on a Carlo Erba 1110 Elemental Analyzer coupled to a Thermo Delta V IRMS or a Costech 4010 Elemental Analyzer coupled to a Thermo Delta Plus XP IRMS. Isotope ratios were calculated as

$$\delta[\ 13C]samples = (\frac{R_{sample}}{R_{standard}} - 1)\ x\ 1000$$

where R$_{sample}$ and R$_{standard}$ are the δ^{13}C/^{12}C molar abundance ratios of samples, with 36-UWSIF-Glutamic 1 and 39-UWSIF-Glutamic 2 used as reference samples. Discrimination of δ^{13}C was calculated as

Discrimination of C^{13} = (-0.008 - (δ^{13}C * 0.001))/(1 + (δ^{13}C * 0.001))*1000

Where the discrimination of C^{13} is independent of the C^{13} values of both the standard used and the air, while δ^{13}C is relative to the standard used (Farquhar et al. 1989). Hereafter, discrimination of C^{13} will be denoted as δ^{13}C.

Demographic Performance and Recovery

We measured survival, recovery, and community functional strategy and diversity across burned sites on both NE and SW aspects. Potential sites were selected based on the presence of a NE and SW aspect, soil burn severity in the medium to high category to keep burn severity consistent, and accessibility by roads and hiking. Final site selection happened after a field visit to validate accessibility and ensure complete vegetation burn, for a total of six burned sites selected (Fig. 1.1). Each site contained a NE and SW aspect with two replicate 30 m transects per aspect type, for a total of 24 recovery transects evenly distributed across aspect types.

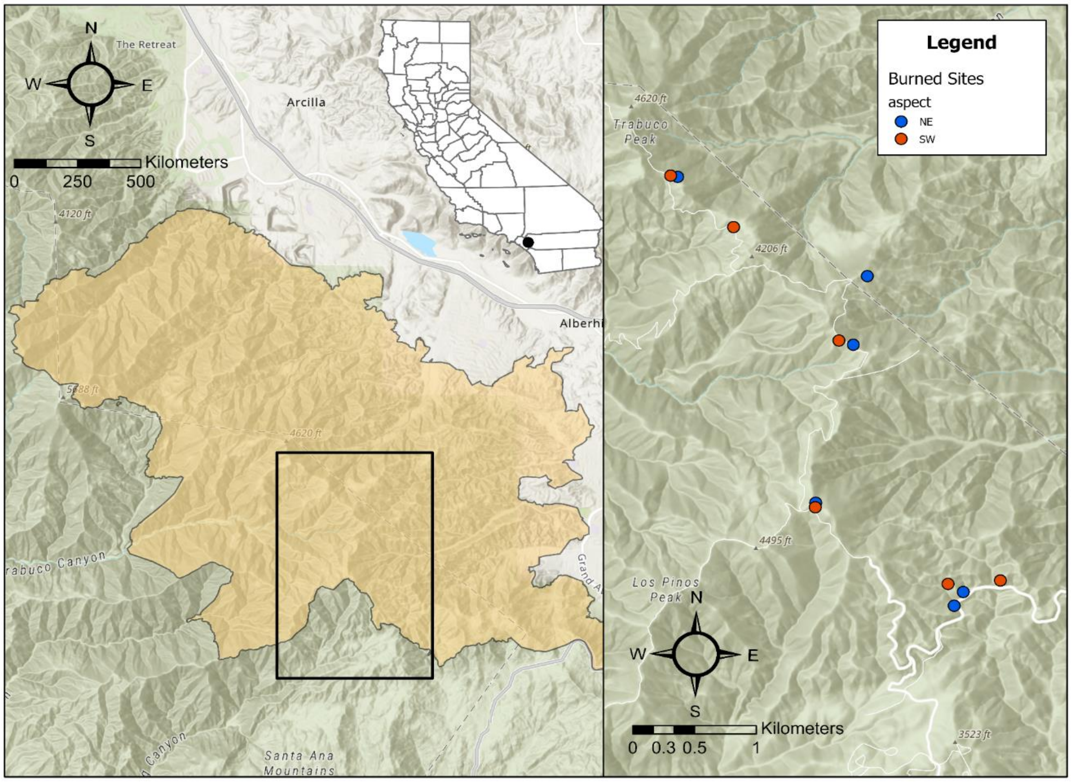

Figure 1.1 Map of the Holy Fire burn scar (left) and burned study sites distributed across Northeast (NE, blue points) and Southwest (SW, red points) aspects in the burn scar (right). Inset map depicts general location of burn scar within California.

To link regeneration traits to survival and growth, a total of 413 individuals of 13 of the same species we collected trait data on were tagged in the first year after fire (2019), distributed across the 24 burned transects. This encompassed 5 obligate resprouters, 4 obligate seeders, and 4 facultative species that were present as both resprouters and seeders. A wide range of individuals were tagged per species based on differing recruitment levels in the field for each species and strategy (see Table S1.3 for details of number of tagged individuals per species, regeneration strategy, and aspect) totaling 86 resprouters and 327 seeders. Survival was surveyed for the first four years after fire (plants tagged in 2019 then surveyed for three years starting in 2020). During the last survey in 2022, growth was measured as volume (length x width x height) for a subset of tagged individuals (minimum of 6-15 individuals per seeder species and aspect type and 3-15 individuals per resprouters were measured).

We estimated community recovery by measuring plant community composition, shrub density and species richness. We sampled community composition along the 30 m transects using the 30 cm point line intercept method (a pole was placed every 30 cm and all living and dead vascular plants and substrate touching the pole were recorded). For each species, we recorded regeneration strategy in the field as described above. Surveys were conducted during the first summer after fire in 2019, which were additionally used to calculate community weighted functional diversity metrics. The transects were resurveyed in 2020, the second year after fire, for a temporal view of recovery. We estimated shrub density in a 1 m belt transect upslope of each composition transect for two years after fire, where every shrub seedling and resprouter was identified to species and counted. The belt transect was split into subsections, where half of the sections were surveyed totaling a $15m^2$ sampling area. In the first year a subset of the transects were split into 10, 1 m x 3 m sections; however, due to sampling constraints the remaining transects were split into 6, 1 m x 5 m sections. In the second year, all transects were sampled in 6, 1 m x 5 m sections. Species richness was additionally recorded in a 1 m x 30 m belt directly above the transect in both years, where every unique shrub, forb, grass, and tree sapling was recorded to summarize site attributes.

Environmental Data Collection

To characterize the environmental conditions across aspects, we measured soil texture and nutrients, and calculated climatic water deficit. Two - four liters of the first 13 cm of soil was collected at multiple locations along each transect and sifted through a 2 mm sieve prior to analysis for soil nutrients and texture. Climatic water deficit, defined as the amount of evapotranspirative demand that exceeds available soil moisture (Stephenson 1998), is used as an indicator of drought stress on soil and plants, and was calculated at each site using USGS Digital Elevation Models, Polaris soil available water capacity, PRISM 30 year normal precipitation and mean temperature, which were downscaled to 10 m resolution using the cwd_function() in R (Redmond 2022).

Analyses

Q1 Life stage trait differences

To test trait differences across life stages, regeneration strategies, and aspects, we used ANOVAs with response variables of each functional trait (i.e. SLA, % N) and predictor variables of life stages (adult vs regenerating plants) and regeneration strategies (regenerating resprouter vs seeder), aspects (NE vs SW), and their interaction, where species mean trait values were the replicates. Tukey post-hoc tests were used on significant main effects using the package emmeans in R. All analysis was done in R version 4.1.1 (R Core Team 2021).

Q2 Linking traits to demographic rates

The percent survival each year was calculated as the number of surviving individuals divided by the total number of tagged individuals relocated that year. To understand survival differences across aspects and regeneration strategies, a non-parametric Scheirer Ray Hare test was used with proportion survival at four years post-fire as the response variable. Due to the consistently high survival rate of resprouters (see results section), we analyzed regeneration trait influence on survival only for seeders, reducing our sample size to eight species. Because regeneration traits were similar across aspects (see results section), regeneration trait data was aggregated across aspects to determine the relationship between regeneration traits and survival. To quantify phylogenetic signal and assess if phylogenetic independent contrasts were needed in subsequent trait analysis, we tested whether Pagel's λ was statistically significant and greater than 0 (Münkemüller et al. 2012) using phylosig() in the phytools R package (Revell 2012). A phylogenetic tree was constructed for the Pagel's λ test using the Zanne et al. 2014 phylogeny. No traits were phylogenetically conserved (Table S1.4), thus phylogenetic independent contrasts were not used in the following linear regression models. Separate multiple linear regression models with a third order polynomial were used for each of the six regeneration traits, where the response variable was proportion survival at four years post-fire and predictor variable a single regeneration trait. A similar analysis was done for the response variable growth, where separate linear regression models were used for each of the six regeneration traits to assess the influence of regeneration traits on growth in year four with the response variable growth and predictor variable a single regeneration trait.

Q3 Recovery over aspects and time

To assess how shrub cover was influenced by aspect, regeneration strategy, and post-fire year, a global linear mixed effects model was used with response variable shrub cover (natural log transformed), fixed categorical effects of aspect, strategy, post-fire year (1 vs 2), and their interactions, and random effects of site and site ID nested within year to account for repeated sampling. The minimal adequate model was selected using the dredge function in R which uses backward selection and AIC methods. Due to the difference in sampling protocols in each year, separate linear mixed effects models were used for year 1 and year 2 to assess shrub density (natural log transformed) across predictors of aspect and regeneration strategy, with a random effect of transect nested within site. For both cover and density analyses, post-hoc tests were conducted for significant main effects using Tukey methods.

To assess shrub function at the community scale, we calculated community weighted means (CWMs) of the dominant regenerating shrubs across aspects (17 species on NE aspects, 15 species on SW) and functional diversity metrics (richness, evenness, divergence, and dispersion) were calculated for the first year of recovery (FD package;

Laliberté et al. 2014). The influence of aspect on shrub community functional strategy was assessed using separate ANOVAs for each functional strategy metric. Functional richness (FRic) describes the range of traits within a community based on the volume of trait space occupied by species in the community (Cornwell et al. 2006). Functional dispersion (FDis) is the degree of trait dissimilarity among species in a community quantified as the mean distance in trait space of individual species to the centroid of the community (Laliberté and Legendre 2010). Functional divergence (FDiv) is the extent to which the abundance of species in a community are distributed at the extremes or edge of the volume of trait space occupied by the community (Villéger et al. 2008, Mouillot et al. 2013). The observed community functional traits and diversity metrics across aspects were then compared to null modeled random communities to test if observed traits were more similar (underdispersed) or more different (overdispersed) than expected by chance. Null model communities were created by randomizing the species matrix, while maintaining abundance and species richness with each transect. Trait values were kept together to conserve functional strategy and traits that evolved together, thus species names were reshuffled across trait and abundance data. 9999 replications were done in separate null models for communities on NE vs SW aspects. Standard effect size (SES) between observed and null modeled community functional traits and diversity metrics was calculated and compared across aspects using an ANOVA.

Q4 Factors predictive of recovery

We identified a set of factors that could be used to predict recovery including abiotic factors (Hanan et al. 2016), site amelioration by resprouting shrubs (Gómez-Aparicio et al. 2004), and diversity of regeneration traits, which this study aimed to test. To test each factor's predictive ability, we took a model fitting approach where we started with a global linear mixed effects model with the response variable of shrub recovery (shrub cover in year two as natural log transformed count data) and predictor variables of functional diversity metrics in year 1 (FRic, FDiv, FDis), soil texture and nutrients (CEC: cation exchange capacity, Mg: Magnesium, Na: Sodium, Ca: Calcium, om.rating: organic matter; K: potassium, SO4S: sulfate, P1: phosphorus, pH) collapsed into PCA axes, climatic water deficit, year 1 resprouter cover, and their interactions with aspect type and random effect of transect nested within site. We first estimated functional diversity metrics using regeneration trait data and the shrub composition from the first year. The minimal adequate model was selected using the dredge function in R which uses backward selection and AIC methods, and we present the results of this best fit model.

To test the predictive ability of adult traits on recovery, an adult trait matrix was used with first year regeneration composition data to calculate functional diversity metrics. We repeated the same model fitting approach using adult traits to estimate functional diversity metrics to compare model outputs between regeneration and adult traits.

Results

We observed mean total vegetation recovery during this study to be 63.1% ± 5.1 cover on NE aspects and 60.4% ± 5.5 on SW aspects. Of this vegetation recovery, on NE aspects 63.4% of cover was composed of shrubs, 34.3% forbs, 2.3% grasses, and 0% tree saplings while on SW aspects 42.2% was composed of shrubs, 57.2% forbs, 0.3%

grasses, and 0.3% tree saplings. We observed 87 unique species (26 shrubs, 52 forbs, 8 grasses, and 1 tree sapling) with an average of 16.58 ± 1.34 species per NE aspect and 13.17 ± 1.04 species per SW aspect. Dominant species on NE aspects included *Quercus berberidifolia* (Fagaceae), *Dendromecon rigida* (Papaveraceae), *Arctostaphylos glandulosa* (Ericaceae), and *Ceanothus oliganthus var. oliganthus* (Rhamnaceae) while dominants on SW aspects included *Arctostaphylos glandulosa*, *Adenostoma fasciculatum* (Rosaceae), *Rhus ovata* (Anacardiaceae), and *Acmispon glaber* (Fabaceae).

Q1 Life stage trait differences

We saw a life stage and regeneration strategy main effect for SLA ($p<0.001$, Table 1.1) and % N ($p=0.002$, Table 1.1). Specifically, regenerating plants (i.e. resprouts and seedlings) had a higher SLA ($p<0.001$) and % N content ($p<0.001$), indicative of a higher photosynthetic capacity and resource acquisitive strategy, compared to adults (Fig. 1.2). Regenerating seeders had a higher SLA compared to resprouters ($p=0.007$), but % N was similar across regeneration strategies ($p=0.92$, Fig. 1.2). Leaf area was similar across life stages and regeneration strategies ($p=0.199$, Table 1.1). We saw a life stage and regeneration strategy main effect for LDMC ($p=0.003$, Table 1.1) where the key difference was life stage - regenerating plants had lower LDMC than adults ($p<0.001$) but similar LDMC across regeneration strategies ($p=0.966$). Discrimination of $\delta^{13}C$ had a significant main effect of life stage and regeneration strategy ($p=0.005$, Table 1.1). Regenerating seeders had a higher discrimination of $\delta^{13}C$, indicating lower intrinsic water use efficiency, than adults ($p<0.001$) and resprouters ($p<0.001$), characteristic of a more resource acquisitive strategy (Fig. 1.2). Adults and regenerating resprouters had similarly high intrinsic water use efficiency (p=0.994) and conservative water strategies (Fig. 1.2). Looking across all traits, regenerating seeders had a more resource acquisitive strategy compared to resprouters (Fig. 1.2). Height varied by regeneration strategy (p<0.001, Table 1.1), where resprouts were taller than seedlings. We found aspect type did not influence traits across life stages or regeneration strategies (Table 1.1).

Table 1.1 Summary model statistics for ANOVAs testing how functional traits differ by life stages and regeneration strategies and across aspects.

	SLA	LA	LDMC	% N	$\delta^{13}C$	Height
Life Stage and Strategy	$22.0759_{2,49}$***	$1.6655_{2,49}$	$6.7432_{2,49}$**	$7.1231_{2,48}$**	$5.8311_{2,48}$**	$54.5445_{1,32}$***
Aspect	$0.0892_{1,49}$	$0.0780_{1,49}$	$0.0044_{1,49}$	$0.2210_{1,48}$	$0.0900_{1,48}$	$1.4332_{1,32}$
Life Stage and Strategy:Aspect	$0.3601_{2,49}$	$0.0497_{2,49}$	$0.0276_{2,49}$	$0.4121_{2,48}$	$0.0279_{2,48}$	$0.5953_{1,32}$

F values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001). SLA: Specific Leaf Area, $cm^2 g^{-1}$; LA: Leaf Area, cm^2; LDMC: Leaf Dry Matter Content, $mg g^{-1}$; % N: percent nitrogen leaf content, %; $\delta^{13}C$: discrimination of $\delta^{13}C$, ‰.

Q2 Linking traits to demographic rates

Total shrub survival across all individuals remained high after the first four post-fire years, where by the second post-fire year (2020) we observed 94.55% survival, by the third year (2021) 85.89%, and by the fourth year (2022) 78.45%. Survival was similar across aspects (p=0.688, Table S1.5) but different across regeneration strategies (p<0.001, Table S1.5), where resprouters had 100% survival, but seeder survival varied from 24% - 96%. For seeders, height during the first growing season influenced survival (p=0.02, Table S1.6), but no other regeneration traits impacted survival (Table S1.6). Plants that were taller during initial regeneration (first year) had higher survival four years after fire (Fig. 1.3), indicating the importance of light availability for survival in post-fire systems. Leaf % N content during the first growing season influenced growth (p=0.046, Table S1.6), but no other regeneration traits impacted growth (Table S1.6). Plants with higher % N in leaf tissue during initial regeneration led to more growth (Fig. 1.4), indicating the importance of initial leaf nitrogen content in post-fire recovery.

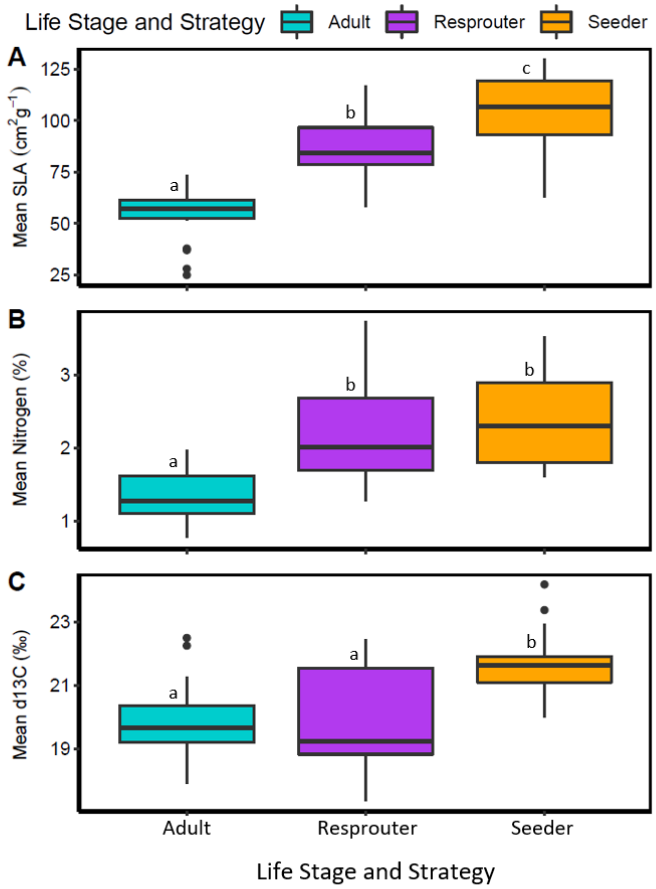

Figure 1.2 Mean trait differences across life stage (adult vs regenerating plants) and regeneration strategy (regenerating resprouters vs seeders) for A) SLA, B) N content, C) discrimination of δ^{13}C. Different letters indicate statistically significant differences between groups.

Q3 Recovery over aspects and time

The minimal adequate model selected for assessing shrub recovery over time included fixed effects of aspect, regeneration strategy, year post fire, and the interaction between

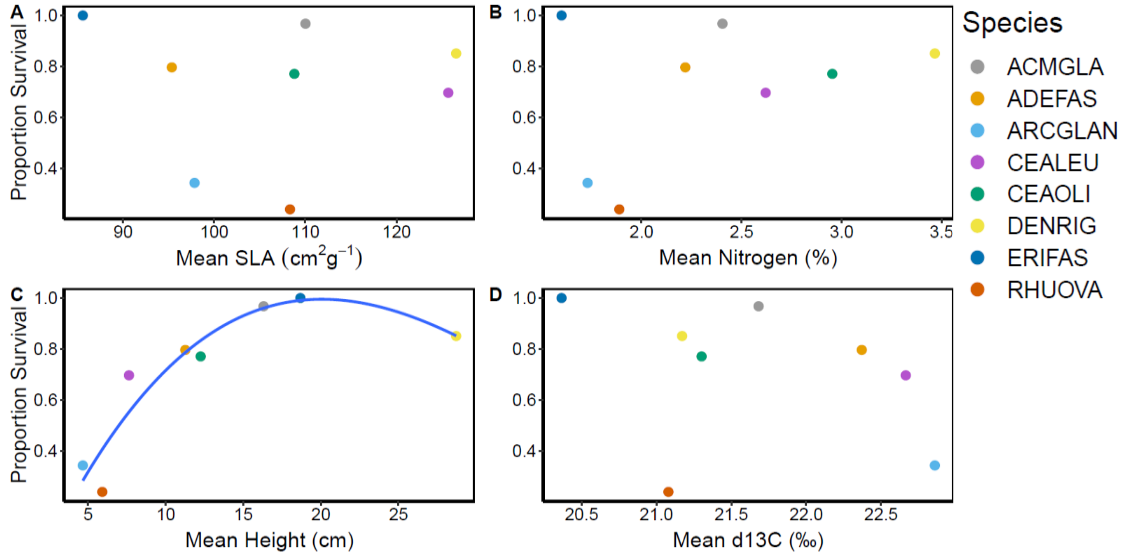

Figure 1.3 Proportion survival across regeneration traits for A) SLA, B) leaf N, C) height, D) discrimination of δ^{13}C. Blue line indicates a significant relationship. ACMGLA: *Acmispon glaber*, ADEFAS: *Adenostoma fasciculatum*, ARCGLAN: *Arctostaphylos glandulosa*, CEALEU: *Ceanothus leucodermis*, CEAOLI: *Ceanothus oliganthus spp. oliganthus*, DENRIG: *Dendromecon rigida*, ERIFAS: *Eriogonum fasciculatum*, RHUOVA: *Rhus ovata*.

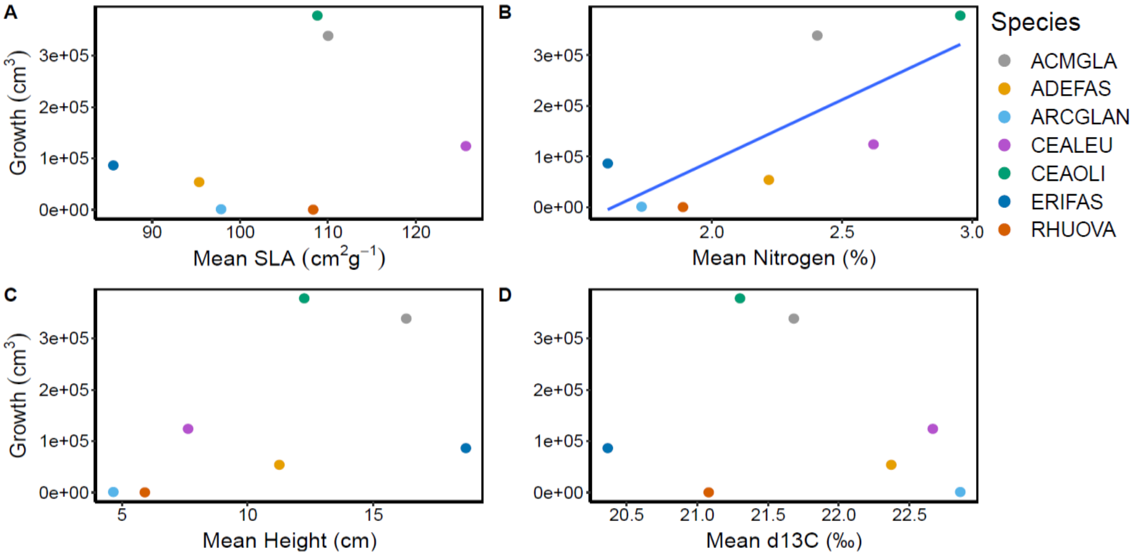

Figure 1.4 Growth across regeneration traits for A) SLA, B) leaf N, C) height, D) discrimination of δ^{13}C. Blue line indicates a significant relationship. See Fig. 1.3 for scientific names associated with species codes.

regeneration strategy and year with random effects of site and site ID nested within year. We found a main effect of aspect (p=0.004, Table 1.2), where shrub cover was higher on NE aspects with 64.8% more recovery compared to SW aspects by year two. Shrub cover varied by regeneration strategy (p<0.001, Table 1.2), year (p<0.001, Table 1.2), and their interaction (p=0.012, Table 1.2) where resprouters contributed more to recovery in year 1 (p<0.001), but by year 2 seeders and resprouters had similar recovery (p=0.728).

In both the first and second years of recovery, shrub density varied by regeneration strategy (p<0.001, Table 1.2) where seeder density was higher compared to resprouter density. In both years, we also observed a significant interaction between aspect and regeneration strategy (yr1: p=0.019, yr2: p=0.025, Table 1.2) where seeders had a higher density on NE aspects compared to SW (post-hoc yr1: p=0.012, yr2: p=0.003) while resprouter density did not vary by aspect (post-hoc yr1: p=1.00, yr2: p=0.888).

Community weighted means (CWMs) of the dominant shrub community in year 1 showed communities on NE aspects had lower CWM discrimination of $\delta^{13}C$ (higher intrinsic water use efficiency, more conservative water use), contrasting predictions for higher resource environments (p=0.012; Table S1.7). There was a main effect of aspect on FRic (p=0.002, Table S1.7) and FDiv (p=0.003, Table S1.7), where on SW aspects functional richness was underdispersed (p=0.002, Fig. S1.1) and functional divergence was overdispersed (p=0.003, Fig. S1.1) compared to random communities, suggesting the presence of fewer strategies that are more distributed towards edges in trait space on SW aspects. We also found functional evenness (FEve) to differ across aspects (p=0.026

Table S1.7), where FEve was higher on SW aspects. No other CWM traits or functional diversity metrics differed across aspects or compared to the null modeled random communities (Table S1.7).

Table 1.2 Summary model statistics for mixed effects model testing how aspect, regeneration strategy, and year post fire influence recovery (a), and for mixed effects models testing how aspect and regeneration strategy influence shrub density across the first two years post fire (b).

(a) Shrub Recovery	Chisq	Pr(>Chisq)		
Aspect	8.3005	0.0039634**		
Regeneration Strategy	13.0614	0.0003014***		
Year	30.7824	2.886e-08***		
Regeneration Strategy:Year	6.2493	0.0124243*		
(b) Shrub Density	Year 1		Year 2	
	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)
Aspect	0.0000	0.99891	0.5186	0.4714
Regeneration Strategy	71.9826	< 2e-16***	53.3912	2.733e-13***
Aspect: Regeneration Strategy	5.5096	0.01891*	5.0519	0.0246*

Recovery was estimated as natural log transformed count data in the first and second year post fire. The recovery model included the random effect of site ID nested within year to account for repeated sampling and random effect of site. Shrub density was estimated as natural log transformed count data in year one and two post fire. The shrub density model included the random effect of transect nested within site. Chisq values are presented. Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001).

Q4 Factors predictive of recovery

The minimal adequate model selected for predicting shrub recovery in year two using regeneration traits included predictor variables of aspect, functional divergence, functional richness, and the interaction between aspect and functional divergence (Fig. 1.5, Table S1.8). Regeneration traits were predictive of recovery, where first-year FRic influenced recovery in year two (p=0.046, Table S1.8) as more functional strategies present in year 1 promoted higher recovery (Fig. S1.2a). Regeneration trait functional divergence interacted with aspect to influence recovery (p<0.001, Table S1.8), where SW aspects had higher recovery as FDiv increased while NE aspects experienced the same recovery level regardless of FDiv (Fig. S1.2b). The PCA axis 1 collapsed environmental variables included CEC, Ca, organic matter, Mg, K and axis 2 contained pH, P1, Mg (Fig. S1.3), but neither axis was included in the minimal adequate model.

Using adult traits, the minimal adequate model selected for predicting shrub recovery in year two included predictor variables of aspect, resprouter cover, and their interaction. Functional diversity metrics estimated with adult traits were not included in the final model, thus adult traits were not predictive of recovery (Fig. 1.5, Table S1.8).

Discussion

This study assessed the role of regeneration traits and strategies across a topographic gradient at different scales of inquiry in post-fire shrub recovery. We found functional traits differed across life stages but not aspect, where regeneration traits were more

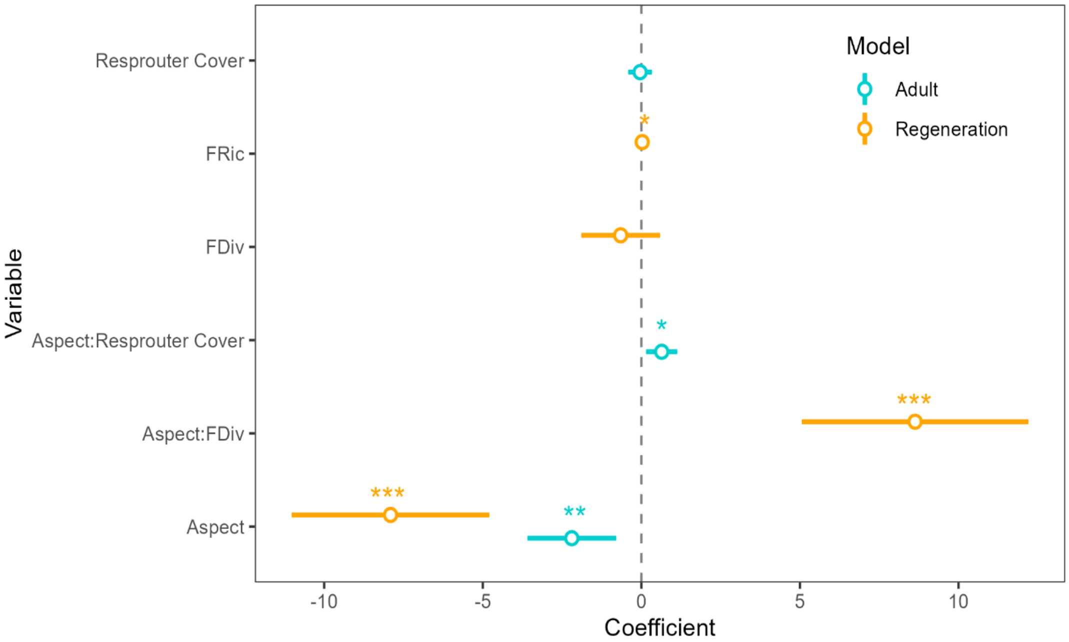

Figure 1.5 Coefficient plot for models using adult (blue) vs regeneration (orange) traits to predict recovery. R.cov: resprouter cover in year one, FRic: functional richness, FDiv: functional divergence. Lines are ± 95% SE.

resource acquisitive (higher SLA, higher δ^{13}C discrimination/lower iWUE, higher % N, lower LDMC) than adult traits (Q1). We linked traits to individual/population demographic processes, finding regeneration height mediated survival while % N mediated growth for seeders, but regeneration traits did not mediate resprouter demographic processes (Q2). At the community scale, we found regeneration strategies drove recovery over time, where resprouters had higher cover than seeders in year one, but by year two, cover was similar across strategies, which was driven by the higher density and acquisitive resource-use strategy of seeders compared to resprouters. We saw NE aspects promoted higher recovery and seeder density but also higher CWM intrinsic water use efficiency (Q3). Finally, we found regeneration traits were more predictive of recovery than adult traits, providing evidence that the functional richness and diversity of early establishing plants can mediate recovery (Q4). Taken together, we demonstrated how traits from the individual to community scales influence post-fire recovery and expand on these findings below.

Q1 Life stage trait differences

Quantifying the differences in traits across life stages and regeneration strategies is the first step to improving our ability to predict recovery, as patterns observed at the seedling stage may have lasting effects on community structure and function (Jakobsson and Eriksson 2000, Larson and Funk 2016). We found leaf economic spectrum traits differed across life stages, where regenerating plants had an acquisitive resource-use strategy and adults had a conservative strategy. This is consistent with recent findings in other systems where traits transitioned from the acquisitive to conservative strategy across early ontogeny (Garbowski et al. 2021, Havrilla et al. 2021) and life stages (Mason et al. 2013, Dayrell et al. 2018, Harrison and LaForgia 2019). In this system with multiple regeneration strategies, we observed SLA, iWUE, and height differed by regeneration strategy where seeders are more resource-acquisitive and resprouters are more conservative during the first year after fire. These results contrast previous studies of chaparral traits during the first few years post-fire where resprouting species were associated with resource-acquisitive traits (characteristic long roots to reach deeper water and higher SLA for faster growth; Anacker et al. 2011, Pratt et al. 2012) while seeder species had more conservative and drought tolerant traits (xylem highly resistant to cavitation, slow growth rates, low SLA, and short heights; Anacker et al. 2011, Pratt et al. 2012). This discrepancy is most likely due to these previous studies missing the true first year regeneration traits, highlighting the importance of using traits at the correct life stage to understand regeneration and community assembly processes or predict recovery. Understanding how traits differ across life stages and regeneration strategies is the first step needed to scale from population demographic processes to community dynamics, but few studies have tested life stage trait differences in field conditions (Laughlin et al. 2017, Dayrell et al. 2018) and connected regeneration traits to community processes (Spasojevic et al. 2014, 2016, Zirbel and Brudvig 2020, Larson et al. 2021).

Q2 Linking traits to demographic rates

Regeneration traits may be integral to the recovery process if these traits dictate successful establishment and survival under post-disturbance stressors (Larson and Funk 2016), but the link between individual trait performance and these demographic processes is often overlooked when predicting variation in recovery (Cadotte et al. 2015, Laughlin et al. 2020). We found two regeneration traits mediated seeder demographic rates; seeder regeneration height influenced survival (Fig. 1.3) while % N influenced growth (Fig. 1.4), indicating the importance of light competition and N content in survival and growth, respectively. Mature chaparral is characterized by a closed canopy structure (Hanes 1971) with low light availability at the soil surface; thus, increased height is likely a key strategy for a species to successfully survive and persist to later stages of recovery (Hanes 1971, Westoby et al. 2002). Competition for light and nitrogen at these early stages of recovery can select for species with higher photosynthetic capacity, growth rate, and total biomass accumulation resulting in secured access to light in the canopy (Westoby et al. 2002). Though not measured in our study due to difficulty of extracting and identifying roots, root traits controlling nutrient and water uptake may be a good indicator of the mechanisms regulating survival, as summer survivorship can be an important bottleneck in dry years. Seedlings in arid systems that expand their root systems quickly (e.g. higher rooting depth) are able to access more soil moisture to increase establishment and survival in arid systems (Padilla and Pugnaire 2007, Harrison and LaForgia 2019). While regeneration traits are increasingly linked to establishment and survival (Larson et al. 2015, 2021, Zirbel and Brudvig 2020, Arend da Silva et al. 2020), identifying the right trait that influences the demographic process of interest is still elusive, especially across different systems and regions. For example, an experimental grassland restoration found trait-environment interactions at the seedling stage structured establishment, such as SLA interacting with light availability (Zirbel and Brudvig 2020), but early life stage traits of coleoptile tissue density (Larson et al. 2015) and seedling root length (Harrison and LaForgia 2019) explained the majority of variation in survival in other grassland regions. Because not all traits influence all demographic processes (i.e., Figs. 1.3, 1.4; Tables S1.4, S1.5; Adler et al. 2014, Salguero-Gómez 2017, Laughlin et al. 2020), there is a clear need to better assess which traits mediate the demographic process at the life stage of interest (Arend da Silva et al. 2020, Larson et al. 2021, Salguero-Gómez and Laughlin 2021).

Regeneration strategies are known to mediate recovery patterns (Keeley 2018), but identifying how their trait differences mediate demographic processes important in recovery has been understudied for first year regeneration traits. Here, we found differences in regeneration strategy mediated overall survival, where resprouters had

100% survival while seeder survival varied. Variation in seeder survival can be impacted by competition (Pausas and Keeley 2014), and we found evidence for this with the presence of higher seeder density compared to resprouters, higher seeder % N content promoting more growth, and taller plants having higher survival, suggesting seeders were experiencing a competitive environment. A caveat to our findings are the method we used to calculate survival may have overestimated resprouter survival, where measuring the proportion of dead burls compared to live ones would better capture resprouter population persistence (Keeley 2006), since once an individual resprouts after fire it has high survival (Table S1.5). One mechanism of resprouter survival is drought avoidance, where resprouters have much deeper roots compared to seeders (Keeley 2018). Since resprouters can have several meter long roots that are difficult to measure in field conditions, discrimination of δ^{13}C may be an alternate trait to better capture resprouter demographics, as δ^{13}C isotope ratio can describe the depth of the water source (i.e. surface vs groundwater) which may be driving the difference in discrimination of δ^{13}C between resprouters and seeders (Fig. 1.2). Further understanding how traits link to the mechanisms regulating demographic processes between regeneration strategies can explain variation in recovery, especially since scaling responses from population to community level recovery is contingent on identifying the right trait-environment relationship for the demographic process of interest.

Q3 Recovery over aspects and time

Identifying the scale at which trait-environment relationships are important is needed to understand what factors influence recovery. Regeneration trait values and survival did not differ across aspects during this study, most likely due to the above average precipitation received in the first two years post fire overwhelming aspect type differences during establishment. While aspect type did not mediate species level regeneration traits or survival in this study (but see Ackerly et al. 2002 for aspect influence on adult traits), it did mediate community level recovery and function. Shrub recovery and seedling density were higher on NE aspects, which is typically a higher resource environment, and interestingly NE aspects supported more conservative water-use community traits. The higher plant abundance on NE aspects may result in a more competitive environment, where plant available water can be lower on NE aspects relative to SW (Ng and Miller 1980). This could indicate NE aspects experience more competition for water, resulting in the lower CWM discrimination of δ^{13}C and a more intrinsic water use efficient strategy that we observed on NE aspects. Aspects additionally influenced community function in the first post-fire year where SW aspects had fewer functional strategies present (underdispersed functional richness) and the abundance of species in the community were more distributed towards the extreme edges of trait space (overdispersed functional divergence) compared to random communities. While we found evidence for how these trait-environment processes scale in wet recovery years, the underlying precipitation conditions during initial regeneration years may alter recovery dynamics and present stronger environmental filtering on traits and establishment (Moreno and Oechel 1994).

The transient dynamics of recovery are apparent as communities transition through different successional states post disturbance (White and Jentsch 2004), but identifying the timing and mechanisms for these transitions can improve recovery predictions. We found the interactions between regeneration strategy and year influenced recovery, where resprouters contributed more to recovery in year one, but by year two recovery was similar across strategies. Previous work has shown similar dynamics (Schmalbach et al. 2007), but here we identified the mechanisms allowing seeders to match resprouter cover within a short recovery period. Seeders have a more acquisitive, faster growth strategy in the first year of recovery compared to resprouters (Fig. 1.2), and coupled with the higher density of seeders compared to resprouters in this moderate to high severity fire (Table 1.2; Minor et al. 2017), these results suggest regeneration strategies and their respective traits are mediating initial recovery. Additionally, regeneration strategies have different spatial and temporal fitness and survival trade-offs after disturbances, which are critical to long term landscape recovery (Pausas and Keeley 2014). The balance of these multiple strategies over time is key to long term recovery, as selective regimes differentially impact survival and reproduction, such that seeders evolved to withstand increasing aridity and fire intensity while resprouters withstand less intense more frequent disturbances from their ability to regenerate from stored energy (Pausas and Keeley 2014). Additionally, the high initial recovery of resprouters may facilitate seeder survival and growth via site amelioration, which we found some evidence for on SW aspects in the predictive recovery model using adult traits (Table S1.8). This highlights the need for long-term studies to disentangle how and when regeneration traits and strategies mediate recovery after a disturbance.

Q4 Factors predictive of recovery

Our ability to predict recovery is contingent on choosing the right traits and measuring them at the appropriate life stage to understand the functional strategies at play. We found that individual regeneration traits linked to performance, but more importantly the diversity of traits present promoted initial recovery. Our results support the positive relationship between diversity and recovery, but we found the diversity of regeneration traits was a better predictor of recovery than adult trait diversity. Specifically, the functional richness of regeneration strategies in the first post-fire year positively correlated with recovery, suggesting more functional traits and strategies present during initial recovery promotes higher recovery. Additionally, the functional divergence of regeneration strategies positively correlated with recovery, but only on SW aspects (Fig. S1.2), suggesting SW aspects may be vulnerable to lower recovery if diversity of functional strategies decreases. Historically, chaparral ecosystems do not exhibit many intermediate successional stages, but researchers have begun to observe that chaparral recovery is stalled on SW aspects when the first post-fire years coincide with extreme drought while other areas recover within normal rates (Underwood et al. 2022). Together the literature and our results point to the vulnerability of SW aspects and the importance of managing for high functional richness in these areas to ensure early establishment that will promote recovery and ultimately the resilience of the community to wildfire and other environmental stressors. Notably, it’s important that functional diversity is estimated for the most appropriate life stage, as we observed that adult functional diversity was not predictive of chaparral recovery.

Conclusion

We linked regeneration traits across multiple scales of inquiry and ecological processes to better elucidate the mechanisms of chaparral post-fire recovery. These results highlight the importance of regeneration traits in the recovery process, where regeneration traits are not ontogenetically conserved, can act differently for seeders and resprouters, link to community function across aspect types, and are more predictive of recovery than adult traits. Regeneration traits should therefore be used to improve recovery predictions with a clear next step of identifying the correct response traits to the demographic process of interest across different systems. We found the diversity of regeneration traits is key to increasing recovery and promoting resilience to disturbances. Taken together our study demonstrates how different dimensions of regenerations traits scale across ecological processes to improve our understanding of recovery and resilience to disturbance.

References

Ackerly, D. D., Knight, C., Weiss, S., Barton, K., & Starmer, K. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia*, *130*(3), 449–457. https://doi.org/10.1007/s004420100805

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 of the United States of America*, *111*(2), 740–745. https://doi.org/10.1073/pnas.1315179111

Anacker, B., Rajakaruna, N., Ackerly, D., Harrison, S., Keeley, J., & Vasey, M. (2011). Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. *Plant Ecology & Diversity*, *4*(2-3), 179–188. https://doi.org/10.1080/17550874.2011.633573

Arend da Silva, I., Guido, A., & Müller, S. C. (2020). Predicting plant performance for the ecological restoration of grasslands: the role of regenerative traits. *Restoration Ecology*, *28*(5), 1183–1191. https://doi.org/10.1111/rec.13182

Armesto, J. J., & Martínez, J. A. (1978). Relations Between Vegetation Structure and Slope Aspect in the Mediterranean Region of Chile. *Journal of Ecology*, *66*(3), 881–889. https://doi.org/10.2307/2259301

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution*, *16*(1), 45–51. https://doi.org/10.1016/s0169-5347(00)02033-4

Browne, L., Markesteijn, L., Manzané-Pinzón, E., Wright, S. J., Bagchi, R., Engelbrecht, B. M. J., Jones, F. A., & Comita, L. S. (2023). Widespread variation in functional trait–vital rate relationships in tropical tree seedlings across a precipitation and soil phosphorus gradient. *Functional Ecology*, *37*, 248–260. https://doi.org/10.1111/1365-2435.14213

Cadotte, M. W., Arnillas, C. A., Livingstone, S. W., & Yasui, S.-L. E. (2015). Predicting communities from functional traits. *Trends in Ecology & Evolution*, *30*(9), 510–511. https://doi.org/10.1016/j.tree.2015.07.001

Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends in Ecology & Evolution*, *31*(5), 382–394. https://doi.org/10.1016/j.tree.2016.02.003

Chang, C., & HilleRisLambers, J. (2016). Integrating succession and community assembly perspectives. *F1000Research, 5(F1000 Faculty Re),* 2294. https://doi.org/10.12688/f1000research.8973.1

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *The American Naturalist*, *111*(982), 1119–1144. https://doi.org/10.1086/283241

Cooper, W. S. (1922). *The Broad-sclerophyll Vegetation of California: An Ecological Study of the Chaparral and Its Related Communities*. Carnegie Institution of Washington. https://market.android.com/details?id=book-W70EAAAAIAAJ

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335–380. https://doi.org/10.1071/bt02124

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, *79*(1), 109–126. https://doi.org/10.1890/07-1134.1

Cornwell, W. K., Schwilk, L. D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, *87*(6), 1465–1471. https://doi.org/10.1890/0012-9658(2006)87[1465:attfhf]2.0.co;2

Cowles, H. C. (1899). The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. Part I.-Geographical Relations of the Dune Floras. *Botanical Gazette* , *27*(2), 95–117. https://doi.org/10.1086/327796

D’Antonio, C. M., & Vitousek, P. M. (1992). Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics*, *23*(1), 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H., & Silveira, F. A. O. (2018). Ontogenetic shifts in plant ecological strategies. *Functional Ecology*, *32*(12), 2730–2741. https://doi.org/10.1111/1365-2435.13221

Dobrowski, S. Z., Abatzoglou, J. T., Greenberg, J. A., & Schladow, S. G. (2009). How much influence does landscape-scale physiography have on air temperature in a mountain environment? *Agricultural and Forest Meteorology*, *149*(10), 1751–1758. https://doi.org/10.1016/j.agrformet.2009.06.006

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in*

Ecology and the Environment, *1*(9), 488–494. https://doi.org/10.1890/1540-9295(2003)001[0488:rdecar]2.0.co;2

Evans, J. R. (1989). Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, *78*(1), 9–19. https://doi.org/10.1007/BF00377192

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*(1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Frenette-Dussault, C., Shipley, B., Meziane, D., & Hingrat, Y. (2013). Trait-based climate change predictions of plant community structure in arid steppes. *Journal of Ecology*, *101*(2), 484–492. https://doi.org/10.1111/1365-2745.12040

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution*, *23*(12), 695–703. https://doi.org/10.1016/j.tree.2008.07.013

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 Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews of the Cambridge Philosophical Society*, *92*(2), 1156–1173. https://doi.org/10.1111/brv.12275

Garbowski, M., Johnston, D. B., & Brown, C. S. (2021). Leaf and root traits, but not relationships among traits, vary with ontogeny in seedlings. *Plant and Soil*, *460*(1), 247–261. https://doi.org/10.1007/s11104-020-04790-z

Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., & Baraza, E. (2004). Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecological Applications: A Publication of the Ecological Society of America*, *14*(4), 1128–1138. https://doi.org/10.1890/03-5084

Hanan, E. J., D'Antonio, C. M., Roberts, D. A., & Schimel, J. P. (2016). Factors Regulating Nitrogen Retention During the Early Stages of Recovery from Fire in Coastal Chaparral Ecosystems. *Ecosystems* , *19*(5), 910–926. https://doi.org/10.1007/s10021-016-9975-0

Hanes, T. L. (1971). Succession after Fire in the Chaparral of Southern California. *Ecological Monographs*, *41*(1), 27–52. https://doi.org/10.2307/1942434

Harrison, S., & LaForgia, M. (2019). Seedling traits predict drought-induced mortality linked to diversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(12), 5576–5581. https://doi.org/10.1073/pnas.1818543116

Havrilla, C. A., Munson, S. M., Yackulic, E. O., & Butterfield, B. J. (2021). Ontogenetic trait shifts: Seedlings display high trait variability during early stages of development. *Functional Ecology*, *35*(11), 2409–2423. https://doi.org/10.1111/1365-2435.13897

Henn, J. J., & Damschen, E. I. (2021). Plant age affects intraspecific variation in functional traits. *Plant Ecology*, *222*(6), 669–680. https://doi.org/10.1007/s11258-021-01136-2

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*(1), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Jacobsen, A. L., & Pratt, R. B. (2018). Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands. *The New Phytologist*, *219*(2), 498–504. https://doi.org/10.1111/nph.15186

Jakobsson, A., & Eriksson, O. (2000). A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* , *88*(3), 494–502. https://doi.org/10.1034/j.1600-0706.2000.880304.x

Keeley, J. E. (2006). Fire Severity and Plant Age in Postfire Resprouting of Woody Plants in Sage Scrub and Chaparral. *Madroño*, *53*(4), 373–379. http://www.jstor.org/stable/41425666

Keeley, J. E. (2018). Drivers of Chaparral Plant Diversity. In E. C. Underwood, H. D. Safford, N. A. Molinari, & J. E. Keeley (Eds.), *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives* (pp. 29–51). Springer International Publishing. https://doi.org/10.1007/978-3-319-68303-4_2

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, *169*(4), 1043–1052. https://doi.org/10.1007/s00442-012-2253-8

Kimball, S., Funk, J. L., Spasojevic, M. J., Suding, K. N., Parker, S., & Goulden, M. L. (2016). Can functional traits predict plant community response to global change? *Ecosphere* , *7*(12), e01602. https://doi.org/10.1002/ecs2.1602

Kutiel, P. (1997). Spatial and Temporal Heterogeneity of Species Diversity in a Mediterranean Ecosystem Following Fire. *International Journal of Wildland Fire*, *7*(4), 307–315. https://doi.org/10.1071/wf9970307

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., & Shipley, B. (2014). Measuring functional diversity from multiple traits, and other tools for functional ecology. *R Package FD*. https://www.imsbio.co.jp/RGM/R_rdfile?f=FD/man/FD-package.Rd&d=R_CC

Larson, J. E., Ebinger, K. R., & Suding, K. N. (2021). Water the odds? Spring rainfall and emergence-related seed traits drive plant recruitment. *Oikos* , *130*(10), 1665–1678. https://doi.org/10.1111/oik.08638

Larson, J. E., & Funk, J. L. (2016). Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, *104*(5), 1284–1298. https://doi.org/10.1111/1365-2745.12613

Larson, J. E., Sheley, R. L., Hardegree, S. P., Doescher, P. S., & James, J. J. (2015). Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. *Journal of Applied Ecology*, *52*(1), 199–209. https://doi.org/10.1111/1365-2664.12350

Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M., & Moore, M. M. (2020). The Net Effect of Functional Traits on Fitness. *Trends in Ecology & Evolution*, *35*(11), 1037–1047. https://doi.org/10.1016/j.tree.2020.07.010

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

Mason, C. M., McGaughey, S. E., & Donovan, L. A. (2013). Ontogeny strongly and differentially alters leaf economic and other key traits in three diverse Helianthus species. *Journal of Experimental Botany*, *64*(13), 4089–4099. https://doi.org/10.1093/jxb/ert249

Minor, J., Falk, D. A., & Barron-Gafford, G. A. (2017). Fire Severity and Regeneration Strategy Influence Shrub Patch Size and Structure Following Disturbance. *Forests, Trees and Livelihoods*, *8*(7), 221. https://doi.org/10.3390/f8070221

Moreno, J. M., & Oechel, W. C. (1994). Fire Intensity as a Determinant Factor of Postfire Plant Recovery in Southern California Chaparral. In J. M. Moreno & W. C. Oechel (Eds.), *The Role of Fire in Mediterranean-Type Ecosystems* (pp. 26–45). Springer New York. https://doi.org/10.1007/978-1-4613-8395-6_3

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews of the Cambridge Philosophical Society*, *88*(2), 349–364. https://doi.org/10.1111/brv.12004

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, *3*(4), 743–756. https://doi.org/10.1111/j.2041-210x.2012.00196.x

Ng, E., & Miller, P. C. (1980). Soil Moisture Relations in the Southern California Chaparral. *Ecology*, *61*(1), 98–107. https://doi.org/10.2307/1937160

Nicita, E., & Halverson, E. (2018). *Holy Fire Burned Area Emergency Response Soil Resource Report*. US Forest Service.

Paddock, W. A. S., III, Davis, S. D., Brandon Pratt, R., Jacobsen, A. L., Tobin, M. F., López-Portillo, J., & Ewers, F. W. (2013). Factors Determining Mortality of Adult Chaparral Shrubs in an Extreme Drought Year in California. *Aliso: A Journal of Systematic and Floristic Botany*, *31*(1), 49–57. https://doi.org/10.5642/aliso.20133101.08

Padilla, F. M., & Pugnaire, F. I. (2007). Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology*, *21*(3), 489–495. https://doi.org/10.1111/j.1365-2435.2007.01267.x

Parker, V. T., Pratt, R. B., & Keeley, J. E. (2016). TWENTY-FOUR. Chaparral. In H. Mooney & E. Zavaleta (Eds.), *Ecosystems of California* (pp. 479–508). University of California Press. https://doi.org/10.1525/9780520962170-028

Park, I. W., & Jenerette, G. D. (2019). Causes and feedbacks to widespread grass invasion into chaparral shrub dominated landscapes. *Landscape Ecology*, *34*(3), 459–471. https://doi.org/10.1007/s10980-019-00800-3

Pausas, J. G., Bradstock, R. A., Keith, D. A., & Keeley, J. E. (2004). Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*, *85*(4), 1085–1100. https://doi.org/10.1890/02-4094

Pausas, J. G., & Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *The New Phytologist*, *204*(1), 55–65. https://doi.org/10.1111/nph.12921

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., & Others. (2013). *New handbook for standardised measurement of plant functional traits worldwide. Aust. Bot. 61, 167--234.*

Pickett, S. T. A., & White, P. S. (1985). Chapter 21 - Patch Dynamics: A Synthesis. In S. T. A. Pickett & P. S. White (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics* (pp. 371–384). Academic Press. https://doi.org/10.1016/B978-0-12-554520-4.50026-5

Pratt, R. B., Jacobsen, A. L., Hernandez, J., Ewers, F. W., North, G. B., & Davis, S. D. (2012). Allocation tradeoffs among chaparral shrub seedlings with different life history types (Rhamnaceae). *American Journal of Botany*, *99*(9), 1464–1476. https://doi.org/10.3732/ajb.1200193

Pratt, R. B., Jacobsen, A. L., Mohla, R., Ewers, F. W., & Davis, S. D. (2008). Linkage between water stress tolerance and life history type in seedlings of nine chaparral species (Rhamnaceae). *Journal of Ecology*, *96*(6), 1252–1265. https://doi.org/10.1111/j.1365-2745.2008.01428.x

PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data created 4 Feb 2014, accessed 24 Jan 2023

R Core Team. (2021). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/*. https://www.R-project.org/

Redmond. (2022). *CWD and AET function (Version V1.0.3). Zenodo. https://doi.org/10.5281/zenodo.6416352*. https://doi.org/10.5281/zenodo.6416352

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

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223. https://doi.org/10.1111/j.2041-210x.2011.00169.x

Salguero-Gómez, R. (2017). Applications of the fast-slow continuum and reproductive strategy framework of plant life histories. *The New Phytologist*, *213*(4), 1618–1624. https://doi.org/10.1111/nph.14289

Salguero-Gómez, R., & Laughlin, D. (2021). Not all traits are functional: the Panglossian paradigm. *Authorea Preprints*. https://doi.org/10.22541/au.163940711.10447233/v1

Schmalbach, H. L., Franklin, J., & O’Leary, J. F. (2007). Patterns of Postfire Regeneration in a Southern California Mixed Chaparral Community. *Madroño; a West American Journal of Botany*, *54*(1), 1–12. https://doi.org/10.3120/0024-9637(2007)54[1:POPRIA]2.0.CO;2

Spasojevic, M. J., Bahlai, C. A., Bradley, B. A., Butterfield, B. J., Tuanmu, M.-N., Sistla, S., Wiederholt, R., & Suding, K. N. (2016). Scaling up the diversity-resilience relationship with trait databases and remote sensing data: the recovery of productivity after wildfire. *Global Change Biology*, *22*(4), 1421–1432. https://doi.org/10.1111/gcb.13174

Spasojevic, M. J., Yablon, E. A., Oberle, B., & Myers, J. A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* , *5*(10), art129. https://doi.org/10.1890/ES14-000159.1

Stephenson, N. (1998). Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, *25*(5), 855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x

Suding, K. N. (2011). Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Suding, K. N., Goldberg, D. E., & Hartman, K. M. (2003). Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology*, *84*(1), 1–16. https://doi.org/10.1890/0012-9658(2003)084[0001:RASTSL]2.0.CO;2

Suding, K. N., Lavorel, S., Chapin, F. S., III, Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., & Navas, M.-L. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, *14*(5), 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Syphard, A. D., Brennan, T. J., & Keeley, J. E. (2019). Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Diversity and Distributions*, *25*(1), 90–101. https://doi.org/10.1111/ddi.12827

Underwood, E. C., Hollander, A. D., Molinari, N. A., Larios, L., & Safford, H. D. (2022). Identifying priorities for post-fire restoration in California chaparral shrublands. *Restoration Ecology*, *30*(3). https://doi.org/10.1111/rec.13513

Van de Water, K. M., & Safford, H. D. (2011). A Summary of Fire Frequency Estimates for California Vegetation before Euro-American Settlement. *Fire Ecology*, *7*(3), 26–58. https://doi.org/10.4996/fireecology.0703026

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

VinZant, K., Howland, J., & Bessemer, A. (2018). *Holy Fire BAER Technical Specialist Botany Report*. US Forest Service.

Walker, L. R., & del Moral, R. (2003). *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press. https://play.google.com/store/books/details?id=fkfr24g-PCkC

Westerband, A. C., & Horvitz, C. C. (2017). Photosynthetic rates influence the population dynamics of understory herbs in stochastic light environments. *Ecology*, *98*(2), 370–381. https://doi.org/10.1002/ecy.1664

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics*, *33*(1), 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

White, P. S. (1979). Pattern, process, and natural disturbance in vegetation. *The Botanical Review; Interpreting Botanical Progress*, *45*(3), 229–299. https://doi.org/10.1007/BF02860857

White, P. S., & Jentsch, A. (2004). Disturbance, succession, and community assembly in terrestrial plant communities. In Temperton, V. M., Hobbs, R. J., Nuttle, T., & Halle, S. (Ed.), *Assembly rules and restoration ecology: bridging the gap between theory and practice* (Vol. 5, pp. 342–366). Island Press. https://books.google.com/books?hl=en&lr=&id=BQm8BwAAQBAJ&oi=fnd&pg=PA342&dq=Disturbance+succession+community+assembly+terrestrial+plant+communities+White+Jentsch&ots=JV4Jy46-Yk&sig=QCSebFHZrgY9JGjQ39WKkHVT9BA

Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., McGlinn, D. J., O’Meara, B. C., Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D. E., Stevens, P. F., Westoby, M., Wright, I. J., Aarssen, L., Bertin, R. I., Calaminus, A., Govaerts, R., … Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, *506*(7486), 89–92. https://doi.org/10.1038/nature12872

Zedler, P. H., Gautier, C. R., & McMaster, G. S. (1983). Vegetation Change in Response to Extreme Events: The Effect of a Short Interval between Fires in California Chaparral and Coastal Scrub. *Ecology*, *64*(4), 809–818. https://doi.org/10.2307/1937204

Zirbel, C. R., & Brudvig, L. A. (2020). Trait–environment interactions affect plant establishment success during restoration. *Ecology*, *101*(3), e02971. https://doi.org/10.1002/ecy.2971

Appendix S1

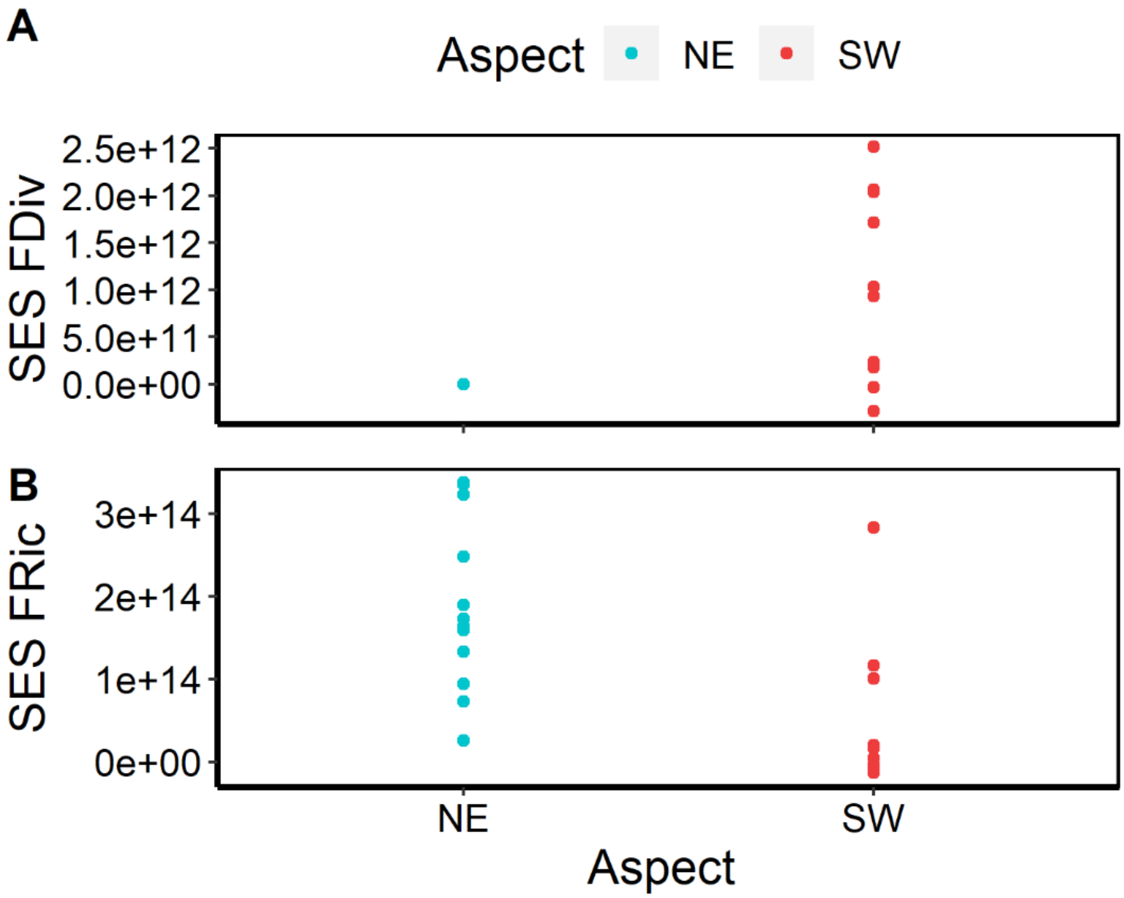

Figure S1.1 Standard effect size (SES) of observed functional diversity metrics compared to null model random communities across aspects. A) SES FDiv (functional divergence) and B) SES FRic (functional richness) across NE (Northeast; blue) and SW (Southwest; red) aspects.

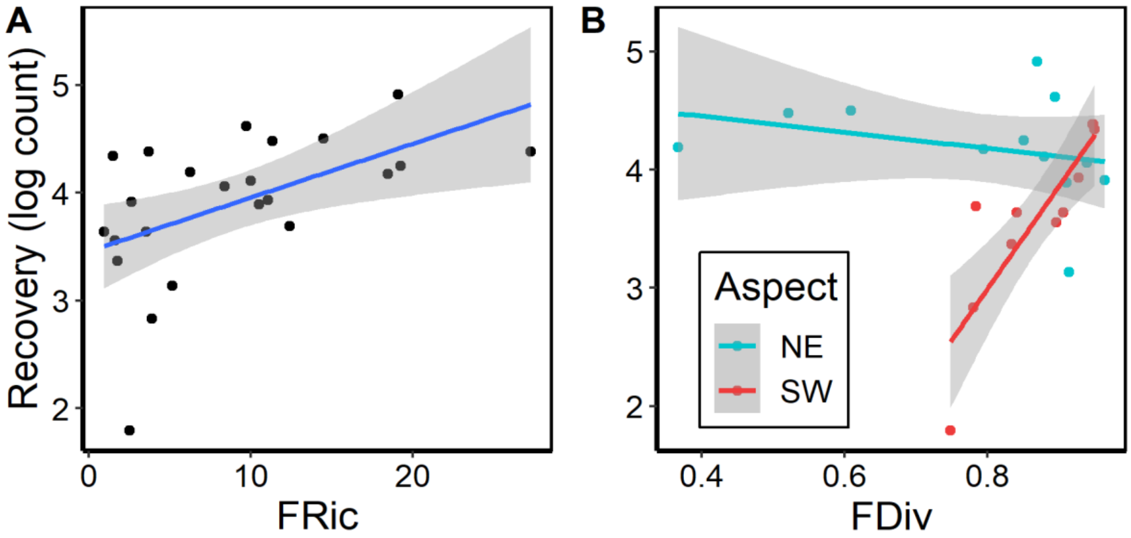

Figure S1.2 Factors predictive of recovery include regeneration trait A) functional richness (FRic) and B) the interaction of functional divergence (FDiv) and aspect (NE, blue vs SW, red).

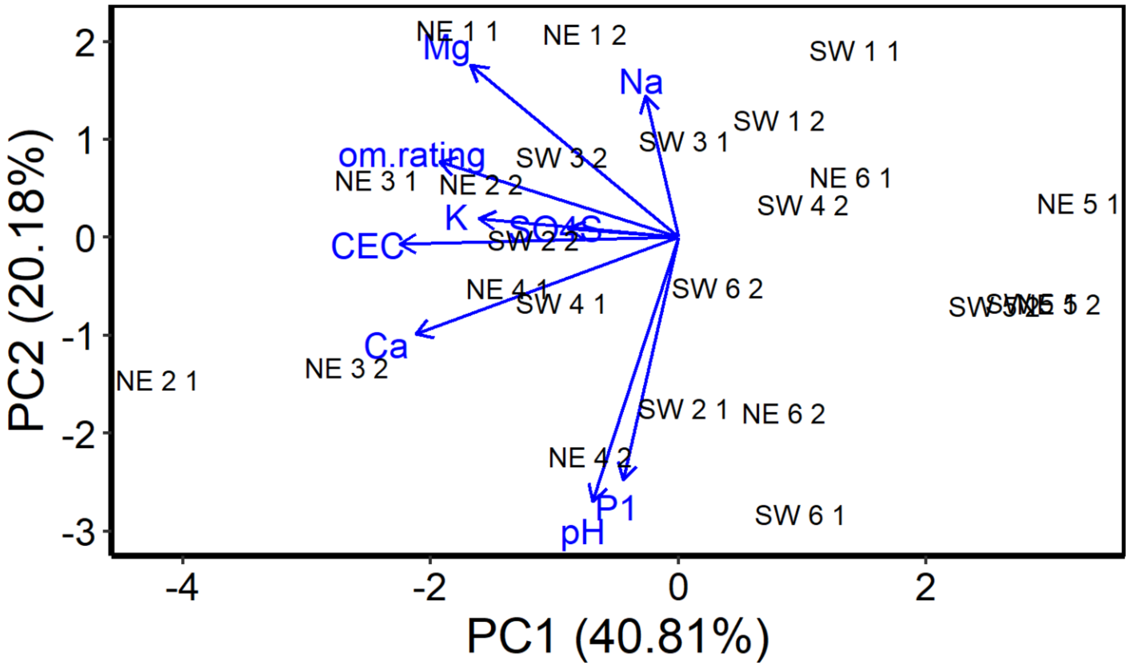

Figure S1.3 PCA of environmental factors across transects. Environmental factors include Mg: Magnesium, Na: Sodium, Ca: Calcium, om.rating: organic matter rating; K: potassium, CEC: cation exchange capacity, SO4S: sulfate, P1: phosphorus, pH.

Table S1.1 Trait collection coordinates. Site indicates site name using the ordered combination of burned (B) or unburned (UB), Northeast (NE) or Southwest (SW) aspect, and site number. Site specific coordinates (decimal degrees), elevation (meters), aspect (degrees), and slope (degrees) are also included.

Site	Latitude	Longitude	Elevation	Aspect	Slope
BNE2	33.69392	-117.465	1252.771	5.815221	21.26689
BNE3	33.69706	-117.471	1302.231	53.65504	25.29422
BNE3.1	33.69685	-117.471	1304.037	74.09906	19.88614
BNE3.2	33.69692	-117.471	1293.28	66.8251	31.76605
BNE4	33.68424	-117.456	1246.799	41.60904	34.33947
BNE5	33.66493	-117.441	1017.058	6.473262	22.33736
BNE6	33.66536	-117.446	1030.724	48.66582	29.36586
BNE7	33.67221	-117.459	1290.222	53.51503	21.92494
BSW1	33.69029	-117.463	1243.407	199.5168	20.52619
BSW2	33.6933	-117.466	1245.662	249.8411	20.13851
BSW3	33.69696	-117.472	1303.418	246.2309	16.79732
BSW3.2	33.69546	-117.471	1270.949	219.8964	32.3133
BSW4	33.68454	-117.457	1264.023	172.4286	18.44042
BSW5	33.66444	-117.441	1016.81	180.5543	30.07737
BSW6	33.66661	-117.446	1040.588	225.292	35.84798
BSW7	33.67164	-117.459	1291.359	223.3288	16.12177
BSW7.1	33.66587	-117.447	1056.497	210.7999	21.15461
BSW8	33.66601	-117.443	1007.728	243.3739	35.19123
UBNE1	33.65973	-117.447	1023.101	330.32	15.85257
UBNE1.1	33.65965	-117.447	1024.572	63.3872	12.74701

Site	Latitude	Longitude	Elevation	Aspect	Slope
UBNE2	33.67019	-117.462	1327.327	27.74414	13.28974
UBNE3	33.66856	-117.457	1266.036	122.5766	13.27348
UBNE6	33.66036	-117.45	1062.068	41.39526	23.93132
UBNE7	33.65338	-117.445	1053.683	92.95339	14.8416
UBSW1	33.6577	-117.449	1022.712	184.3161	9.667078
UBSW2	33.66866	-117.464	1361.401	297.4321	14.61569
UBSW3	33.66856	-117.457	1268.851	228.0163	7.74294
UBSW4	33.67108	-117.458	1314.557	160.8367	9.202979
UBSW5	33.66793	-117.454	1226.369	164.2694	12.08885
UBSW6	33.66066	-117.449	1049.321	207.5909	24.50748

Table S1.2 Species mean traits across aspect, life stage, regeneration strategy. Strategy is life stage (a: adult) or regeneration strategy (r: resprouter, s: seeder), Species is the six letter species code, Count is number of individuals used to calculate trait means, LA: Leaf Area (cm^2), SLA: Specific Leaf Area (cm^2/g), LDMC: Leaf Dry Matter Content (mg/g), % N: percent nitrogen leaf content (%), δ13C: discrimination of δ13C (‰). See Table S1.9 for species names.

Aspect	Strategy	Species	Count	LA	SLA	LDMC	Height	% N	δ13C
NE	a	ADEFAS	12	0.334	60.251	471.849	NA	1.100	20.367
NE	a	ARCGLAN	12	5.465	36.981	507.894	NA	0.800	20.122
NE	a	CEACRA	12	1.562	27.942	498.370	NA	1.233	19.108
NE	a	CEAOLI	12	1.362	70.755	464.836	NA	1.633	22.260
NE	a	DENRIG	8	2.512	58.658	338.953	NA	1.900	19.318
NE	a	HETARB	11	13.935	57.450	442.469	NA	1.700	19.948
NE	a	QUEBER	13	3.254	51.579	549.263	NA	1.533	19.597
NE	a	RHAILI	12	4.890	62.431	423.520	NA	1.700	18.797
NE	a	RHUOVA	13	19.025	53.768	393.798	NA	1.033	18.272
NE	r	ADEFAS	10	0.188	78.761	378.469	44.740	2.000	21.470
NE	r	ARCGLAN	10	8.027	84.290	329.360	47.310	1.267	21.874
NE	r	CEALEU	9	1.942	116.950	358.516	38.278	2.633	22.470
NE	r	CERBET	10	1.443	84.414	389.958	57.530	2.000	21.838
NE	r	DENRIG	12	6.718	96.976	246.677	99.992	3.333	19.143
NE	r	FRACAL	5	13.088	106.273	348.924	92.800	3.733	18.376
NE	r	HETARB	7	15.862	80.364	350.037	80.143	1.867	19.354
NE	r	QUEBER	16	3.164	95.004	367.790	98.825	1.833	19.143
NE	r	QUEWIZ	9	2.051	58.034	454.879	95.278	1.267	17.367
NE	r	RHAILI	12	6.706	109.639	315.429	78.417	2.467	18.725
NE	r	RHUOVA	11	16.156	78.465	299.119	64.964	1.533	18.099
NE	s	ACMGLA	11	0.214	112.837	311.991	18.118	2.500	21.732

NE	s	ADEFAS	6	0.218	104.768	443.093	8.917	2.000	21.417
Aspect	Strategy	Species	Count	LA	SLA	LDMC	Height	% N	δ13C
NE	s	ARCGLAN	9	0.819	105.906	420.282	4.178	1.767	24.194
NE	s	CEACRA	12	1.215	62.528	415.375	7.275	1.867	21.102
NE	s	CEALEU	10	1.447	121.071	361.318	7.580	2.900	21.875
NE	s	CEAOLI	13	1.944	110.506	363.123	11.938	2.967	20.928
NE	s	DENRIG	12	9.681	125.351	211.643	31.617	3.400	20.926
NE	s	RHUOVA	10	3.292	113.307	346.468	5.870	1.933	21.628
SW	a	ADEFAS	11	0.335	56.868	505.014	NA	1.200	20.366
SW	a	ARCGLAN	12	5.523	37.782	513.830	NA	0.767	19.982
SW	a	CEACRA	13	1.404	24.873	503.291	NA	1.267	17.888
SW	a	CEALEU	10	0.542	73.459	459.517	NA	1.600	20.786
SW	a	DENRIG	6	4.380	57.016	342.885	NA	1.967	19.283
SW	a	ERIFAS	13	0.733	70.271	413.880	NA	0.933	22.505
SW	a	HETARB	6	13.909	70.097	402.644	NA	1.400	19.667
SW	a	QUEBER	15	2.340	53.100	539.202	NA	1.267	19.423
SW	a	RHAILI	11	3.714	59.613	450.104	NA	1.267	21.279
SW	a	RHUOVA	7	18.313	53.671	394.180	NA	1.100	18.237
SW	r	ADEFAS	14	0.227	72.390	466.898	49.129	1.650	21.592
SW	r	ARCGLAN	9	8.760	74.461	341.316	46.167	1.567	21.662
SW	r	CERBET	7	1.442	64.283	457.964	107.071	2.700	20.018
SW	r	DENRIG	12	3.952	95.443	244.589	94.583	3.100	19.284
SW	r	HETARB	10	13.230	105.560	296.463	90.110	2.833	19.179
SW	r	RHAILI	9	5.319	88.086	375.963	103.667	2.567	19.179
SW	r	RHUOVA	16	17.060	79.751	314.808	88.856	2.033	17.679
SW	s	ACMGLA	10	0.356	106.924	346.932	14.320	2.300	21.627
SW	s	ADEFAS	10	0.155	89.697	463.549	12.670	2.350	22.944

SW	s	ARCGLAN	11	1.302	91.245	423.434	5.055	1.700	21.768
Aspect	Strategy	Species	Count	LA	SLA	LDMC	Height	% N	δ13C
SW	s	CEACRA	12	1.015	62.612	410.330	10.067	1.800	22.259
SW	s	CEALEU	11	1.460	129.896	338.603	7.682	2.367	23.384
SW	s	CEAOLI	8	1.293	106.026	346.742	12.763	2.933	21.909
SW	s	CEASPP	4	3.629	129.934	329.380	16.250	NA	NA
SW	s	DENRIG	12	13.123	127.762	177.835	25.817	3.533	21.417
SW	s	ERIFAS	10	0.479	85.583	390.978	18.680	1.600	20.367
SW	s	RHUOVA	5	3.417	98.347	355.232	6.000	1.800	19.985

Table S1.3 Number of tagged individuals used to assess species survival across regeneration strategies and aspects. Strategy is regeneration strategy (r: resprouter, s: seeder), Species is the six letter species code, Count is the number of individuals used to calculate species proportion survival. See Table S1.9 for full species names.

Species	Strategy	Aspect	Count
ACMGLA	s	SW	31
ADEFAS	r	NE	4
ADEFAS	r	SW	14
ADEFAS	s	NE	11
ADEFAS	s	SW	48
ARCGLAN	r	NE	12
ARCGLAN	r	SW	12
ARCGLAN	s	NE	22
ARCGLAN	s	SW	10
CEALEU	r	NE	5
CEALEU	s	NE	20
CEALEU	s	SW	13
CEAOLI	s	NE	52
CEAOLI	s	SW	31
CERBET	r	SW	4
DENRIG	s	NE	32
DENRIG	s	SW	15
ERIFAS	s	NE	4
ERIFAS	s	SW	13
HETARB	r	NE	11
QUEBER	r	NE	3
QUEWIZ	r	NE	11
RHAILI	r	NE	3

Species	Strategy	Aspect	Count
RHUOVA	r	NE	3
RHUOVA	r	SW	4
RHUOVA	s	NE	25

Table S1.4 Summary model statistics for Pagel’s λ test assessing phylogenetic signal in traits across closely related species. Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001).

Trait	Pagel’s λ	p-value
SLA	6.6107e-05	1
LA	0.999934	0.0947982
LDMC	0.999934	0.179537
Height	0.91477	0.396034
% N	0.958673	0.281158
δ13C	6.6107e-05	1

Table S1.5 Summary model statistics for non-parametric Scheirer Ray Hare test assessing how aspect and regeneration strategy influence shrub survival. Survival was calculated as the proportion survival during the last survey in 2022. H values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001).

	H value	p-value
Aspect	$0.1608_{1,22}$	0.68838
Regeneration Strategy	$16.3217_{1,22}$	0.00005 ***
Aspect: Regeneration Strategy	$0.1226_{1,22}$	0.72628

Table S1.6 Summary model statistics for third order polynomial regression models testing how regeneration traits influence survival and linear regression models testing how regeneration traits influence growth. Survival was calculated as the proportion survival during the last survey in 2022 for only seeders. Growth was calculated as the plant volume (length X width X height) during the last survey in 2022 for only seeders. F values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001). SLA: Specific Leaf Area, LA: Leaf Area, LDMC: Leaf Dry Matter Content, % N: percent nitrogen leaf content, δ13C: discrimination of δ13C.

Trait	Survival		Growth	
	F	p-value	F	p-value
SLA	$0.6148_{3,4}$	0.640686	$0.6096_{1,5}$	0.4703
LA	$1.9261_{3,4}$	0.267006	$0.2484_{1,5}$	0.6394
LDMC	$0.125_{3,4}$	0.940492	$2.2411_{1,5}$	0.1946
Height	$11.416_{3,4}$	0.01978 *	$1.8679_{1,5}$	0.2300
% N	$0.3849_{3,4}$	0.770585	$7.0070_{1,5}$	0.04559 *
δ13C	$1.894_{3,4}$	0.271817	$0.2182_{1,5}$	0.6600

Table S1.7 Summary model statistics for ANOVAs assessing how community weighted mean (CWM) traits and standard effect size (SES) between observed and null modeled random community traits differ across aspects. CWMs were calculated from year one composition data. Null model communities were calculated from year one composition data. F values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001). SLA: Specific Leaf Area, LA: Leaf Area, LDMC: Leaf Dry Matter Content, % N: percent nitrogen leaf content, δ13C: discrimination of δ13C, FRic: functional richness, FEve: functional evenness, FDiv: functional divergence, FDis: functional dispersion.

	CWM		SES	
	F	p-value	F	p-value
FDis	$0.4308_{1,22}$	0.5184	$0.3449_{1,22}$	0.563
FDiv	$1.5627_{1,21}$	0.225	$11.643_{1,21}$	0.002622 **
FRic	$2.9819_{1,21}$	0.09888	$11.862_{1,21}$	0.002432 **
FEve	$5.7398_{1,21}$	0.02598 *	$1.2938_{1,21}$	0.2682
SLA	$3.202_{1,22}$	0.08733	$1.2092_{1,22}$	0.2834
LA	$0.0353_{1,22}$	0.8528	$2.0454_{1,22}$	0.1667
LDMC	$0.7957_{1,22}$	0.382	-	-
%N	$0.3116_{1,22}$	0.5823	$0.8692_{1,22}$	0.3613
δ13C	$7.4793_{1,22}$	0.01209 *	$3.654_{1,22}$	0.06905
Height	$2.6902_{1,22}$	0.1152	$2.5313_{1,22}$	0.1259

Table S1.8 Summary model statistics for the best fit models for how functional traits at the regeneration stage and adult stage influence shrub recovery across aspects. Recovery was estimated as natural log transformed count data in year two. F values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001). FDiv: functional divergence, FRic: functional richness.

	Regeneration		Adult	
	F value	p-value	F value	p-value
Aspect	$24.7437_{1,18}$	9.815e-05 ***	$9.4498_{1,20}$	0.005987 **
FDiv	$1.0626_{1,18}$	0.3162794		
FRic	$4.5907_{1,18}$	0.0460653 *		
Aspect:FDiv	$22.4389_{1,18}$	0.0001646 ***		
Resprouter cover			$0.0430_{1,20}$	0.837783
Aspect: resprouter cover			$6.6051_{1,20}$	0.018271*

Table S1.9 Species six letter codes and scientific names for the shrub species used for functional trait collections.

Code	Scientific Name
ACMGLA	*Acmispon glaber*
ADEFAS	*Adenostoma fasciculatum*
ARCGLAN	*Arctostaphylos glandulosa*
CEACRA	*Ceanothus crassifolius*
CEALEU	*Ceanothus leucodermis*
CEAOLI	*Ceanothus oliganthus spp. oliganthus*
CEASPP	*Ceanothus sp.*
CERBET	*Cercocarpus betuloides*
DENRIG	*Dendromecon rigida*
ERIFAS	*Eriogonum fasciculatum*
FRACAL	*Frangula californica*
HETARB	*Heteromeles arbutifolia*
QUEBER	*Quercus berberidifolia*
QUEWIZ	*Quercus wislizeni*
RHAILI	*Rhamnus ilicifolia*
RHUOVA	*Rhus ovata*

Chapter 2: The interaction between life stages and spatial scales impacts the strength of trait filtering and drivers of trait variation

Abstract

Plant functional traits are commonly used to understand how environmental gradients shape plant assembly, but this is dependent on the scale and source of trait variation. Early life stage traits (regeneration traits) may mediate the recovery process, yet are largely understudied and differ from adult traits commonly used to determine community structure and function. Here, we examined 1) how functional traits change across life stages and regeneration strategies, 2) how life stage, regeneration strategy, and scale of resource gradient influence the direction and magnitude of trait filtering, and 3) how the importance of a driver of trait variation changes relative to other drivers of variation (i.e., variation between local environment, regeneration strategies, species) across life stages and a regional stress gradient. We collected leaf functional traits in chaparral shrublands for regenerating shrub species within three burn scars across a regional increasing elevation gradient from the coast moving inland in Southern California and for adults in nearby unburned areas across northeast and southwest aspects. We found regeneration traits were indicative of resource-acquisitive functional strategies (higher SLA, higher $\delta^{13}C$ discrimination/lower iWUE, higher % N, lower LDMC) relative to adults, and regenerating seeders had the most resource-acquisitive traits. Life stage, regeneration strategy, and scale of resource gradient influence the direction of trait filtering similarly (i.e., traits became conservative over time and more stressful conditions), but the magnitude of trait filtering differed where the environment filtered regeneration traits more strongly than adult traits. The interaction between ontogeny and spatial scale influenced trait variation, where the role of interspecific variation was larger for adults compared to regenerating plants for most traits. Furthermore, the regional stress gradient regulated the amount each driver of variation contributed to leaf trait variation, where regeneration strategy and topography drove trait variation under certain life stage and regional stress combinations. Our results show that the magnitude rather than direction of trait filtering and the contribution of different drivers of trait variation changes across life stages and spatial scales, highlighting the importance of identifying how ontogeny and spatial scales impact traits to better apply trait-based approaches in community assembly and recovery.

Introduction

Patterns of plant functional traits and their variation have improved understanding of how environmental gradients and disturbances shape vegetation assembly (Díaz et al. 1999; Lavorel and Garnier 2002; McGill et al. 2006; Mouillot et al. 2013). Trait values within a community can change predictably across environmental gradients, and this trait-environment matching results in different functional community compositions (Diaz et al. 1998; Cornwell and Ackerly 2009). However, the inference gained from trait-based approaches is dependent on identifying the relevant scale and source of trait variation (Violle et al. 2012; Laughlin et al. 2012; Shipley et al. 2016). One key source of functional trait variation is ontogeny, developmental changes throughout a species' lifespan, which can result in species shifting from one functional strategy (i.e., stress tolerant) to another (i.e., resource acquisitive) over time (Spasojevic et al. 2014; Dayrell et al. 2018; Garbowski et al. 2021; Henn and Damschen 2021). However, less research has focused on disentangling how drivers of trait variation (e.g., adaptive trait variation at the species vs individual level) differ between early life stage and adult plants compared to the influence of environmentally driven trait variation. The spatial scale of the environmental gradient can also differentially influence trait variation, such that regional scale gradients create more trait variation at the species level (i.e., interspecific variation) while local scale gradients create more trait variation at the individual level (i.e., intraspecific variation; Lajoie and Vellend 2015). Thus, identifying how life stage and spatial scale interact to drive trait variation will improve our ability to apply trait-based approaches to community assembly and recovery processes.

Environmental trait filtering can vary with ontogeny with strong implications for plant performance and community assembly (Spasojevic et al. 2014; Larson and Funk 2016; Larson et al. 2021). Resource environments can differ between stages of establishment (i.e., regeneration stage) and persistence (i.e., adult stage; Grubb 1977), resulting in seedlings exhibiting different trait values related to a higher resource acquisition strategy (e.g., higher specific leaf area (SLA) than adults; Spasojevic et al. 2014; Dayrell et al. 2018; Henn and Damschen 2021). Moreover, the regeneration stage may experience stronger niche selection due to resource conditions, resulting in stronger species sorting and species being more functionally similar (Ramachandran et al. 2023). These dynamics contribute to regenerating and adult individuals differing in their niche breadth and expressing ontogenetic niche shifts (i.e., changes in niche breadth or position throughout development; Parish and Bazzaz 1985). Seedlings may have larger niche breadth and trait variation compared to adults when early-successional heterogeneous environmental conditions become more homogenous as plants mature (e.g. available nutrients becoming limited as plants grow; Niinemets 2010). Alternatively, adults may experience and occupy a broader range of regional environmental conditions than seedlings (e.g., experience more fluctuations in annual precipitation and temperature over longer timescales), resulting in adults with larger niche breadth and trait variation (Gabler and Siemann 2012). While many studies have assessed trait differences across life stages (e.g., saplings vs adults; Spasojevic et al. 2014; Dayrell et al. 2018), they miss sampling at the critical initial regeneration stage for long lived species (i.e., establishment niche) and may not detect the full extent of trait filtering that occurs early in establishment.

Trait-environment matching at the species level can result in different relationships depending on the spatial scale of focus (Lajoie and Vellend 2015; Messier et al. 2017; Li et al. 2019; Guzmán-Jacob et al. 2022). While the regional scale climate consistently filters traits to be more similar (i.e., lower SLA and a smaller range of SLA values as resources become limited; Weiher and Keddy 1995; Reich et al. 1997; Grime 2006), more trait variation can occur within a local community than across regional climatic gradients (Wright et al. 2004; Li et al. 2019). Furthermore, the direction and magnitude of a biological response to an environmental gradient is dependent on the spatial scale in which it is measured (i.e., scale of effect, optimal spatial scale to measure an environmental variable based on how an organism perceives the landscape; Miguet et al. 2016). For example, seed traits influencing germination were found to vary more at the local scale of post-fire resource availability than at the regional climatic scale, highlighting the effect of local scales for regenerating plants (Moreira et al. 2012). In contrast, adult traits may be more influenced by regional climatic fluctuations influencing their persistence over time (Weiher and Keddy 1995; Reich et al. 1997; Grime 2006). To understand how functional trait patterns may change with time, it is integral to test the effects of both regional and local scales on trait-environment matching across life stages.

Different selective forces and environmental gradients can simultaneously act on the same trait, thus identifying the appropriate drivers of trait variation is key (Shipley et al. 2016). Spatial scale is predicted to be a main factor in differentiating environmental drivers of trait variation, where regional spatial scales may select species trait means while local scale heterogeneity may select for plasticity within species (Lajoie and Vellend 2015). Spatial scale may then result in interspecific differences driving trait variation at regional scales and (Lajoie and Vellend 2015). Moreover, plants experience the combined stress of multiple environmental gradients acting at the same time, but few trait-environment matching studies focus on interacting environmental gradients (Niinemets 2010; Anacker et al. 2011; Lajoie and Vellend 2015; Li et al. 2019). The stress-dominance hypothesis predicts a shift from more trait variation under mild resource conditions to less trait variation under harsh, limited resource conditions (Weiher and Keddy 1995), but it is unclear how this functions across multiple environmental gradients simultaneously acting on a trait (i.e., does the contribution of one environmental gradient to trait variation change based on the amount of stress of another environmental gradient?). Therefore, integrating multivariate environmental changes at different spatial scales may better identify shifts in the contribution of trait variation.

The drivers of trait variation may differ across life stages, as niche requirements shift through ontogeny (Li et al. 2019). Stronger environmental filtering for regenerating plants (Grubb 1977) may necessitate a higher proportion of individual level trait variation to overcome environmental conditions during the sensitive regeneration stage compared to established adults (Dayrell et al. 2018; Larson et al. 2021). For example, topographic factors and space contributed more to trait variation for seedlings than adults (Li et al. 2019). In contrast, environmental filtering for adult plants may necessitate more species level trait variation to coexist in a community and persist through fluctuating environmental conditions over long lifespans. Understanding drivers of trait variation is important to accurately use trait-based approaches in community assembly (Laughlin et al. 2012; Shipley et al. 2016), thus evaluating how drivers of trait variation change across life stages and spatial scales is needed.

Disturbances like fire occur over broad heterogeneous landscapes and provide an opportunity to assess how interacting multi-scale environmental gradients and ontogeny influence trait dynamics. The first year post-fire has a huge flush of recruitment, due to the influx of nutrient and light availability mixed with serotinous germination, followed by high mortality (Bond and van Wilgen 1996; Keeley et al. 2005) suggesting first year regeneration is an important demographic stage. Overall landscape level resource availability is high post-fire, but topography creates local scale heterogeneity. Aspect type can influence resource availability, where Northeast (pole-facing) aspects receive less solar insolation creating cooler air and soil temperatures and wetter soils while Southwest (equator-facing) aspects receive more solar insolation and have hotter air and soil temperatures and drier soils (Martínez and Armesto 1983), differently impacting trait means and variation (Ackerly et al. 2002). Moreover, how a plant regenerates after a disturbance (i.e., germinates from seed, resprouts from energy storage structures), can also be a driver of trait variation (Anacker et al. 2011). Plants regenerating from seed (seeders) should have traits representative of the resource acquisitive strategy, since they must growth fast to reach establishment, while adults should have traits indicative of the conservative strategy conferring persistence, with regenerating resprouters having intermediate traits as their persistent root structure essentially surpasses the establishment stage but they must regrow aboveground photosynthetic tissues. The post-fire setting provides an opportunity to assess how the multiple interacting factors filter traits in the regeneration niche (e.g., post-fire) vs adult niche (e.g., pre-fire or unburned), and disentangle if the contribution of these drivers of trait variation are maintained throughout different life stages and across regional scales.

To assess what drives trait variation at different life stages and understand how spatial scale influences this during post-fire recovery of long-lived shrubland communities, we designed an observational study across three burn scars spanning a regional resource gradient and a local topographic gradient. We asked: 1) how do functional traits change across life stages and regeneration strategies, 2) how does life stage, regeneration strategy, and scale of resource gradient influence the direction and magnitude of trait filtering, and 3) does the importance of a driver of trait variation change relative to other drivers of variation (i.e., variation between local environment, regeneration strategies, species) across life stages and are changes dependent on a regional environmental gradient? Specifically, we predict that: 1) regeneration traits will have a more resource acquisitive strategy than adult traits, and regenerating seeders will have the most resource acquisitive strategy, 2) traits will become more resource conservative as the environmental gradients become harsher at both spatial scales, with stronger filtering at regional scales and for regeneration traits, and 3) interspecific variation will drive trait variation more at the adult stage compared to regenerating plant stage, and the regional resource gradient will regulate the amount each source of variation contributes to leaf trait variation.

Methods

Study Location

This study was conducted in three chaparral shrublands which all experienced a wildfire in 2018: the Aliso Fire in the Aliso and Wood Canyons Wilderness Park, Laguna Niguel, Ca (33.55215, -117.744), the Holy Fire in the Cleveland National Forest, Lake Elsinore, CA (33.67169, -117.459), and the Cranston Fire in the San Bernardino National Forest, Idyllwild, CA (33.69679, -116.699). Chaparral is dominated by thick leaved, sclerophyllous shrubs that create a short, closed canopy. Study sites ranged in elevation from an average of 93 m at Aliso, 1182 m at Holy, and 1541 m at Cranston. The historic annual growing season (Oct. - Aug. from 1970-2019) total precipitation at Aliso is 328.14 mm, at Holy is 495.73 mm, and at Cranston is 580.29 mm and historic annual growing season mean temperature at Aliso is 17.19 °C, at Holy is 15.63 °C, and at Cranston is

12.74 °C (PRISM Climate Group 2023), characteristic of the Mediterranean climate with cool, wet winters and hot, dry summers. During the study period in 2019, total growing season precipitation was 501.22 mm at Aliso, 779.63 mm at Holy, and 797.94 mm at Cranston. The mean annual growing season temperature was 16.89 °C at Aliso, 14.98 °C at Holy, and 12.66 °C at Cranston. The focal vegetation community was kept constant between the three study locations and included montane mixed chaparral (*Arctostaphylos glandulosa* and *Ceanothus* spp. dominant) and chamise chaparral (*Adenostoma fasciculatum* dominant; Nelson and Howland 2018; VinZant et al. 2018). The vegetation community collected in Aliso also included sagebrush-buckwheat (*Artemisia californica*, *Eriogonum fasciculatum*) and scrub-chaparral (*Salvia* spp.; Almanza n.d.).

The Aliso Fire burned 71 hectares from June 2, 2018 through June 10, 2018, the Holy Fire burned 9,362 hectares from August 6, 2018 through September 13, 2018, and the Cranston Fire burned 5,317 hectares from July 25, 2018 through August 10, 2018. All three fires were caused by arson. These fires burned in a patchy mosaic pattern with small unburned areas remaining on the landscape. These unburned areas were used to compare traits of adult communities, in addition to unburned areas outside of the burn scar boundary. The Aliso Fire had no previous record of wildfire at the study location (data records start in 1878 from the Department of Forest and Fire Protection CAL FIRE - Fire Perimeter data “Firep21_2”, https://www.fire.ca.gov/what-we-do/fire-resource-assessment-program/fire-perimeters). The Holy Fire was within the normal 30-100 year fire return interval for chaparral (Hanes 1971; Van de Water and Safford 2011), as the time since the last burn ranged from 38 to 64 years in the burn scar and 64 to 93 years in the nearby unburned areas. The Cranston Fire was within the normal fire return interval, as the time since the last burn ranged from 37 to 75 years in the burn scar and 27 to 94 years in the nearby unburned areas.

Trait Data Collection

To determine tradeoffs in resource-use and growth strategies across life stages and regeneration strategies, we measured a suite of traits that are indicative of resource-use strategies. We measured morphological traits including: specific leaf area (SLA), leaf area (LA), and leaf dry matter content (LDMC) and chemical traits including % Nitrogen (% N) content and discrimination of $\delta^{13}C$ following standard functional trait protocols (Pérez-Harguindeguy et al. 2013). These morphological traits were selected as SLA and LDMC are associated with a plant's ability to acquire and use resources, while LA is associated with leaf energy and water balance while coping with temperature, drought, and nutrient stressors (Pérez-Harguindeguy et al. 2013). These chemical traits were selected as % N is indicative of photosynthetic capacity (Evans 1989), while discrimination of $\delta^{13}C$ is used as an indicator of intrinsic water use efficiency (iWUE) reflecting the efficiency of carbon gain through photosynthesis relative to water transpired (Farquhar et al. 1989). These traits are also associated with the leaf economic spectrum (Reich 2014) which captures key tradeoffs in acquisitive (high SLA, high LA, low LDMC, high % N, high discrimination of $\delta^{13}C$/low iWUE) vs conservative (low SLA, low LA, high LDMC, low % N, low discrimination of $\delta^{13}C$/high iWUE) resource-use strategies.

We collected leaf functional traits from 5-21 individuals for each of 11-15 dominant regenerating species within the burn scar (regeneration traits) and for adult species in nearby unburned areas (adult traits) across Northeast (NE) and Southwest (SW) aspects for a total of 25 different species sampled across the study (Table S2.1 collection coordinates; Table S2.2 species trait means across burn scar, aspect, life stage, regeneration strategy). All regeneration traits were collected on less than one year old seedlings or new aboveground biomass of regenerating resprouters (leaves collected at the end of the first growing season). Regeneration strategy was recorded for each species as either seeder or resprouter, where facultative species were assigned based on their recruitment in the field (i.e., *Adenostoma fasciculatum* resprouter, *Adenostoma fasciculatum* seeder) in burned areas, but not in the unburned areas since it was not possible to tell if facultative species present originated as resprouters or seeders during the last disturbance. To evaluate trait trade-offs at a local scale, we selected collection sites within each burn scar on NE and SW aspects that were accessible by roads and hiking. Within these sites we kept soil burn severity consistent in the medium to high category.

After collection in the field, leaves were re-hydrated overnight in dark conditions to reach saturated wet weight. The following day, excess moisture was wiped off the saturated leaves, weighed to measure wet weight, then scanned to measure leaf area (ImageJ, https:// imagej.nih.gov/ij/). Leaves were dried at 60 °C for a minimum of 72 h then weighed to measure dry weight. These data were used to calculate SLA as fresh LA (cm^2) divided by dry weight (g) and LDMC as dry weight (mg) divided by wet weight (g). For isotope analysis, leaf tissue was ground at UC Riverside for a total of 3 replicates per species, aspect, and life stage and strategy comprised of leaves from 1-5 individuals. Leaf δ^{13}C and % N content were measured at the University of Wyoming Stable Isotope Facility (http://www.uwyo.edu/sif/) where samples were analyzed for δ^{13}C and % N on a Carlo Erba 1110 Elemental Analyzer coupled to a Thermo Delta V IRMS or a Costech 4010 Elemental Analyzer coupled to a Thermo Delta Plus XP IRMS. Isotope ratios were calculated as

$$\delta[\ 13C]samples = (\frac{R_{sample}}{R_{standard}} - 1)\ x\ 1000$$

where R_{sample} and $R_{standard}$ are the $\delta^{13}C/^{12}C$ molar abundance ratios of samples, with 36-UWSIF-Glutamic 1 and 39-UWSIF-Glutamic 2 used as reference samples.

Discrimination of δ^{13}C was calculated as

$$\text{Discrimination of } C^{13} = (-0.008 - (\delta^{13}C * 0.001))/(1 + (\delta^{13}C * 0.001))*1000$$

where the discrimination of C^{13} is independent of the C^{13} values of both the standard used and the air, while δ^{13}C is relative to the standard used (Farquhar et al. 1989). Hereafter, discrimination of C^{13} will be denoted as δ^{13}C.

Resource Gradients Across Spatial Scales

The three study locations follow a regional resource and elevation gradient from the coast (Aliso) moving inland (Cranston, Fig. 2.1). We used a Principal Component Analysis (PCA) to collapse multiple environmental variables (elevation, precipitation, temperature, available water capacity, climatic water deficit, and slope) into two axes to quantify the resource gradient present at the regional vs local spatial scale. Climatic water deficit, defined as the amount of evapotranspirative demand that exceeds available soil moisture (Stephenson 1998), is used as an indicator of drought stress on soil and plants, and was calculated at each site using USGS Digital Elevation Models, Polaris soil available water capacity, PRISM 30 year normal precipitation and mean temperature, which were downscaled to 10 m resolution using the cwd_function() in R (Redmond 2022). PC1 captured 62.36% of variation and PC2 captured 18.04% of variation. The regional gradient was expressed on PC1 where Aliso was characterized by low elevation, low

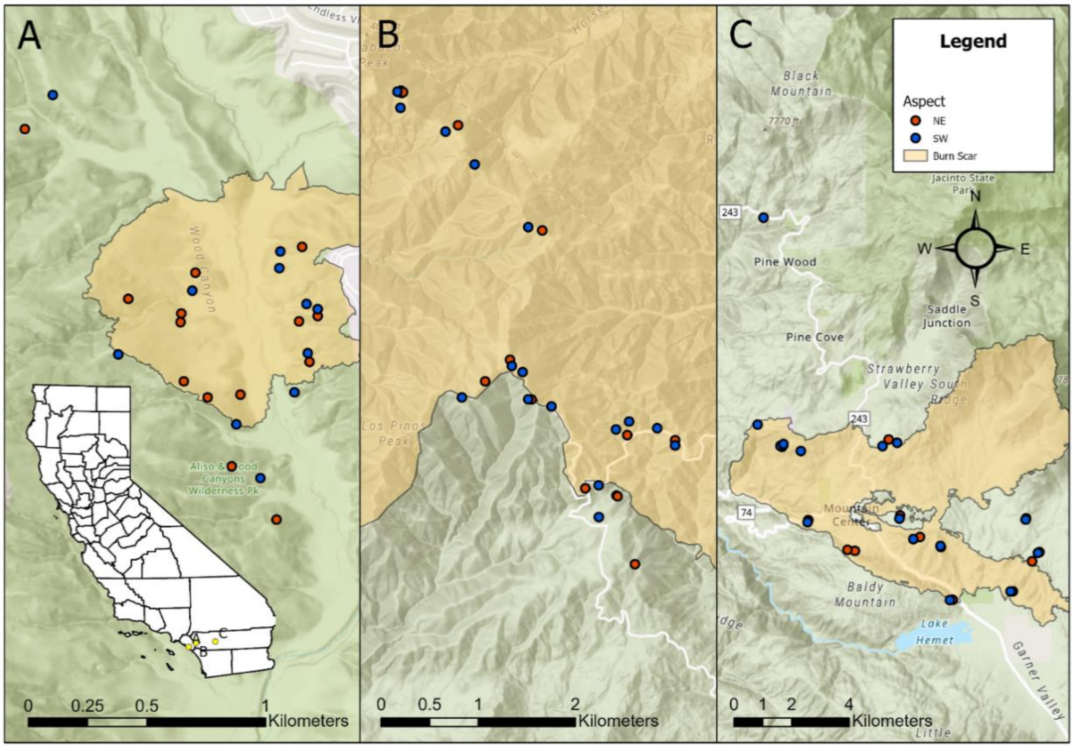

Figure 2.1 Maps of trait collection sites in each regional burn scar A) Aliso, B) Holy, and C) Cranston. Sites were sampled in burn scars (orange) for regeneration traits and outside of burn scars for adult traits. Color represents aspect (blue: NE Northeast, red: SW Southwest). Inset map of California with relative locations of burn scars starting from the left: Aliso, Holy, Cranston.

mean precipitation, and higher mean temperature at the low end of PC1 while Cranston was characterized by high elevation, high precipitation, and lower mean temperature at the high end of PC1, and Holy had values in between the other two locations (Fig. 2.2). While Aliso is the hottest and driest of the sites, it is mild relative to the other sites of Holy and Cranston that have very cold growing season temperatures (see Methods: Study Site description section) which can limit photosynthesis. Additionally, elevation is a main driver of the PC1 gradient where Aliso is near sea level and Cranston is around 1500 m further supporting the harsher conditions at higher elevation (mainly driven by low temperature, but also high winds causing higher transpiration). The local topographic gradient was expressed on PC2 where NE aspects were characterized by low climatic water deficit indicating low drought stress, high available water capacity, and steeper slopes while SW aspects were characterized by high climatic water deficit indicating high drought stress, low available water capacity, and less steep slopes (Fig. 2.2).

Analyses

To test how functional traits differed by life stages and regeneration strategies (Q1) and across resource gradients at different spatial scales (regional burn scar, local topography; Q2), we used linear mixed-effects models with response variables of each functional trait (e.g., SLA, % N) and predictor variables of life stage and regeneration strategy (adult, regenerating resprouter, seeder), regional resource gradient collapsed into PC1, local topographic resource gradient collapsed into PC2, and their interactions, with a random effect of species to account for phylogenetic signal in traits between closely related species, and variance weighted by life stage and regeneration strategy to account for

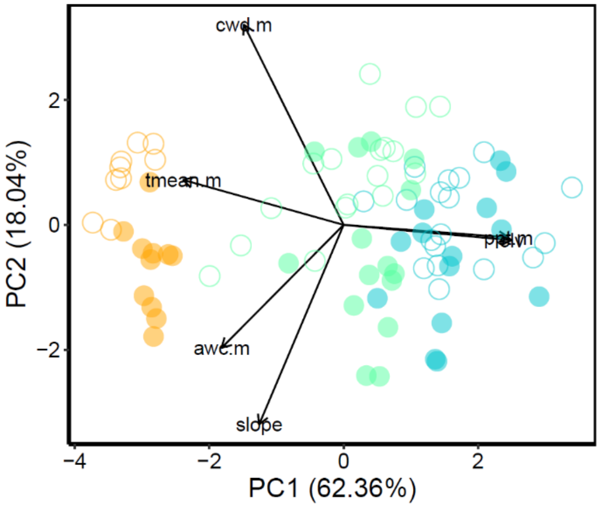

Figure 2.2 Principal Components Analysis (PCA) of sites and environmental variables. Colors represent the regional burn scar (orange: aliso, green: holy, blue: cranston), and shape fill represent aspect type (solid: NE Northeast, open: SW Southwest).

heteroscedasticity between these groups. The replicates were individuals within a species, and the models were created using the lme() function from the nlme package. To quantify phylogenetic signal, we tested whether Pagel's λ was statistically significant and greater than 0 (Münkemüller et al. 2012) using phylosig() in the phytools R package (Revell 2012). A phylogenetic tree was constructed for the Pagel's λ test using the (Zanne et al. 2014) phylogeny. Only LDMC was phylogenetically conserved (Table S2.3); therefore we did not do any further corrections in our models beyond specifying species as a random effect. Tukey post-hoc tests were used on significant main effects using the package emmeans in R. R2 marginal and conditions were calculated using the r.squaredGLMM() function in the MuMIn package. All analyses were done in R version 4.1.1 (R Core Team 2021).

To evaluate how the importance of sources of trait variation (i.e., variation between local environment, regeneration strategies, species) may change across life stages and if these changes are dependent on a regional environmental gradient (Q3), we conducted a variance partitioning analysis with general linear models that consisted of nested and crossed (i.e., specifying more than one nested random term) factors. For each trait, we analyzed how variance is partitioned between regeneration strategies nested within local aspect crossed with individuals nested within species (i.e., (aspect/regeneration strategy)+(species/individual)), and we did this separately for adults and regenerating plants to compare how the importance of sources of trait variation differ across life stages. We also evaluated how the regional resource gradient, categorized by the three burn scars (Fig. 2), influenced the source of trait variation and amount of variation it contributed to leaf traits. We did this by performing the variance partitioning analysis separately for each burn scar. The individual level was not calculated due to the model lumping individual leaf trait variation with unexplained variance. The models were created based on code from (Messier et al. 2017; Messier 2017).

Results

We found a life stage and regeneration strategy main effect for all traits (p<0.001, Table 2.1). Specifically, regenerating plants (i.e., resprouts and seedlings) had higher SLA (p<0.001), lower LDMC (p<0.001), higher discrimination of δ^{13}C (i.e., lower intrinsic water use efficiency; p<0.001), and higher % N content (p<0.001) compared to adults, indicating regenerating plants exhibited an overall resource acquisitive strategy (Fig. 2.3). Compared to regenerating resprouters, regenerating seeders had a higher SLA (p<0.001), higher discrimination of δ^{13}C (p<0.001), higher % N content (p<0.001), but LDMC was similar across regeneration strategies (p=0.596). LA differed across life stage and regeneration strategy, where adults had lower LA than resprouts (p=0.018) but higher LA then seedlings ($p<0.001$) and regenerating resprouts had higher LA then seedlings ($p<0.001$). Looking across all traits, regenerating seeders had a more resource acquisitive strategy compared to resprouters (Fig. 2.3).

Table 2.1 Summary model statistics for linear mixed-effects models testing how functional traits differ by life stages and regeneration strategies and across different spatial scales (regional, PC1; local, PC2). Chisquare values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001). SLA: Specific Leaf Area (cm^2/g), LA: Leaf Area (cm^2), LDMC: Leaf Dry Matter Content (mg/g), % N: percent nitrogen leaf content (%), δ13C: discrimination of δ13C (‰).

	SLA	LA	LDMC	% N	$\delta^{13}C$
PC1	$0.2108_{1,1407}$	$0.3378_{1,1442}$	$5.2223_{1,1396}$*	$7.5275_{1,1287}$**	$18.8491_{1,1287}$***
PC2	$10.3164_{1,1407}$**	$6.9080_{1,1442}$**	$10.5668_{1,1396}$**	$5.4860_{1,1287}$*	$9.9298_{1,1287}$**
Life Stage and Strategy	$653.7306_{2,1407}$***	$37.6769_{2,1442}$***	$524.6133_{2,1396}$***	$3578.2321_{2,1287}$***	$120.1983_{2,1287}$***
PC1: Life Stage and Strategy	$41.4978_{2,1407}$***	$34.0078_{2,1442}$***	$11.7356_{2,1396}$**	$178.0539_{2,1287}$***	$17.1299_{2,1287}$***
PC2: Life Stage and Strategy	$1.1958_{2,1407}$	$3.6676_{2,1442}$	$3.2959_{2,1396}$	$12.8067_{2,1287}$**	$8.6394_{2,1287}$*
R^2 conditional	0.4794	0.7027502	0.5266732	0.9118415	0.469959
R^2 marginal	0.1592	0.01545548	0.1292121	0.3928588	0.06197717

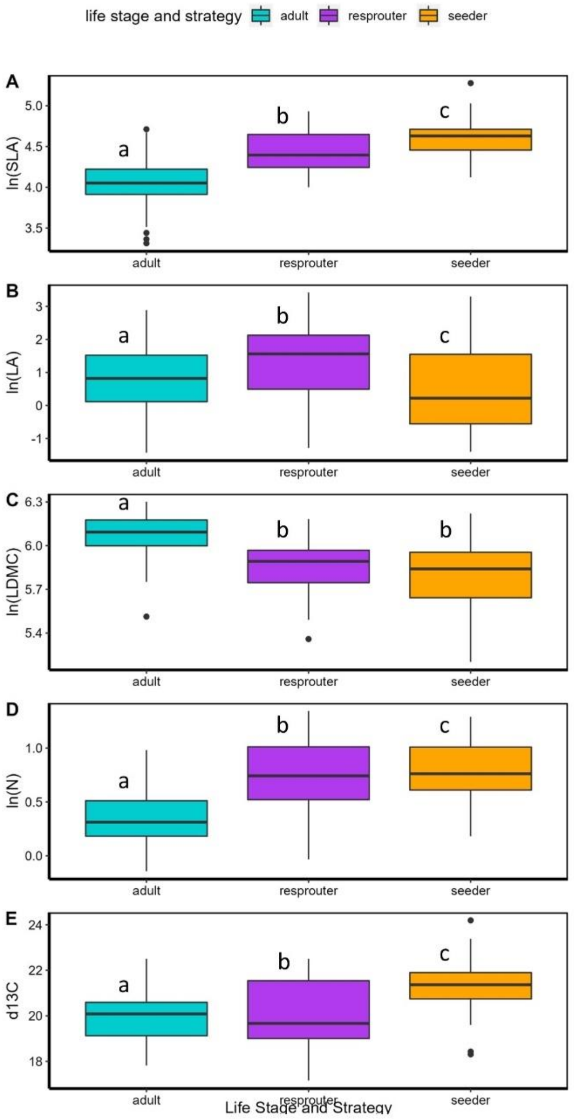

Figure 2.3 Trait values at different life stages and regeneration strategies for A) SLA: Specific Leaf Area (cm^2/g), B) LA: Leaf Area (cm^2), C) LDMC: Leaf Dry Matter Content (mg/g), D) % N: percent leaf nitrogen content (%), E) $\delta^{13}C$: discrimination of $\delta^{13}C$ (‰). Colors represent life stage and regeneration strategy (teal: adult, purple: resprouter, orange: seeder).

We observed a significant interaction between PC1 and life stage and regeneration strategy for all traits (SLA, LA, $\delta^{13}C$, %N $p<0.001$; LDMC $p=0.003$, Table 2.1). SLA decreased along the PC1 regional gradient (higher elevation and precipitation, lower temperature at high end of PC1) for both life stages but decreased less strongly for regenerating plants than for adults (Fig. 2.4A). LA, % N, and $\delta^{13}C$ decreased along the

PC1 regional gradient for both life stages but decreased more strongly for regenerating plants than for adults (Fig. 2.4B,D,E). LDMC increased along the PC1 regional gradient for both life stages but increased more strongly for regenerating plants than for adults (Fig. 2.4C). Trait differences between life stages were conserved across the regional resource gradient (PC1), where regeneration traits were more resource-acquisitive than adults (higher SLA, lower LDMC, higher discrimination of δ^{13}C, and higher % N content, Fig. 2.4). Generally, seeders were more acquisitive than resprouters, but resprouts had higher %N than seeders at the low end of PC1 (low elevation, milder conditions) and consistently had a higher leaf area than seeders. LA, LDMC, δ^{13}C, and %N had a steeper slope for regenerating plants compared to adults, but SLA had a steeper slope for adults compared to regenerating plants (Fig. 2.4).

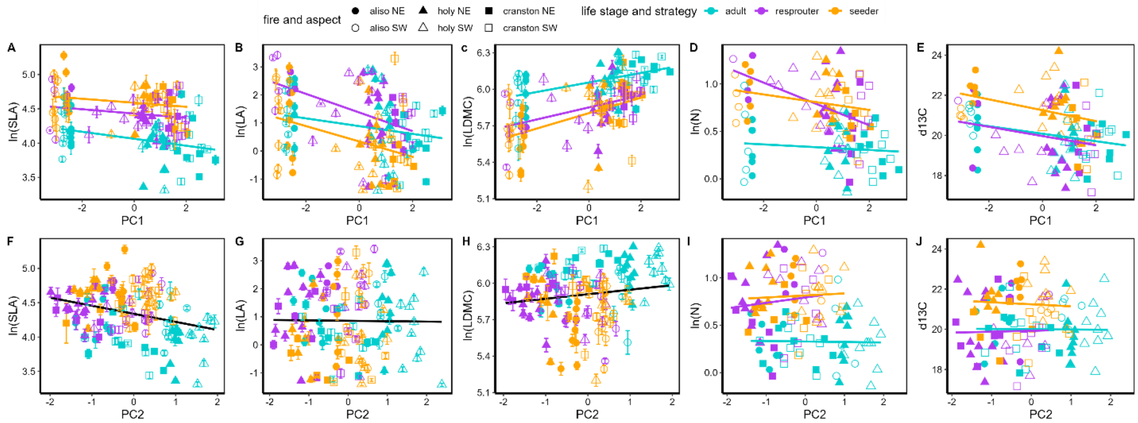

Figure 2.4 Linear regressions of traits at different life stages and regeneration strategies across regional (PC1) and local (PC2) scales of resource gradients for A) SLA: Specific Leaf Area, B) LA: Leaf Area, C) LDMC: Leaf Dry Matter Content, D) % N: percent leaf nitrogen content, E) δ^{13}C: discrimination of δ^{13}C. Colors represent life stage and regeneration strategy (teal: adult, purple: resprouter, orange: seeder). Black lines indicate a statistically significant relationship between resource gradient and trait ($p<0.05$), while colored lines additionally indicate the presence of an interaction with life stage and regeneration strategy.

Morphological traits varied along PC2 (SLA, LA, LDMC $p<0.01$, Table 2.1). Specifically, SLA strongly decreased along the PC2 topographic gradient from NE to SW (higher climatic water deficit indicating higher drought stress on SW aspects), while LA slightly decreased and LDMC strongly increased along the PC2 topographic gradient (Fig. 2.4F,G,H). Overall, morphological traits became more conservative as drought stress increased along a topographic gradient from NE to SW (Fig. 2.4F,G,H). Chemical traits varied in their strength and direction of relationship to drought stress along the PC2 topographic gradient from NE to SW. We observed a significant interaction between PC2 and life stage and regeneration strategy for chemical traits (δ^{13}C $p=0.013$, %N $p=0.002$, Table 2.1). %N slightly increased for seeders, more strongly increased for resprouters, and slightly decreased for adults along the PC2 topographic gradient (Fig. 2.4I). δ^{13}C more strongly decreased for seeders than adults but slightly increased for resprouters along the PC2 topographic gradient (Fig. 2.4J).

Morphological and chemical traits differed in drivers of trait variation across life stages and spatial scales (Table S2.4). For morphological traits, the regional scale (i.e., burn scars from lower elevation milder resource conditions at Aliso to higher elevation with increasingly harsher conditions at Cranston) influenced when each level of organization drove trait variation and the amount of variation. For SLA, interspecific variation contributed to trait variation more for the adult than regeneration stage regardless of regional scale, but regional scale influenced the amount of interspecific variation with greater contributions from interspecific variation across both life stages as

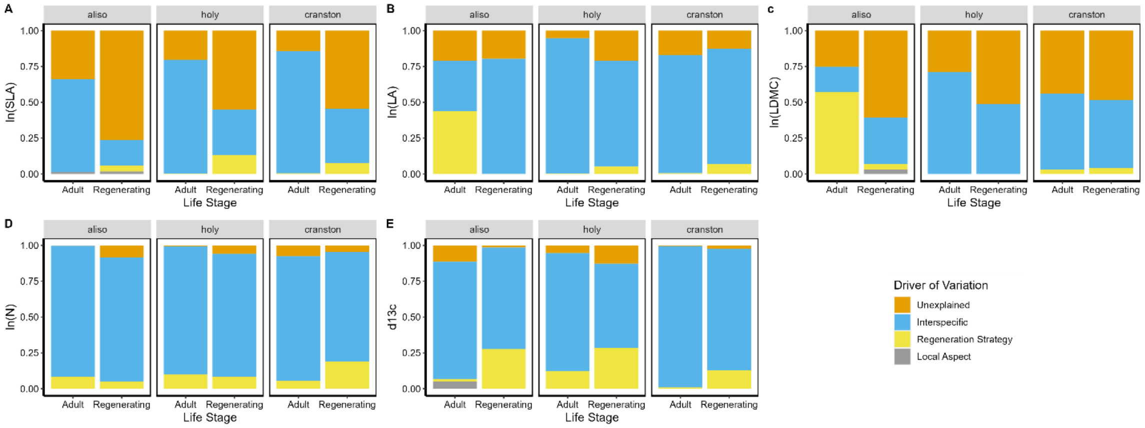

Figure 2.5 Variance partitioning across spatial scales and life stages for A) SLA: Specific Leaf Area (cm^2/g), B) LA: Leaf Area (cm^2), C) LDMC: Leaf Dry Matter Content (mg/g), D) % N: percent leaf nitrogen content (%), E) $\delta^{13}C$: discrimination of $\delta^{13}C$ (‰). Life stage (adult or regenerating) is nested within the regional scale burn scar (aliso, holy, cranston) to compare the drivers of trait variation (orange: unexplained, blue: interspecific or species level, yellow: regeneration strategy, grey: local aspect) and their relative contribution to trait variation. Note that individual level (i.e., intraspecific) variation is captured within unexplained variation.

sites experienced harsher resource conditions (Fig. 2.5A). For LA and LDMC, interspecific variation contributed to trait variation more for the adult than regeneration stage at Holy and Cranston under harsher regional conditions but had the opposite effect at Aliso under mild conditions (Fig. 2.5B,C). The regional scale and life stage also influenced the contribution of regeneration strategy to trait variation, where regeneration strategy contributed more in the regeneration stage for SLA but more in the adult stage at Aliso under mild conditions for LA and LDMC (Fig. 2.5A,B,C). Regeneration strategy created trait variation in morphological traits mainly for regenerating plants, except for LA and LDMC under mild conditions where regeneration strategy played a large role for adults and reduced the contribution of interspecific variation (Fig. 2.5B,C). Local scale aspect played a slight role under mild regional conditions for adult and regenerating SLA and regenerating LDMC (Fig. 2.5A,C).

For chemical traits, interspecific variation contributed to trait variation more for the adult than regeneration stage regardless of regional scale (Fig. 2.5D,E). Compared to morphological traits, chemical trait variation was mediated by regeneration strategy more often across both life stages and regional scale. The regional scale influenced the amount that regeneration strategy contributed to trait variation across life stages, where regeneration strategy was a larger driver in % N variation for regenerating plants than adults at Cranston under harsher conditions but regeneration strategy contributed overall less to trait variation and similarly across life stages at Aliso and Holy (Fig. 2.5D). The majority of variation in $\delta^{13}C$ is explained by interspecific variation and regeneration strategy, leaving very little unexplained variation (Fig. 2.5E). Regeneration strategy created more chemical trait variation for regenerating plants than adults, but adults consistently had variation attributed to regeneration strategy across the regional scale compared to morphological traits. Local scale aspect played a slight role under mild regional conditions for adult $\delta^{13}C$ (Fig. 2.5E), similar to morphological traits (Fig. 2.5A,C).

Discussion

Assessing what drives trait variation at different life stages and how spatial scale influences trait variation is important for improving application of trait-based approaches to predict community (re)assembly. Here, we found regeneration traits were more resource acquisitive (higher SLA, higher $\delta^{13}C$ discrimination/lower iWUE, higher % N, lower LDMC) than adult traits, and regenerating seeders had the most resource acquisitive strategy (Q1). Traits became more resource conservative as the environmental gradients became harsher at both spatial scales, with stronger filtering shown at regional scales (Q2). Stronger filtering was also shown for regeneration traits compared to adult traits, except for SLA at the regional scale and all morphological traits at the local scale (Q2). We found interspecific variation to drive trait variation more at the adult compared to regenerating plant stage for most traits, and the regional resource gradient to strongly regulate the amount each driver of variation contributed to morphological leaf trait variation but weakly for chemical leaf trait variation (Q3). We also found the contribution of regeneration strategy and topography to trait variation differed based on the interaction between ontogeny and spatial scale (Q3).

Trait differences across ontogeny can be used to assess resource acquisition strategies, plant performance, and community assembly (Spasojevic et al. 2014; Larson and Funk 2016; Garbowski et al. 2021; Larson et al. 2021). Here, we found leaf economic spectrum traits differed across life stages, where regenerating plants had an acquisitive resource-use strategy and adults had a conservative strategy, consistent with recent findings in other systems (Spasojevic et al. 2014; Dayrell et al. 2018; Henn and Damschen 2021). Our findings support the prediction that resource acquisition strategies become more conservative over time, as light and nutrient availability is high immediately post-fire but over time soil moisture availability becomes a main driver of community assembly and resource acquisition strategies in chaparral systems (Cornwell and Ackerly 2009). For example, we observed regenerating seeders had the most resource acquisitive strategy during the sensitive establishment stage, followed by regenerating resprouters that surpassed the establishment stage by maintaining deep root structures (having similar iWUE to adults, where reaching deeper soil moisture influences $\delta^{13}C$) but must regrow aboveground photosynthetic tissue to persist after a disturbance, and adults utilizing a conservative strategy to remain in the persistence stage. These results contrast previous studies of chaparral traits during the first few years post-fire where resprouting species were associated with resource-acquisitive traits (long roots to reach deeper water and higher SLA for faster growth; Mooney and Dunn 1970; Anacker et al. 2011; Pratt et al. 2012; Parker et al. 2016) while seeder species had more conservative and drought tolerant traits (xylem highly resistant to cavitation, slow growth rates, low SLA, and short heights; Anacker et al. 2011; Pratt et al. 2012). This discrepancy is most likely due to these previous studies missing the true first year regeneration traits, vital to the establishment niche. Tracking ontogenetic changes in regeneration strategies can help identify how trait-environment matching regulates community assembly differently over time.

Ontogenetic niche shifts driven by environmental gradients can influence species distributions and population dynamics (Parish and Bazzaz 1985; Eriksson 2002) and succession (Young et al. 2005), thus identifying how traits are filtered differently across life stages and spatial scales is integral for identifying assembly processes throughout development. At both spatial scales, we found that traits became more resource conservative as the environmental gradients became harsher, consistent with decades of environmental filtering studies (Weiher and Keddy 1995; Reich et al. 1997). The strength of filtering was stronger at regional than local scales (Fig. 2.4), potentially driven by more heterogeneity at the regional scale (Miguet et al. 2016; Messier et al. 2017) resulting in a more severe stress gradient (Weiher and Keddy 1995). We found life stages and regeneration strategies experienced different strengths of environmental filtering for morphological traits along the regional but not local scale and for chemical traits along both scales. Guzmán-Jacob et al. (2022) found similar patterns in morphological and chemical trait relationships across regional and local scales, and additionally found phylogenetic and species level differences were the main drivers of trait variation compared to environmental gradients. Morphological traits are known to be highly sensitive to many factors (Pérez-Harguindeguy et al. 2013; Messier et al. 2017), where trait environment filtering at local scales may be overpowering the detection of ontogenetic differences. In contrast, chemical traits are less sensitive to environmental factors and remain relatively consistent in their trait values at the species level (Farquhar et al. 1989; Pérez-Harguindeguy et al. 2013), allowing detection of ontogenetic differences even in the presence of local scale environmental filters. The strength of filtering was generally stronger on regeneration traits compared to adult traits (Fig. 2.4). This demonstrates that trait-environment matching and niche selection play a stronger role for regenerating plants (Ramachandran et al. 2023), where seedlings can be more vulnerable to environmental conditions during the establishment stage and may experience a more narrow niche than adults that have already established (i.e., smaller breadth of establishment niche than persistence niche; Grubb 1977; Gabler and Siemann 2012). The changes in strength of environmental filtering, rather than direction, is driven by ontogeny and spatial scales.

Identifying sources of adaptive trait variation is necessary for understanding how trait-environment matching is maintained (Ackerly 2003) and predicting ecosystem functioning under changing environmental conditions (Laughlin et al. 2012; Lajoie and Vellend 2015). We found interspecific variation to drive trait variation more at the adult stage compared to regenerating plant stage for most traits (Fig. 2.5). At the regeneration stage, large amounts of individual level trait variation (i.e., intraspecific variation) can occur from plastic responses to local heterogeneous environments, ontogenetic differences, and trait variation not yet being filtered out by abiotic and biotic conditions that occur over a lifespan (Jiang et al. 2021). This individual variation may not be as necessary over time as adults have already established, and our results support that species level differences (i.e., interspecific variation) play a larger role in the persistence rather than establishment niche (Gabler and Siemann 2012; Jiang et al. 2021). The amount of interspecific variation generally increased across the regional scale for morphological traits but not chemical traits, indicating species level differences drive trait variation more under harsh conditions while other factors can contribute to variation at mild conditions. These patterns may be weaker for chemical traits due to our method of pooling multiple leaves together for species with low leaf mass and their less plastic nature, which together may also contribute to the low unexplained variation found for chemical traits. We found local scale aspect played a slight role only under mild regional conditions, further supporting the stress-dominance hypothesis with multiple interacting environmental gradients, where the regional context influences the scale of effect which can be due to variation in landscape variables, species traits, or indirect variables that differ by region (Miguet et al. 2016). Our study provides evidence for considering more nuance in the sources of trait variation particularly as environmental gradients at certain spatial scales may have primacy in trait patterns.

Understanding how ontogeny and spatial scale interact to influence trait variation can improve our ability to apply trait-based approaches to community assembly and recovery processes (Li et al. 2019; Jiang et al. 2021; Hulshof and Umaña 2022). We found strong evidence to support that life stages and spatial scale/stress gradients interact to mediate the drivers of trait variation. For example, we observed differences in interspecific variation between life stages were maintained across regional scales. Our results align with previous studies showing interspecific variation contributes to more trait variation in adults compared to regenerating plants (Dayrell et al. 2018; Jiang et al. 2021) and the proportion of interspecific variation varies along regional resource conditions due to increased heterogeneity at larger spatial scales (Lajoie and Vellend 2015; Hulshof and Umaña 2022). Furthermore, we found evidence to support the combination of stressors and tolerance to them changes throughout ontogeny (Niinemets 2010). For example, we observed local scale topography only created trait variation at mild regional conditions but at different life stages depending on the trait. A study conducted in a subtropical forest showed topography consistently contributed more to trait variation for seedlings than adults (Li et al. 2019), highlighting the need for studying the relationship between local topography and life stages across different systems. We found new evidence that regeneration strategy mediated trait variation differently for regenerating plants vs adults depending on the regional conditions and that this was more nuanced for morphological vs chemical traits. More studies are needed to disentangle regeneration strategy differences over time, spatial scale, and trait types to better apply trait-based approaches in community assembly. Unexplained variation was generally higher for regenerating plants compared to adults. We were not able to quantify intraspecific variation, which is shown to play a larger role for regenerating plants (Dayrell et al. 2018; Jiang et al. 2021; Henn and Damschen 2021) and may make up a significant portion of the unexplained variation seen here for regenerating plants. Together, our results show trait variation is highly dependent on ontogeny and its interaction with resource gradients at different spatial scales.

Conclusion

Assessing what drives trait variation at different life stages and spatial scales is important for improving application of trait-based approaches in community recovery. We found regeneration traits differed from adults, were filtered more strongly, and had different contributions of drivers of trait variation, supporting the use of regeneration traits in understanding establishment and recovery. The regional environmental gradient filtered traits more strongly than at the local scale and regulated the contribution of each driver of trait variation. Overall, the magnitude of trait filtering and the contribution of different drivers of trait variation changed across life stages and spatial scales, highlighting the importance of identifying how ontogeny and spatial scales impact traits to better apply trait-based approaches in community assembly and recovery.

References

Ackerly, D. D. (2003). Community Assembly, Niche Conservatism, and Adaptive Evolution in Changing Environments. *International Journal of Plant Sciences, 164*(S3), S165–S184. https://doi.org/10.1086/368401

Ackerly, D. D., Knight, C., Weiss, S., Barton, K., & Starmer, K. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia*, *130*(3), 449–457. https://doi.org/10.1007/s004420100805

Almanza, E. (n.d.). *ADAR-Based Mapping of the Nature Reserve of Orange County*. The Nature Conservancy.

Anacker, B., Rajakaruna, N., Ackerly, D., Harrison, S., Keeley, J., & Vasey, M. (2011). Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. *Plant Ecology & Diversity*, *4*(2-3), 179–188. https://doi.org/10.1080/17550874.2011.633573

Bond, W. J., & van Wilgen, B. W. (1996). Fire, competition and the organization of communities. In W. J. Bond & B. W. van Wilgen (Eds.), *Fire and Plants* (pp. 148–187).

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, *79*(1), 109–126. https://doi.org/10.1890/07-1134.1

Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H., & Silveira, F. A. O. (2018). Ontogenetic shifts in plant ecological strategies. *Functional Ecology*, *32*(12), 2730–2741. https://doi.org/10.1111/1365-2435.13221

Diaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science, 9*(1), 113–122. https://doi.org/10.2307/3237229

Díaz, S., Cabido, M., & Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. *Ecological Assembly Rules: Perspectives, Advances, Retreats*, 338–362. https://books.google.com/books?hl=en&lr=&id=RIZDYJ0zKaAC&oi=fnd&pg=PA338&dq=diaz+1999+functional+implications&ots=JkEnT7CYUE&sig=AQQDj3js41g5vLcTDE_-GXuVEg0

Eriksson, O. (2002). Ontogenetic niche shifts and their implications for recruitment in three clonal Vaccinium shrubs: Vaccinium myrtillus, Vaccinium vitis-idaea, and

Vaccinium oxycoccos. *Canadian Journal of Botany-Revue Canadienne De Botanique*, *80*(6), 635–641. https://doi.org/10.1139/B02-044

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*(1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Gabler, C. A., & Siemann, E. (2012). Environmental Variability and Ontogenetic Niche Shifts in Exotic Plants May Govern Reinvasion Pressure in Restorations of Invaded Ecosystems. *Restoration Ecology*, *20*(5), 545–550. https://doi.org/10.1111/j.1526-100X.2012.00901.x

Garbowski, M., Johnston, D. B., & Brown, C. S. (2021). Leaf and root traits, but not relationships among traits, vary with ontogeny in seedlings. *Plant and Soil*, *460*(1), 247–261. https://doi.org/10.1007/s11104-020-04790-z

Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science*, *17*(2), 255–260. https://doi.org/10.1111/j.1654-1103.2006.tb02444.x

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, *52*(1), 107–145. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-185X.1977.tb01347.x

Guzmán-Jacob, V., Guerrero-Ramírez, N. R., Craven, D., Brant Paterno, G., Taylor, A., Krömer, T., Wanek, W., Zotz, G., & Kreft, H. (2022). Broad- and small-scale environmental gradients drive variation in chemical, but not morphological, leaf traits of vascular epiphytes. *Functional Ecology*, *36*(8), 1858–1872. https://doi.org/10.1111/1365-2435.14084

Hanes, T. L. (1971). Succession after Fire in the Chaparral of Southern California. *Ecological Monographs*, *41*(1), 27–52. https://doi.org/10.2307/1942434

Henn, J. J., & Damschen, E. I. (2021). Plant age affects intraspecific variation in functional traits. *Plant Ecology*, *222*(6), 669–680. https://doi.org/10.1007/s11258-021-01136-2

Hulshof, C. M., & Umaña, M. N. (2022). Power laws and plant trait variation in spatio-temporally heterogeneous environments. *Global Ecology and Biogeography: A Journal of Macroecology*. https://doi.org/10.1111/geb.13620

Jiang, F., Cadotte, M. W., & Jin, G. (2021). Individual-level leaf trait variation and correlation across biological and spatial scales. *Ecology and Evolution*, *11*(10), 5344–5354. https://doi.org/10.1002/ece3.7425

Keeley, J. E., Fotheringham, C. J., & Baer-Keeley, M. (2005). Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecological Applications: A Publication of the Ecological Society of America*, *15*(5), 1515–1534. https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/04-1005

Lajoie, G., & Vellend, M. (2015). Understanding context dependence in the contribution of intraspecific variation to community trait–environment matching. *Ecology*, *96*(11), 2912–2922. https://doi.org/10.1890/15-0156.1

Larson, J. E., Ebinger, K. R., & Suding, K. N. (2021). Water the odds? Spring rainfall and emergence-related seed traits drive plant recruitment. *Oikos* , *130*(10), 1665–1678. https://doi.org/10.1111/oik.08638

Larson, J. E., & Funk, J. L. (2016). Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, *104*(5), 1284–1298. https://doi.org/10.1111/1365-2745.12613

Laughlin, D. C., Joshi, C., van Bodegom, P. M., Bastow, Z. A., & Fulé, P. Z. (2012). A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*, *15*(11), 1291–1299. https://doi.org/10.1111/j.1461-0248.2012.01852.x

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

Li, Y., Bin, Y., Xu, H., Ni, Y., Zhang, R., Ye, W., & Lian, J. (2019). Understanding Community Assembly Based on Functional Traits, Ontogenetic Stages, Habitat Types and Spatial Scales in a Subtropical Forest. *Forests, Trees and Livelihoods*, *10*(12). https://doi.org/10.3390/f10121055

Martínez, J. A., & Armesto, J. J. (1983). Ecophysiological plasticity and habitat distribution in three evergreen sclerophyllous shrubs of the Chilean matorral. *Acta Oecologica: Oecologia Plantarum*. http://agris.fao.org/agris-search/search.do?recordID=US201302165631

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Messier, J. (2017, August 18). *Variance Partitioning Code*. Julie Messier. https://juliemessier.org/code/

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

Miguet, P., Jackson, H. B., Jackson, N. D., Martin, A. E., & Fahrig, L. (2016). What determines the spatial extent of landscape effects on species? *Landscape Ecology*, *31*(6), 1177–1194. https://doi.org/10.1007/s10980-015-0314-1

Mooney, H. A., & Dunn, E. L. (1970). Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. *Evolution; International Journal of Organic Evolution*, *24*(2), 292–303. https://doi.org/10.1111/j.1558-5646.1970.tb01762.x

Moreira, B., Tavsanoglu, C., & Pausas, J. G. (2012). Local versus regional intraspecific variability in regeneration traits. *Oecologia*, *168*(3), 671–677. https://doi.org/10.1007/s00442-011-2127-5

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., & Thuiller, W. (2012). How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, *3*(4), 743–756. https://doi.org/10.1111/j.2041-210x.2012.00196.x

Nelson, D., & Howland, J. (2018). *Cranston BAER Technical Specialist Report Botany.pdf*. US Forest Service.

Niinemets, Ü. (2010). Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*, *260*(10), 1623–1639. https://doi.org/10.1016/j.foreco.2010.07.054

Parish, J. A. D., & Bazzaz, F. A. (1985). Ontogenetic niche shifts in Old-Field annuals. *Ecology*, *66*(4), 1296–1302. https://doi.org/10.2307/1939182

Parker, V. T., Pratt, R. B., & Keeley, J. E. (2016). TWENTY-FOUR. Chaparral. In H. Mooney & E. Zavaleta (Eds.), *Ecosystems of California* (pp. 479–508). University of California Press. https://doi.org/10.1525/9780520962170-028

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. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167. https://doi.org/10.1071/bt12225

Pratt, R. B., Jacobsen, A. L., Hernandez, J., Ewers, F. W., North, G. B., & Davis, S. D. (2012). Allocation tradeoffs among chaparral shrub seedlings with different life history types (Rhamnaceae). *American Journal of Botany*, *99*(9), 1464–1476. https://doi.org/10.3732/ajb.1200193

PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data created 4 Feb 2014, accessed 06 Aug 2023

Ramachandran, A., Huxley, J. D., McFaul, S., Schauer, L., Diez, J., Boone, R., Madsen-Hepp, T., McCann, E., Franklin, J., Logan, D., Rose, M. B., & Spasojevic, M. J. (2023). Integrating ontogeny and ontogenetic dependency into community assembly. *Journal of Ecology*, *111*(7), 1561–1574. https://doi.org/10.1111/1365-2745.14132

R Core Team. (2021). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/*. https://www.R-project.org/

Redmond. (2022). *CWD and AET function (Version V1.0.3). Zenodo. https://doi.org/10.5281/zenodo.6416352*. https://doi.org/10.5281/zenodo.6416352

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

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(25), 13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223. https://doi.org/10.1111/j.2041-210x.2011.00169.x

Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, *180*(4), 923–931. https://doi.org/10.1007/s00442-016-3549-x

Spasojevic, M. J., Yablon, E. A., Oberle, B., & Myers, J. A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* , *5*(10), art129. https://doi.org/10.1890/ES14-000159.1

Stephenson, N. (1998). Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography*, *25*(5), 855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x

Van de Water, K. M., & Safford, H. D. (2011). A Summary of Fire Frequency Estimates for California Vegetation before Euro-American Settlement. *Fire Ecology*, *7*(3), 26–58. https://doi.org/10.4996/fireecology.0703026

VinZant, K., Howland, J., & Bessemer, A. (2018). *Holy Fire BAER Technical Specialist Botany Report*. US Forest Service.

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. In *Trends in Ecology & Evolution* (Vol. 27, Issue 4, pp. 244–252). https://doi.org/10.1016/j.tree.2011.11.014

Weiher, E., & Keddy, P. A. (1995). Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. *Oikos* , *74*(1), 159–164. https://doi.org/10.2307/3545686

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

Young, T. P., Petersen, D. A., & Clary, J. J. (2005). The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters*, *8*(6), 662–673. https://doi.org/10.1111/j.1461-0248.2005.00764.x

Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., McGlinn, D. J., O'Meara, B. C., Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D. E., Stevens, P. F., Westoby, M., Wright, I. J., Aarssen, L., Bertin, R. I., Calaminus, A., Govaerts, R., … Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, *506*(7486), 89–92. https://doi.org/10.1038/nature12872

Appendix S2

Table S2.1 Trait collection coordinates.

Table S2.2 Species mean traits across fire, aspect, life stage, regeneration strategy.

Table S2.3 Summary model statistics for Pagel's λ test assessing phylogenetic signal in traits across closely related species.

Table S2.4 Summary model statistics for trait variance partitioning models across fires and life stages.

Table S2.5 Species six letter codes, scientific names, and regeneration strategies for the shrub species used for functional trait collections.

Table S2.1 Trait collection coordinates. Fire is the regional site (A, Aliso; H, Holy; C, Cranston), burned indicates if the site was burned (B) or unburned (UB), aspect is Northeast (NE) or Southwest (SW), and site number is the sampling location of different aspects (i.e. 1, 2, 3, etc.) and location within an aspect (i.e. 1 and 1.2 are different locations on the same aspect). Site specific coordinates (decimal degrees), elevation (meters), aspect (degrees), and slope (degrees) are also included.

Fire	Burned	Aspect	Site	Latitude	Longitude	Elevation	Aspect	Slope
A	B	NE	1	33.54821	-117.742	58.69364	77.68421	27.84827
A	B	NE	1.2	33.5481	-117.743	105.2685	37.5154	21.79972
A	B	NE	2	33.54945	-117.739	72.75109	298.7153	20.86223
A	B	NE	3	33.55119	-117.739	89.86649	320.2112	23.81705
A	B	NE	3.2	33.55099	-117.74	94.13902	300.3135	24.80326
A	B	NE	4	33.55282	-117.744	87.01639	75.07806	17.30698
A	B	NE	5	33.5538	-117.74	102.5779	288.6263	29.28462
A	B	NE	6	33.54872	-117.744	96.66834	52.41905	22.499
A	B	NE	7.1	33.55128	-117.744	73.18628	72.0023	21.38577
A	B	NE	7.2	33.55096	-117.744	76.04823	61.30688	20.32019
A	B	NE	8.1	33.55183	-117.746	134.4539	118.959	26.08926
A	B	SW	2	33.54978	-117.739	80.30965	216.0016	23.55996
A	B	SW	3	33.55145	-117.739	92.92754	216.7226	29.33762

Fire	Burned	Aspect	Site	Latitude	Longitude	Elevation	Aspect	Slope
A	B	SW	3.2	33.55165	-117.739	92.01738	244.6214	28.61303
A	B	SW	4	33.55215	-117.744	68.75771	199.7565	20.0391
A	B	SW	5	33.55363	-117.74	86.91357	333.8387	28.62256
A	B	SW	6	33.553	-117.74	85.47923	220.9209	18.3399
A	UB	NE	1	33.5455	-117.742	110.7809	41.58272	27.59704
A	UB	NE	4	33.55827	-117.75	101.2994	101.8526	14.0727
A	UB	NE	6	33.54348	-117.74	84.46943	38.45553	29.62245
A	UB	SW	1.1	33.54709	-117.742	76.61664	177.6462	29.51633
A	UB	SW	2	33.5483	-117.74	59.87967	235.0305	20.7115
A	UB	SW	3	33.54973	-117.746	166.618	151.6766	14.95
A	UB	SW	4	33.55955	-117.749	136.0677	180.8676	14.88438
A	UB	SW	6	33.54505	-117.741	73.42297	146.6474	15.13787
H	B	NE	2	33.69392	-117.465	1252.771	5.815221	21.26689
H	B	NE	3	33.69706	-117.471	1302.231	53.65504	25.29422
H	B	NE	3.1	33.69685	-117.471	1304.037	74.09906	19.88614
H	B	NE	3.2	33.69692	-117.471	1293.28	66.8251	31.76605

Fire	Burned	Aspect	Site	Latitude	Longitude	Elevation	Aspect	Slope
H	B	NE	4	33.68424	-117.456	1246.799	41.60904	34.33947
H	B	NE	5	33.66493	-117.441	1017.058	6.473262	22.33736
H	B	NE	6	33.66536	-117.446	1030.724	48.66582	29.36586
H	B	NE	7	33.67221	-117.459	1290.222	53.51503	21.92494
H	B	SW	1	33.69029	-117.463	1243.407	199.5168	20.52619
H	B	SW	2	33.6933	-117.466	1245.662	249.8411	20.13851
H	B	SW	3	33.69696	-117.472	1303.418	246.2309	16.79732
H	B	SW	3.2	33.69546	-117.471	1270.949	219.8964	32.3133
H	B	SW	4	33.68454	-117.457	1264.023	172.4286	18.44042
H	B	SW	5	33.66444	-117.441	1016.81	180.5543	30.07737
H	B	SW	6	33.66661	-117.446	1040.588	225.292	35.84798
H	B	SW	7	33.67164	-117.459	1291.359	223.3288	16.12177
H	B	SW	7.1	33.66587	-117.447	1056.497	210.7999	21.15461
H	B	SW	8	33.66601	-117.443	1007.728	243.3739	35.19123
H	UB	NE	1	33.65973	-117.447	1023.101	330.32	15.85257
H	UB	NE	1.1	33.65965	-117.447	1024.572	63.3872	12.74701

Fire	Burned	Aspect	Site	Latitude	Longitude	Elevation	Aspect	Slope
H	UB	NE	2	33.67019	-117.462	1327.327	27.74414	13.28974
H	UB	NE	3	33.66856	-117.457	1266.036	122.5766	13.27348
H	UB	NE	6	33.66036	-117.45	1062.068	41.39526	23.93132
H	UB	NE	7	33.65338	-117.445	1053.683	92.95339	14.8416
H	UB	SW	1	33.6577	-117.449	1022.712	184.3161	9.667078
H	UB	SW	2	33.66866	-117.464	1361.401	297.4321	14.61569
H	UB	SW	3	33.66856	-117.457	1268.851	228.0163	7.74294
H	UB	SW	4	33.67108	-117.458	1314.557	160.8367	9.202979
H	UB	SW	5	33.66793	-117.454	1226.369	164.2694	12.08885
H	UB	SW	6	33.66066	-117.449	1049.321	207.5909	24.50748
C	B	NE	1	33.69679	-116.699	1577.466	17.95983	13.56983
C	B	NE	3	33.69235	-116.723	1517.469	63.77394	27.35761
C	B	NE	4	33.69267	-116.726	1527.723	16.51028	22.4269
C	B	NE	5	33.70192	-116.741	1310.15	32.38945	22.96752
C	B	NE	6	33.69372	-116.691	1549.178	81.8632	10.35037
C	B	NE	7	33.67994	-116.664	1386.278	136.1373	20.73119

Fire	Burned	Aspect	Site	Latitude	Longitude	Elevation	Aspect	Slope
C	B	SW	1	33.69615	-116.701	1573.952	240.4239	6.829834
C	B	SW	2	33.72484	-116.751	1601.726	216.4653	23.1298
C	B	SW	2.1	33.72511	-116.751	1601.21	242.0429	18.65918
C	B	SW	2.2	33.72549	-116.75	1629.244	229.9143	13.04338
C	B	SW	3	33.73176	-116.76	1445.414	229.8551	17.7383
C	B	SW	4	33.72352	-116.744	1603.144	187.2848	15.99613
C	B	SW	5	33.70131	-116.741	1312.27	183.9952	19.12282
C	B	SW	6	33.72516	-116.713	1732.706	218.5855	19.51368
C	B	SW	7	33.69398	-116.691	1550.871	215.8738	7.49049
C	B	SW	8	33.67996	-116.665	1362.199	246.3599	17.57312
C	UB	NE	1	33.70352	-116.706	1476.303	349.3359	19.69286
C	UB	NE	2	33.67717	-116.686	1438.292	71.40533	16.06628
C	UB	NE	3	33.72726	-116.711	1745.447	17.94502	15.175
C	UB	NE	4	33.70281	-116.659	1624.703	69.43088	12.34181
C	UB	NE	5	33.6893	-116.657	1503.247	78.11044	9.536138
C	UB	NE	5.1	33.69225	-116.654	1500.18	113.0626	13.7781

Fire	Burned	Aspect	Site	Latitude	Longitude	Elevation	Aspect	Slope
C	UB	SW	1	33.70257	-116.707	1505.762	233.7087	11.18511
C	UB	SW	2	33.67712	-116.688	1454.691	220.2272	15.34236
C	UB	SW	3	33.72623	-116.708	1778.938	256.8516	13.26786
C	UB	SW	4	33.70236	-116.659	1616.61	205.0628	28.5156
C	UB	SW	5	33.69199	-116.655	1498.321	242.8809	17.89738
C	UB	SW	6	33.79653	-116.758	1632.844	244.6849	11.74443
C	UB	SW	7	33.72568	-116.75	1631.853	256.4433	13.42102

Table S2.2 Species mean traits across fire, aspect, life stage, regeneration strategy. Strat is life stage (a: adult) or regeneration strategy (r: resprouter, s: seeder), species is the six letter species code, SLA: Specific Leaf Area (cm^2/g), LA: Leaf Area (cm^2), LDMC: Leaf Dry Matter Content (mg/g), % N: percent nitrogen leaf content (%), δ13C: discrimination of δ13C (‰), count is number of individuals used to calculate trait means for LA, % N, and $\delta^{13}C$, count.r is the reduced count used to calculate trait means for SLA and LDMC as specified. See Table S2.5 for species names and regeneration strategies.

fire	aspect	strat	species	SLA	LA	LDMC	% N	$\delta^{13}C$	count	count.r
aliso	NE	a	ARTCAL	4.547	0.098	5.770	0.511	21.523	9	
aliso	NE	a	DIPLON	4.552	0.806	5.962	0.182	22.049	8	
aliso	NE	a	ERIFAS	4.150	0.065	6.074	0.182	20.544	10	
aliso	NE	a	HETARB	4.006	2.568	6.113	0.236	18.273	10	
aliso	NE	a	RHAILI	4.206	1.570	6.117	0.624	20.892	8	
aliso	NE	a	RHUINT	3.956	2.362	6.070	0.033	19.283	10	
aliso	NE	a	SALMEL	4.081	1.286	5.846	0.511	20.366	9	
aliso	NE	r	HETARB	4.701	2.818	5.697	0.833	22.294	14	
aliso	NE	r	RHAILI	4.809	2.210	5.687	1.299	21.592	14	13 SLA
aliso	NE	r	RHUINT	4.510	2.079	5.691	0.930	18.376	16	
aliso	NE	s	ACMGLA	4.512	-0.775	5.615	1.131	22.084	14	13 SLA
aliso	NE	s	ARTCAL	4.663	0.179	5.510	1.204	22.470	14	11 LDMC
aliso	NE	s	DIPLON	4.513	1.101	5.788	0.606	21.597	17	
aliso	NE	s	ENCCAL	5.029	1.702	5.296	NA	NA	9	
aliso	NE	s	ERIFAS	4.452	-0.265	5.846	0.765	23.261	9	8 LDMC
aliso	NE	s	MALFAS	5.278	2.986	5.323	NA	NA	11	8 SLA
aliso	NE	s	MALLAU	4.578	2.518	5.707	NA	NA	17	
aliso	NE	s	SALMEL	4.629	2.081	5.530	1.018	22.401	11	
aliso	SW	a	ARTCAL	4.473	0.121	5.751	NA	NA	10	
aliso	SW	a	DIPLON	4.421	0.589	NA	0.095	21.174	5	
aliso	SW	a	ENCCAL	4.671	1.142	5.513	0.981	21.524	12	9 SLA, 8 LDMC
aliso	SW	a	ERIFAS	4.198	0.038	6.058	-0.034	21.349	13	
aliso	SW	a	HETARB	4.115	2.442	6.017	0.288	19.982	5	
aliso	SW	a	RHAILI	4.066	1.472	6.127	0.676	20.576	11	
aliso	SW	a	RHUINT	3.767	2.155	6.093	NA	NA	14	
aliso	SW	a	SALMEL	3.997	0.986	5.888	NA	NA	13	12 LDMC

fire	aspect	strat	spp	SLA	LA	LDMC	% N	δ^{13}C	count	count.r
aliso	SW	r	ENCCAL	4.932	1.438	5.359	1.262	21.733	9	8 LDMC
aliso	SW	r	HETARB	4.186	3.330	5.964	NA	NA	5	
aliso	SW	r	MALLAU	4.775	3.422	5.625	NA	NA	5	
aliso	SW	r	RHUINT	4.052	2.132	5.892	NA	NA	15	14 SLA
aliso	SW	s	ACMGLA	4.472	-0.846	5.976	1.099	20.996	13	12 LDMC
aliso	SW	s	ARTCAL	4.708	0.199	5.599	0.903	20.962	13	
aliso	SW	s	DIPLON	4.914	1.437	5.694	0.758	20.825	13	
aliso	SW	s	ENCCAL	4.939	1.840	5.294	NA	NA	10	8 LDMC
aliso	SW	s	ERIFAS	4.352	-0.635	5.864	0.588	21.347	12	11 SLA
aliso	SW	s	MALFAS	5.001	2.636	5.544	NA	NA	11	10 SLA, 10 LDMC
aliso	SW	s	MALLAU	4.443	2.551	5.675	NA	NA	12	
aliso	SW	s	SALMEL	4.221	1.585	5.631	NA	NA	15	14 SLA
holy	NE	a	ADEFAS	4.090	-0.923	6.152	0.182	20.367	12	
holy	NE	a	ARCGLAN	3.606	1.691	6.230	-0.105	20.122	12	
holy	NE	a	CEACRA	3.363	0.503	6.207	0.288	19.108	11	10 SLA
holy	NE	a	CEAOLI	4.249	0.348	6.115	0.550	22.260	12	11 LDMC
holy	NE	a	DENRIG	4.065	0.878	5.820	0.693	19.318	8	
holy	NE	a	HETARB	4.061	2.567	6.081	0.588	19.948	12	
holy	NE	a	QUEBER	3.937	1.120	6.301	0.491	19.597	13	12 LDMC
holy	NE	a	RHAILI	4.119	1.579	6.046	0.588	18.797	12	
holy	NE	a	RHUOVA	3.974	2.887	5.974	0.125	18.272	13	
holy	NE	r	ADEFAS	4.358	-1.285	5.923	0.742	21.470	10	
holy	NE	r	ARCGLAN	4.387	2.051	5.786	0.312	21.874	10	
holy	NE	r	CEALEU	4.653	0.520	5.873	1.006	22.470	9	8 SLA
holy	NE	r	CERBET	4.414	0.314	5.962	0.742	21.838	10	
holy	NE	r	DENRIG	4.540	1.785	5.491	1.234	19.143	12	
holy	NE	r	FRACAL	4.658	2.490	5.853	1.344	18.376	5	
holy	NE	r	HETARB	4.401	2.797	5.824	0.676	19.354	9	
holy	NE	r	QUEBER	4.479	0.936	5.900	0.659	19.143	17	
holy	NE	r	QUEWIZ	4.024	0.636	6.182	0.312	17.367	9	8 LDMC
holy	NE	r	RHAILI	4.680	1.871	5.748	0.943	18.725	12	
holy	NE	r	RHUOVA	4.313	2.829	5.720	0.491	18.099	15	
holy	NE	s	ACMGLA	4.713	-1.200	5.741	0.956	21.732	11	

fire	aspect	strat	spp	SLA	LA	LDMC	% N	δ^{13}C	count	count.r
holy	NE	s	ADEFAS	4.836	-1.241	5.835	0.742	21.417	9	
holy	NE	s	ARCGLAN	4.657	-0.291	6.036	0.624	24.194	9	
holy	NE	s	CEACRA	4.124	0.226	6.027	0.676	21.102	12	
holy	NE	s	CEALEU	4.706	0.229	5.880	1.099	21.875	10	
holy	NE	s	CEAOLI	4.689	0.546	5.888	1.121	20.928	13	
holy	NE	s	DENRIG	4.827	2.175	5.351	1.253	20.926	12	
holy	NE	s	RHUOVA	4.652	0.895	5.856	0.710	21.628	9	
holy	SW	a	ACMGLA	NA	-1.427	NA	NA	NA	4	
holy	SW	a	ADEFAS	4.028	-0.870	6.179	0.262	20.366	11	10 LDMC
holy	SW	a	ARCGLAN	3.614	1.654	6.246	-0.143	19.982	11	
holy	SW	a	CEACRA	3.313	0.394	6.223	0.312	17.888	14	9 SLA
holy	SW	a	CEALEU	4.279	-0.489	6.121	0.531	20.786	10	
holy	SW	a	DENRIG	4.043	1.445	5.837	0.726	19.283	6	
holy	SW	a	ERIFAS	4.238	-0.242	6.021	0.033	22.505	13	
holy	SW	a	HETARB	4.227	2.597	5.992	0.405	19.667	6	
holy	SW	a	QUEBER	3.966	0.820	6.289	0.312	19.423	15	
holy	SW	a	RHAILI	4.136	1.355	6.088	0.312	21.279	7	
holy	SW	a	RHUOVA	3.959	2.881	5.969	0.182	18.237	7	
holy	SW	r	ADEFAS	4.251	-1.148	6.066	0.560	21.592	14	13 LDMC
holy	SW	r	ARCGLAN	4.291	2.111	5.825	0.511	21.662	9	
holy	SW	r	CERBET	4.123	0.356	6.083	1.030	20.018	7	6 LDMC
holy	SW	r	DENRIG	4.532	1.334	5.534	1.163	19.284	12	10 LDMC
holy	SW	r	HETARB	4.634	2.497	5.684	1.076	19.179	10	
holy	SW	r	RHAILI	4.451	1.686	5.927	0.981	19.179	9	
holy	SW	r	RHUOVA	4.347	2.781	5.746	0.758	17.679	17	
holy	SW	s	ACMGLA	4.644	-0.820	5.813	0.875	21.627	10	
holy	SW	s	ADEFAS	4.607	-1.399	5.938	0.896	22.944	13	12 LDMC
holy	SW	s	ARCGLAN	4.500	0.192	6.043	0.588	21.768	11	
holy	SW	s	CEACRA	4.123	0.074	6.012	0.642	22.259	12	
holy	SW	s	CEALEU	4.850	0.371	5.817	0.903	23.384	11	
holy	SW	s	CEAOLI	4.656	0.215	5.848	1.110	21.909	8	
holy	SW	s	DENRIG	4.828	2.484	5.202	1.290	21.417	12	10 LDMC
holy	SW	s	ERIFAS	4.442	-0.560	5.962	0.531	20.367	10	
holy	SW	s	RHUOVA	4.582	1.245	5.869	0.642	19.985	5	

fire	aspect	strat	spp	SLA	LA	LDMC	% N	δ^{13}C	count	count.r
cranston	NE	a	ADEFAS	3.846	-1.101	6.165	0.033	19.144	11	
cranston	NE	a	ARCGLAN	3.754	1.434	6.143	0.095	20.052	6	
cranston	NE	a	CEALEU	4.362	0.257	6.106	0.642	20.576	21	
cranston	NE	a	CEAPER	3.513	0.105	6.187	0.182	18.829	12	
cranston	NE	a	CERBET	3.793	0.079	6.244	0.360	20.087	13	
cranston	NE	a	LONSUB	4.712	0.489	5.838	0.470	20.611	5	
cranston	NE	a	QUEWIZ	3.886	1.288	6.210	0.336	17.819	20	
cranston	NE	r	ADEFAS	4.215	-1.171	5.984	0.262	19.702	10	9 LDMC
cranston	NE	r	ARCGLAN	4.001	1.904	6.002	-0.034	22.505	9	
cranston	NE	r	CERBET	4.390	0.003	5.949	1.018	20.366	8	7 SLA, 7 LDMC
cranston	NE	r	LONSUB	4.740	0.222	5.962	0.427	19.671	11	
cranston	NE	r	QUEWIZ	4.237	1.006	5.968	0.531	18.132	11	10 SLA, 10 LDMC
cranston	NE	r	RHAILI	4.571	1.377	5.857	0.659	19.179	6	5 SLA
cranston	NE	s	ACMGLA	4.824	-1.262	5.724	0.930	21.382	10	9 LDMC
cranston	NE	s	ADEFAS	4.398	-1.089	6.220	0.560	18.428	10	
cranston	NE	s	ARCGLAN	4.201	-0.290	6.055	0.427	20.856	11	7 SLA
cranston	NE	s	CEALEU	4.632	0.224	6.033	0.693	19.597	11	
cranston	NE	s	CEAPER	4.147	-0.549	5.955	0.550	20.017	11	
cranston	SW	a	ADEFAS	3.946	-1.225	6.070	0.262	19.040	12	
cranston	SW	a	ARCGLAN	3.776	1.612	6.158	-0.034	20.088	16	
cranston	SW	a	CEALEU	4.413	0.289	6.074	0.588	20.331	12	
cranston	SW	a	CEAPER	3.441	-0.100	6.285	0.312	19.073	7	6 LDMC
cranston	SW	a	CERBET	3.934	0.446	6.176	0.470	20.302	11	
cranston	SW	a	ERIFAS	4.122	0.138	6.061	0.095	22.119	15	
cranston	SW	a	LONSUB	4.624	0.659	5.999	0.360	20.191	6	
cranston	SW	a	QUEWIZ	3.906	1.331	6.268	0.210	17.993	11	
cranston	SW	a	RHAILI	3.993	1.003	6.126	0.336	18.831	10	
cranston	SW	r	ADEFAS	4.243	-1.022	5.979	0.312	19.667	10	
cranston	SW	r	ARCGLAN	4.099	1.940	5.939	0.154	21.488	12	
cranston	SW	r	CERBET	4.339	0.210	5.987	0.981	20.087	14	13 SLA
cranston	SW	r	DENRIG	4.770	1.853	NA	1.099	18.934	5	
cranston	SW	r	LONSUB	4.842	0.485	5.762	0.875	19.807	11	8 SLA
cranston	SW	r	QUEWIZ	4.104	1.288	6.101	0.550	17.159	13	

fire	aspect	strat	spp	SLA	LA	LDMC	% N	$\delta^{13}C$	count	count.r
cranston	SW	r	RHAILI	4.261	1.369	5.986	0.624	19.074	12	
cranston	SW	s	ACMGLA	4.675	-1.253	5.725	0.981	20.716	10	
cranston	SW	s	ADEFAS	4.481	-1.334	5.979	0.588	19.633	15	
cranston	SW	s	ARCGLAN	4.501	0.606	6.031	0.470	20.859	13	
cranston	SW	s	CEALEU	4.705	0.403	5.910	0.833	20.472	15	
cranston	SW	s	CEAPER	4.235	-0.396	5.955	0.693	19.772	13	
cranston	SW	s	DENRIG	4.840	1.730	5.412	1.110	18.309	11	10 SLA
cranston	SW	s	ERICRA	4.620	3.299	5.721	NA	NA	7	
cranston	SW	s	ERIFAS	4.254	-0.295	5.951	0.182	22.645	10	

Table S2.3 Summary model statistics for Pagel’s λ test assessing phylogenetic signal in plant functional traits across closely related species. Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001).

Trait	Pagel’s λ	p-value
SLA	0.41214	0.508504
LA	0.916899	0.0915639
LDMC	0.911152	0.00383864**
% N	6.6107e-05	1
$\delta^{13}C$	0.63714	0.0821306

Table S2.4 Summary model statistics for trait variance partitioning models across regional burn scars and life stages. Fire is the regional burn scar (aliso, holy, cranston), life stage is adult or regenerating, trait includes SLA: Specific Leaf Area (cm^2/g), LA: Leaf Area (cm^2), LDMC: Leaf Dry Matter Content (mg/g), % N: percent leaf nitrogen content (%), δ^{13}C: discrimination of δ^{13}C (‰), and driver is the source of trait variation (unexplained, interspecific, regeneration strategy, local aspect), and value is the amount of trait variation explained (%).

Fire	Life Stage	Trait	Driver	Value
aliso	adult	SLA	unexplained	33.73001
aliso	adult	SLA	individual	0
aliso	adult	SLA	interspecific	64.92598
aliso	adult	SLA	regeneration strategy	0
aliso	adult	SLA	aspect	1.344015
aliso	adult	LA	unexplained	20.72664
aliso	adult	LA	individual	0.889112
aliso	adult	LA	interspecific	35.11832
aliso	adult	LA	regeneration strategy	43.26594
aliso	adult	LA	aspect	0
aliso	adult	LDMC	unexplained	25.20371
aliso	adult	LDMC	individual	0

Fire	Life Stage	Trait	Driver	Value
aliso	adult	LDMC	interspecific	17.52159
aliso	adult	LDMC	regeneration strategy	57.27471
aliso	adult	LDMC	aspect	0
aliso	adult	$\delta^{13}C$	unexplained	11.45776
aliso	adult	$\delta^{13}C$	individual	1.55E-09
aliso	adult	$\delta^{13}C$	interspecific	81.68524
aliso	adult	$\delta^{13}C$	regeneration strategy	1.91906
aliso	adult	$\delta^{13}C$	aspect	4.937935
aliso	adult	N	unexplained	0.322713
aliso	adult	N	individual	0
aliso	adult	N	interspecific	91.32293
aliso	adult	N	regeneration strategy	8.35435
aliso	adult	N	aspect	2.70E-06
aliso	regenerating	SLA	unexplained	76.28696
aliso	regenerating	SLA	individual	0
aliso	regenerating	SLA	interspecific	17.87998

Fire	Life Stage	Trait	Driver	Value
aliso	regenerating	SLA	regeneration strategy	4.132328
aliso	regenerating	SLA	aspect	1.700731
aliso	regenerating	LA	unexplained	19.64725
aliso	regenerating	LA	individual	0
aliso	regenerating	LA	interspecific	80.31919
aliso	regenerating	LA	regeneration strategy	0.033554
aliso	regenerating	LA	aspect	0
aliso	regenerating	LDMC	unexplained	59.69422
aliso	regenerating	LDMC	individual	1.551623
aliso	regenerating	LDMC	interspecific	31.82738
aliso	regenerating	LDMC	regeneration strategy	3.846658
aliso	regenerating	LDMC	aspect	3.080118
aliso	regenerating	N	unexplained	8.303376
aliso	regenerating	N	individual	0
aliso	regenerating	N	interspecific	86.85552
aliso	regenerating	N	regeneration strategy	4.841107

Fire	Life Stage	Trait	Driver	Value
aliso	regenerating	N	aspect	1.66E-07
aliso	regenerating	$\delta^{13}C$	unexplained	1.491845
aliso	regenerating	$\delta^{13}C$	individual	0
aliso	regenerating	$\delta^{13}C$	interspecific	70.84569
aliso	regenerating	$\delta^{13}C$	regeneration strategy	27.66247
aliso	regenerating	$\delta^{13}C$	aspect	4.21E-08
holy	adult	SLA	unexplained	20.24641
holy	adult	SLA	individual	0
holy	adult	SLA	interspecific	79.53009
holy	adult	SLA	regeneration strategy	0.223503
holy	adult	SLA	aspect	0
holy	adult	LA	unexplained	5.169409
holy	adult	LA	individual	0.888593
holy	adult	LA	interspecific	93.56007
holy	adult	LA	regeneration strategy	0.38193
holy	adult	LA	aspect	9.84E-10

Fire	Life Stage	Trait	Driver	Value
holy	adult	LDMC	unexplained	28.5573
holy	adult	LDMC	individual	1.384648
holy	adult	LDMC	interspecific	70.05805
holy	adult	LDMC	regeneration strategy	0
holy	adult	LDMC	aspect	0
holy	adult	N	unexplained	0.54274
holy	adult	N	individual	0
holy	adult	N	interspecific	89.61403
holy	adult	N	regeneration strategy	9.843225
holy	adult	N	aspect	6.53E-07
holy	adult	$\delta^{13}C$	unexplained	5.366652
holy	adult	$\delta^{13}C$	individual	0
holy	adult	$\delta^{13}C$	interspecific	82.22464
holy	adult	$\delta^{13}C$	regeneration strategy	12.40871
holy	adult	$\delta^{13}C$	aspect	6.11E-07
holy	regenerating	SLA	unexplained	54.915

Fire	Life Stage	Trait	Driver	Value
holy	regenerating	SLA	individual	0
holy	regenerating	SLA	interspecific	31.77245
holy	regenerating	SLA	regeneration strategy	13.31254
holy	regenerating	SLA	aspect	0
holy	regenerating	LA	unexplained	21.00205
holy	regenerating	LA	individual	0
holy	regenerating	LA	interspecific	73.87998
holy	regenerating	LA	regeneration strategy	5.117964
holy	regenerating	LA	aspect	0
holy	regenerating	LDMC	unexplained	51.12994
holy	regenerating	LDMC	individual	0.293284
holy	regenerating	LDMC	interspecific	48.57677
holy	regenerating	LDMC	regeneration strategy	1.29E-08
holy	regenerating	LDMC	aspect	0
holy	regenerating	N	unexplained	5.943957
holy	regenerating	N	individual	0

Fire	Life Stage	Trait	Driver	Value
holy	regenerating	N	interspecific	85.77002
holy	regenerating	N	regeneration strategy	8.28602
holy	regenerating	N	aspect	1.09E-06
holy	regenerating	$\delta^{13}C$	unexplained	12.69487
holy	regenerating	$\delta^{13}C$	individual	0
holy	regenerating	$\delta^{13}C$	interspecific	58.87648
holy	regenerating	$\delta^{13}C$	regeneration strategy	28.42865
holy	regenerating	$\delta^{13}C$	aspect	0
cranston	adult	SLA	unexplained	14.21559
cranston	adult	SLA	individual	9.01E-09
cranston	adult	SLA	interspecific	85.24899
cranston	adult	SLA	regeneration strategy	0.535422
cranston	adult	SLA	aspect	0
cranston	adult	LA	unexplained	16.63615
cranston	adult	LA	individual	1.72057
cranston	adult	LA	interspecific	81.09205

Fire	Life Stage	Trait	Driver	Value
cranston	adult	LA	regeneration strategy	0.551233
cranston	adult	LA	aspect	2.94E-09
cranston	adult	LDMC	unexplained	43.98103
cranston	adult	LDMC	individual	0
cranston	adult	LDMC	interspecific	52.89499
cranston	adult	LDMC	regeneration strategy	3.12398
cranston	adult	LDMC	aspect	0
cranston	adult	N	unexplained	7.600593
cranston	adult	N	individual	0
cranston	adult	N	interspecific	86.95061
cranston	adult	N	regeneration strategy	5.448797
cranston	adult	N	aspect	1.08E-07
cranston	adult	$\delta^{13}C$	unexplained	0.411899
cranston	adult	$\delta^{13}C$	individual	0
cranston	adult	$\delta^{13}C$	interspecific	98.69213
cranston	adult	$\delta^{13}C$	regeneration strategy	0.89597

Fire	Life Stage	Trait	Driver	Value
cranston	adult	$\delta^{13}C$	aspect	1.24E-09
cranston	regenerating	SLA	unexplained	54.6036
cranston	regenerating	SLA	individual	0
cranston	regenerating	SLA	interspecific	37.70706
cranston	regenerating	SLA	regeneration strategy	7.689346
cranston	regenerating	SLA	aspect	0
cranston	regenerating	LA	unexplained	12.71797
cranston	regenerating	LA	individual	0
cranston	regenerating	LA	interspecific	80.13793
cranston	regenerating	LA	regeneration strategy	7.144092
cranston	regenerating	LA	aspect	0
cranston	regenerating	LDMC	unexplained	48.40263
cranston	regenerating	LDMC	individual	6.67E-09
cranston	regenerating	LDMC	interspecific	47.51482
cranston	regenerating	LDMC	regeneration strategy	4.082548
cranston	regenerating	LDMC	aspect	9.67E-08

Fire	Life Stage	Trait	Driver	Value
cranston	regenerating	N	unexplained	4.634791
cranston	regenerating	N	individual	0
cranston	regenerating	N	interspecific	76.34907
cranston	regenerating	N	regeneration strategy	18.82448
cranston	regenerating	N	aspect	0.191662
cranston	regenerating	$\delta^{13}C$	unexplained	2.396778
cranston	regenerating	$\delta^{13}C$	individual	0
cranston	regenerating	$\delta^{13}C$	interspecific	84.80969
cranston	regenerating	$\delta^{13}C$	regeneration strategy	12.79353
cranston	regenerating	$\delta^{13}C$	aspect	0

Table S2.5 Species six letter codes, scientific names, and regeneration strategies for the shrub species used for functional trait collections.

Code	Scientific Name	Regeneration Strategy
ACMGLA	*Acmispon glaber*	Obligate Seeder
ADEFAS	*Adenostoma fasciculatum*	Facultative
ARCGLAN	*Arctostaphylos glandulosa*	Facultative
ARTCAL	*Artemisia californica*	Obligate Seeder
CEACRA	*Ceanothus crassifolius*	Obligate Seeder
CEALEU	*Ceanothus leucodermis*	Facultative
CEAOLI	*Ceanothus oliganthus spp. oliganthus*	Obligate Seeder
CEAPER	*Ceanothus perplexans*	Obligate Seeder
CERBET	*Cercocarpus betuloides*	Obligate Resprouter
DENRIG	*Dendromecon rigida*	Facultative
DIPLON	*Diplacus longiflorus*	Obligate Seeder
ENCCAL	*Encelia californica*	Facultative
ERICRA	*Eriodictyon crassifolium*	Obligate Seeder
ERIFAS	*Eriogonum fasciculatum*	Obligate Seeder
FRACAL	*Frangula californica*	Obligate Resprouter
HETARB	*Heteromeles arbutifolia*	Obligate Resprouter
LONSUB	*Lonicera subspicata*	Obligate Resprouter
MALFAS	*Malacothamnus fasciculatus*	Obligate Seeder
MALLAU	*Malosma laurina*	Facultative
QUEBER	*Quercus berberidifolia*	Obligate Resprouter

Code	Scientific Name	Regeneration Strategy
QUEWIZ	*Quercus wislizeni*	Obligate Resprouter
RHAILI	*Rhamnus ilicifolia*	Obligate Resprouter
RHUINT	*Rhus integrifolia*	Obligate Resprouter
RHUOVA	*Rhus ovata*	Facultative
SALMEL	*Salvia mellifera*	Obligate Seeder

Chapter 3: Regeneration trait functional strategies and timing mediate post-fire restoration planting success in chaparral

Abstract

Increasing habitat type conversions due to altered disturbance regimes and climate change requires innovative perspectives on how to improve restoration efficacy. Functional traits can be used to select species with different resource use strategies associated with restoration goals, and using traits at the early life stage where restoration operates (i.e., regeneration traits) may improve restoration success. The timing of restoration after a disturbance may also influence restoration success, as resource conditions change over time and the window for plant establishment shifts. We co-produced restoration and trait-based science with practitioners to assess post-fire planting success of chaparral shrubs. We experimentally tested how 1) restoration timing (i.e., time since fire) and 2) communities of different resource use strategies selected using regeneration traits influenced restoration planting establishment and survival success. Using 8 species of chaparral shrub species, we developed three planting pallets using regeneration traits – acquisitive (fast growing), conservative (stress tolerant), and diverse (both acquisitive and conservative) – and planted them into two burn scars at one year post-fire (Lake Fire) and eight years post-fire (Powerhouse Fire) in the Angeles National Forest, Lake Hughes, CA. We compared survival and cover in these treatments with nearby control plots to assess restoration efficacy compared to natural recovery. We found survival and cover were higher when seedlings were planted sooner after a fire. Survival was mediated by functional community type, where conservative treatments had higher survival when planted sooner after a fire, but survival was similar across all treatments when planted in the eight years post fire site. We found restoration effectively increased shrub cover in planted plots compared to control plots; however, treatment plots had similar cover regardless of the community functional strategy. Overall, our results show the timing of restoration impacts restoration success and can mediate the outcomes of regeneration trait-based restoration strategies.

Introduction

With increasing alterations to natural fire regimes and the interaction between fire and other environmental change stressors (e.g., drought, invasion), fire-prone ecosystems are experiencing weakened, patchy recovery and becoming more susceptible to plant invasion and habitat type conversion (Houghton et al., 2001; Keeley & Brennan, 2012; Park & Jenerette, 2019; Pausas, 2004). Underlying ecological processes can change when disturbance regimes are altered, resulting in altered recovery regardless of species adaptations to disturbance (Falk et al. 2022). Restoration, therefore, can be necessary across a gradient of conditions from immediately post fire (e.g., high severity stand replacing fire) to several years later (e.g., stalled recovery, invasion, type conversion). While trait-based approaches can be used in restoration to achieve both functional and compositional goals across this broad range of restoration settings (Funk et al. 2008; Perring et al. 2015), understanding how to match the appropriate functional strategy to these varied starting conditions is vital to improving restoration efficacy.

The use of functional targets has been effective in restoration of degraded ecosystems (Funk and McDaniel 2010) and creating resilience to future disturbances and stressors (Kimball et al. 2016). Traits commonly used in restoration relate to resource acquisition, growth, and reproduction (Gornish et al. 2023) and can be categorized into different functional strategies (i.e., acquisitive vs conservative) that relate to differing restoration goals (Laughlin 2014; Gornish et al. 2023). For example, species with conservative traits can be selected to promote survival in drought-prone systems (Balachowski and Volaire 2018), while species with acquisitive traits can be selected when the goal is to quickly establish and grow after a disturbance and preempt invasive species establishment (Funk et al. 2008), while a diverse mix with both strategies can be beneficial as a bet-hedging strategy under fluctuating environmental conditions. Selecting species palettes based on trait strategies therefore can be used to meet restoration goals that take into consideration current or changing environmental conditions. For example, in post-fire restoration, selecting species with fire tolerant traits (e.g., resprouting ability and rapid and abundant recruitment from seed) has successfully been used to promote resilience to fire (Loh et al. 2009). However, few studies experimentally test the success of different trait-based approaches (e.g., multiple community functional strategies) in active restoration (Carlucci et al. 2020; Gornish et al. 2023). Most work has used adult traits to inform restoration efforts, but given that restoration aims to re-establish species into disturbed or degraded areas, there is a clear opportunity to enhance restoration success by considering traits that are more relevant at the regeneration life stage post-disturbance (Grubb 1977; Perring et al. 2015). Notably, regeneration traits regularly differ from adults (Spasojevic et al. 2014; Dayrell et al. 2018; Garbowski et al. 2021) highlighting a mismatch between the traits used and life stage at which restoration operates (Larson and Funk 2016). Regeneration traits have been successfully used to guide restoration in grassland systems (Larson et al. 2015; Zirbel and Brudvig 2020) and have the potential to be used more broadly to improve restoration outcomes of post-disturbance scenarios.

The timing of restoration after a disturbance may influence restoration success (Brudvig 2011), as resource conditions differ with time post-disturbance, changing which plant strategies may be the most successful (Bashirzadeh et al. 2023). For example, after a fire, the initial post burn environment has a high resource input of nutrients from ash and light availability, which is rapidly utilized and depleted in the first few years post-fire by both native and invasive growth (Parker et al. 2016; Hanan et al. 2016; Allen et al. 2018). Restoration actions during this window could leverage these favorable growing conditions, to ensure successful revegetation outcomes while minimizing inputs (Kimball et al. 2015). As time post-disturbance increases, resources become limited as competition for light, nutrients, and water ensues, especially in invaded areas (Allen et al. 2018). Thus, planting at a longer time since fire may have less suitable establishment conditions and reduce restoration success. Therefore, management actions taken at this point may require more resources (e.g., cost and labor for site amelioration) to successfully restore (Kimball et al. 2015). However, the need for restoration may not be immediately evident or funds to facilitate restoration may not be readily available, resulting in restoration happening much later after the disturbance has occurred, particularly in post-fire settings (Lopes et al. 2022). Trait-based approaches may help mediate some of the challenges with implementing revegetation efforts in these less ideal settings, as matching traits suitable for a given environmental condition may improve establishment (Weiher and Keddy 1995). Therefore, there is a need to investigate how trait-based approaches can improve planting success in different time since disturbance scenarios.

Restoration of fire-prone habitats, such as chaparral, have largely been unsuccessful due to drought, increasing fire frequency, and non-native plant invasion (Allen et al. 2018), creating a need to experimentally test when and how to restore to improve management efforts. Type conversion from chaparral to non-native annual grasslands is a widespread problem in Southern California largely driven by frequent, short interval fires (Syphard et al. 2022). While chaparral restoration is increasingly implemented, it is often unsuccessful due to interacting abiotic and biotic factors (Allen et al. 2018), as well as occurring well after the natural recovery window. This delay is often caused by delays in funding where restoration does not occur until several years after the disturbance. The method of restoration can also impact success, where sowing seeds has largely been unsuccessful due to drought and competition with invasive species (Allen et al. 2018) leaving outplanting as the recommended restoration method (VinZant 2013). Outplanting is costly, time intensive, and still has relatively low survival rates, especially in dry systems, creating a need for improved outplanting establishment techniques (Leverkus et al. 2021). One method is to use a trait-based approach to select species mixes for different resource and growth strategies based on restoration goals, but it is unclear how different functional groups influence establishment success in the post-fire setting.

We co-produced restoration and trait-based science with practitioners to meet the needs of both groups (Covey 1989; Gornish et al. 2023) to assess and improve chaparral post-fire planting success. Specifically, we designed an experimental study planting shrubs of different resource-use strategies into two burn scars at different times since fire. We asked how 1) restoration timing (i.e., time since fire) and 2) regeneration trait-based communities influence restoration planting establishment and survival success.

Methods

Study Location

This study was conducted in chaparral shrublands in the Angeles National Forest, Lake Hughes, CA, which experienced two bordering wildfires in 2013 (Powerhouse Fire; 34.60295, -118.489) and 2020 (Lake Fire; 34.68887, -118.54986). Study sites ranged in elevation from 819 m - 1181 m in the Powerhouse burn scar and 1365 m - 1565 m in the Lake burn scar. The historic annual total growing season (Oct. - Aug. from 1970-2023) precipitation at the Powerhouse Fire and Lake Fire study locations are 470.22 mm and 578.41 mm, respectively, and mean annual growing season temperatures are 15.43 °C and 13.49 °C, respectively (PRISM Climate Group 2023), characteristic of the Mediterranean climate with cool, wet winters and hot, dry summers. During the study period, total growing season precipitation for Powerhouse Fire was 343.58 mm in 2022 and 997.21 mm in 2023 and for Lake Fire was 389.91 mm in 2022 and 1143.17 mm in 2023. The mean annual growing season temperature for Powerhouse Fire was 16.66 °C in 2022, and 14.01 °C in 2023 and for Lake Fire was 14.22 °C in 2022, and 12.05 °C in 2023. The vegetation community is characterized as manzanita-chamise chaparral

(*Arctostaphylos spp.* and *Adenostoma fasciculatum* dominant) and ceanothus chaparral (*Ceanothus spp.* dominant; Burned Area Report Lake Fire 2020).

The Powerhouse Fire burned 12,251 hectares from May 30, 2013 through June 10, 2013 and was caused by downed power lines. The Lake Fire burned 12,581 hectares from August 12, 2020 through September 28, 2020 and the cause is still unknown. The majority of area burned (i.e., Powerhouse Fire: 66% of hectares, Lake Fire: 72.4% of hectares) was in the moderate to high soil burn severity categories (Staley et al. 2013; 2020). The Powerhouse wildfire was within the normal 30-100 year fire return interval for chaparral (Hanes 1971; Van de Water and Safford 2011), as the time since the last burn ranged from 33 to 92 years (data records start in 1878 from the Department of Forest and Fire Protection CAL FIRE - Fire Perimeter data "Firep22_1", https://www.fire.ca.gov/what-we-do/fire-resource-assessment-program/fire-perimeters). The Lake Fire reburned part of the Powerhouse burn scar (7 years since last burn), but Lake Fire study sites were located in areas within the normal fire return interval, where time since last burn was 79 to 96 years.

Experimental Design

In Winter 2022, we set up a factorial experiment evaluating time since fire and functional community strategy effects on restoration success. Within each burn scar (Powerhouse Fire, 2013 and Lake Fire, 2020), we selected five sites based on burn severity, south facing aspect, degradation level, lack of evidence of erosion (rills, gullies, flow paths) in the planting plots, similar surrounding dominant vegetation, similar amounts of invasion, soil texture, and site accessibility determined from multiple site visits (Fig. 3.1). The outplanting communities consisted of one of three trait-based community mixes: resource acquisitive, conservative, and high diversity (both of the previous mixes combined). At each site, six 2 m x 2 m plots were randomly assigned to one of these treatments for two replicates of each, and a seventh plot was used as a control to compare natural recovery of the species selected for planting. Each treatment plot was planted with four species and four replicates per species for a total of 16 plants per plot (Fig. 3.2). Within each treatment plot we set up a 4 x 4 grid and randomly assigned a species to a planting location. A total of 960 individuals were planted and tagged in Jan. - Feb. 2022 via digging a shallow hole (~15 cm) to put a 10 cm deep seedling plug in. Holes were wet with 237 mL of water prior to planting and plants were watered with 237 mL after planting. All plant material was sourced, grown, and screened for *Phytophthora* fungal

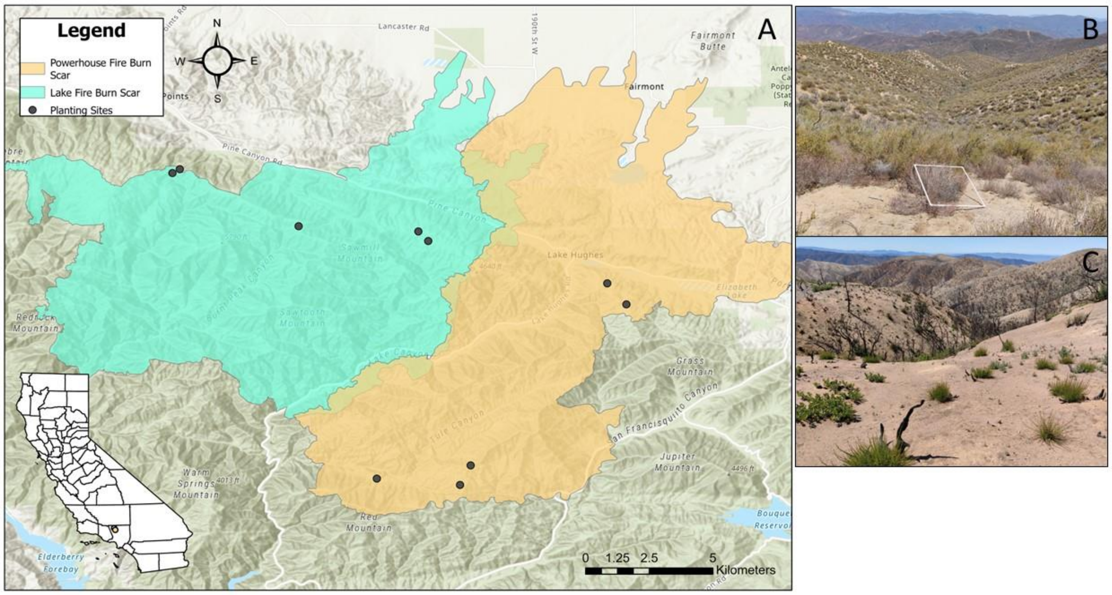

Figure 3.1 Map of study sites within each burn scar (A). The Powerhouse Fire (2013) burn scar is orange and Lake Fire (2020) burn scar is blue. Landscape views of natural recovery in Powerhouse Fire (B) and Lake Fire (C). Inset map of California with relative locations of burn scars by color.

Figure 3.2 Pictures of the planting process. A) treatment plot design with four species and four replicates per species for a total of 16 plants per plot being prepared for planting at the Lake Fire, B) pre-wetting the dug hole before planting seedlings, C) planted seedling with a berm to hold water.

infection by the California Botanic Garden from seed sources in the Angeles National Forest. Plants were hand watered with 474 ml of water the first week after planting and 237 ml the second week after planting. All sites were given 474 ml of water at the end of June to help the plants during summer drought conditions. Two acquisitive strategy species (*Eriophyllum confertiflorum*, Asteraceae; *Keckiella cordifolia*, Plantaginaceae) were placed in an herbivore (i.e., deer, rabbit, squirrel) exclosure for the first growing year to prevent herbivory of the most susceptible species. Plants that died from transplant shock were replanted within 2-4 weeks. Seedling survival was surveyed in Spring (May) 2022 for a measure of establishment success, Fall (October) 2022 for a measure of survival through the Summer drought season, and Spring (May) 2023 for a measure of survival one year post-establishment. Percent cover of the planted seedlings and naturally recovering vegetation (including all shrubs, forbs, and grasses) was measured during the Spring 2022 and 2023 surveys.

Trait Data Collection to Determine Species Mixes

We used functional strategy goals to create restoration planting mixes, using regeneration trait values rather than adult traits to experimentally test how regeneration traits influence restoration planting success. The trait-based community mixes included the resource acquisitive strategy aimed at rapid shrub growth preventing establishment of non-native forbs and grasses, the conservative strategy aimed at maintaining shrub survival under stressful growing conditions like drought, and high diversity strategy of both of the previous mixes combined aimed at bet hedging under variable weather conditions.

To determine species selection based on tradeoffs in resource-use and growth strategies, we measured a suite of traits that are indicative of resource-use strategies across 25 chaparral shrub species. We measured specific leaf area (SLA), leaf area (LA), and leaf dry matter content (LDMC) following standard protocols (Pérez-Harguindeguy et al. 2013). These morphological traits were selected as SLA and LDMC are associated with a plant’s ability to acquire and use resources, while LA is associated with leaf energy and water balance while coping with temperature, drought, and nutrient stressors (Pérez-Harguindeguy et al. 2013). These traits are also associated with the leaf economic spectrum(Reich 2014) which captures key tradeoffs in acquisitive (high SLA, high LA, low LDMC) vs conservative (low SLA, low LA, high LDMC) resource-use strategies. We collected leaf functional traits from 5-48 individuals for each of 25 candidate species at the regeneration stage (Table S3.1 species trait means). All regeneration traits were collected on less than one year old seedlings in the post-fire field setting in previous studies (i.e., not measured in the Lake and Powerhouse burn scars) or at the California Botanical Garden nursery. After collection, leaves were re-hydrated overnight in dark conditions to reach saturated wet weight. The following day, excess moisture was wiped off the saturated leaves, weighed to measure wet weight, then scanned to measure leaf area (ImageJ, https:// imagej.nih.gov/ij/). Leaves were dried at 60 °C for a minimum of 72 h then weighed to measure dry weight. These data were used to calculate SLA as fresh LA (cm^2) divided by dry weight (g) and LDMC as dry weight (mg) divided by wet weight (g).

Because of strong correlations between SLA, LA, and LDMC, we ordered species based on their SLA trait values, with high values indicating an acquisitive strategy and low values a conservative one. Based on seed availability, the potential species list was reduced. We then selected the top and bottom 4 species as the acquisitive and conservative mix, respectively. The diverse mix was made up of 2 species from each of the other mixes. This resulted in the following species mixes: 1) acquisitive: *Artemisia californica* (Asteraceae), *Eriophyllum confertiflorum* (Asteraceae), *Keckiella cordifolia* (Plantaginaceae), and *Ribes aureum* (Grossulariaceae)*;* 2) conservative: *Atriplex canescens* (Amaranthaceae), *Eriogonum fasciculatum* (Polygonaceae), *Salvia apiana* (Lamiaceae), and *Salvia mellifera* (Lamiaceae)*;* 3) diverse: *Eriophyllum confertiflorum*, *Ribes aureum*, *Eriogonum fasciculatum*, and *Salvia apiana* (Table 3.1).

Table 3.1 Species palettes used in functional strategy planting treatments.

Species Name	**Functional Strategy Planting Mix**		
	Conservative	Acquisitive	Diverse
Artemisia californica		X	
Atriplex canescens	X		
Eriogonum fasciculatum	X		X
Eriophyllum confertiflorum		X	X
Keckiella cordifolia		X	
Ribes aureum		X	X
Salvia apiana	X		X
Salvia mellifera	X		

Analyses

To assess how time since fire and functional community strategy treatment influenced survival of post-fire restoration planting, we used a Cox proportional hazards model with response variable overall survival probability at one year post-planting (Spring 2023) and predictor variables fire (indicating time since fire), functional strategy planting treatment, and their interaction. The Cox proportional hazard model allows us to incorporate survivorship from all sampling points to assess how survivorship changed throughout the course of the study. Overall survival probability was calculated using the surv() function from the survival package (Therneau 2023) in R. One site at each burn scar was dropped due to high herbivory. A type 3 Anova using the car package (Fox and Weisberg 2019) was used to view the model outputs. A Tukey post-hoc test was used on significant main effects using the emmeans package (Lenth 2021). To identify vulnerable time points for plants, we also report how mortality changed throughout the year (i.e., spring establishment, summer drought, one year survival) and across time since fire by calculating mortality between each survey relative to the amount that survived. To assess how time since fire and functional community strategy treatment planting influenced shrub cover compared to natural recovery, we used a non-parametric Scheirer Ray Hare test using the rcompanion package (Mangiafico 2022) with percent cover of species of planted shrubs at one year after planting as the response variable and predictor variables fire (indicating time since fire), functional strategy planting treatment, and their interaction. A Dunn post-hoc test was used on significant main effects using the package FSA (Ogle et al. 2022). All analysis was done in R version 4.1.1 (R Core Team 2021).

Results

We observed mean (± standard deviation) total vegetation recovery (i.e., total plant cover) during this study to be 9.7% ± 9.7 cover at Lake Fire and 12.9% ± 16.1 at Powerhouse Fire. Of this vegetation recovery, at Lake Fire an average of 83.3% of cover was composed of shrubs, 9.8% forbs, and 6.9% grasses while at Powerhouse Fire an average of 5.6% was composed of shrubs, 78% forbs, and 16.4% grasses. We observed 44 unique species (17 shrubs, 25 forbs, and 3 grasses) with an average of 6.6 ± 3.2 species per plot at Lake Fire and 5.8 ± 3.1 species per plot at Powerhouse Fire. Dominant species recorded in plots at Lake Fire included *Eriophyllum confertiflorum* (Asteraceae), *Salvia apiana* (Lamiaceae), *Atriplex canescens* (Amaranthaceae), and *Adenostoma fasciculatum* (Rosaceae), while dominants at plots in Powerhouse Fire included

Cryptantha intermedia (Boraginaceae), *Schismus spp.* (Poaceae), *Calyptridium monandrum* (Portulacaceae), and *Eriodictyon crassifolium* (Boraginaceae).

We found a main effect of time since fire on survival (p<0.001, Table S3.2). Specifically, survival was higher when planted sooner after fire in the Lake Fire burn scar (Fig. 3.3). Survival at one year post-planting (survey 3) was 55.6% in the one year post-fire site, while only 7.9% within the eight years post-fire site. We found a significant main effect of functional strategy planting treatment (p=0.002, Table S3.2) and its interaction with time since fire (p=0.008, Table S3.2) on survival. Functional strategy planting treatment impacted survival only when planted sooner after a fire, where conservative functional strategy treatments had higher survival than diverse treatments (p=0.008, Fig. 3.3). Over the duration of this study, acquisitive treatments had similar survival to both conservative (p=0.086, Fig. 3.3) and diverse treatments (p=0.954, Fig. 3.3) when planted sooner after a fire. When planted sooner after a fire, average survival was 54.4% in acquisitive plots, 64.4% in conservative plots, and 48.1% in diverse plots, while average survival ranged from 5% - 11.9% when planted later after fire.

Mortality over time provides a complementary perspective to these survivorship dynamics. During the establishment phase (surveyed Spring 2022) mortality was 22.7% at Lake Fire and 44% at Powerhouse Fire, during the first summer drought (surveyed Fall 2022) mortality of the remaining plants was 3% at Lake Fire and 14.5% at Powerhouse Fire, and after the summer (i.e., during the Fall and Winter; surveyed Spring 2023) mortality of the remaining plants was 25.8% at Lake Fire and 83.5% at Powerhouse Fire.

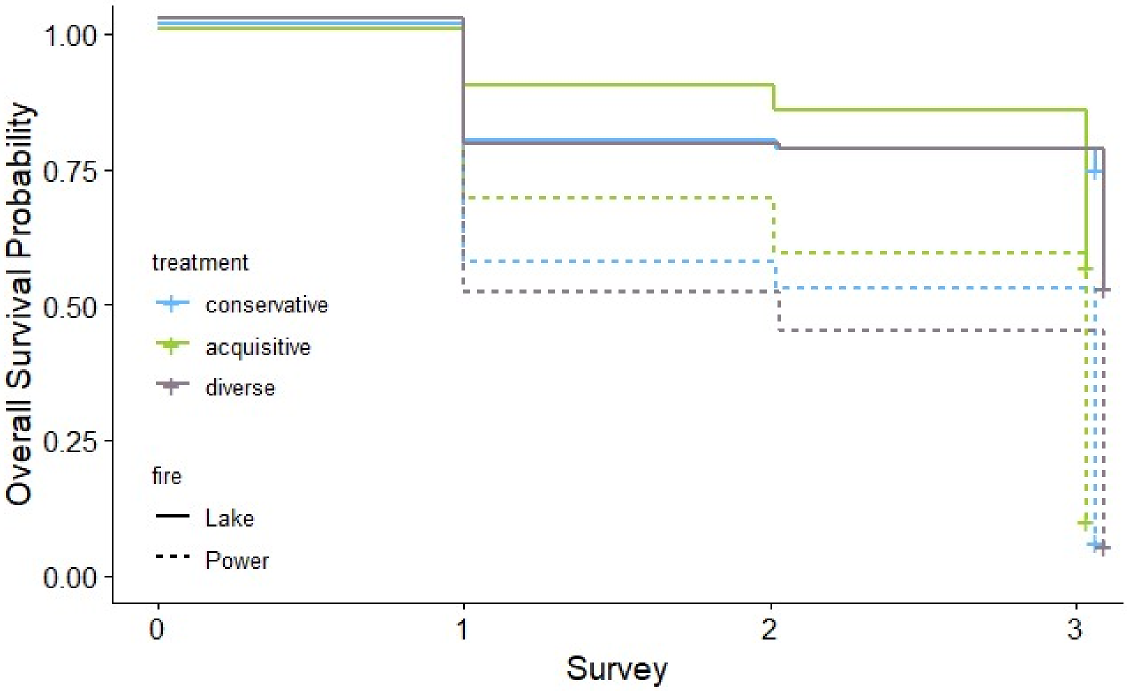

Figure 3.3 Survival probability curve over time for different functional strategy planting treatments and time since fire. Surveys represent different timepoints where survey 0 is winter 2022 planting, survey 1 is spring 2022 establishment, survey 2 is fall 2022 summer survival, and survey 3 is spring 2023 year 1 survival. Colors indicate different functional strategy planting treatments (blue: conservative, green: acquisitive, gray: diverse). Line types are different burn scars with different time since fire (solid: Lake Fire planted one year post-fire, dashed: Powerhouse Fire planted eight years post-fire). Lines represent the pooled response across all individuals and species within a given treatment.

We found a main effect of time since fire on percent shrub cover of planted species (p=0.008, Table S3.3). Shrub cover was higher in the Lake Fire burn scar that more recently burned. We also found a main effect of planting treatment (p=0.001, Table S3.3). Shrub cover was higher in planted plots compared to control plots that were not planted for the species that were selected for planting (acquisitive - control p<0.001, conservative - control p=0.001, diverse - control p=0.003, Fig. 3.4); however treatment plots had similar cover regardless of the community functional strategy (Fig. 3.4).

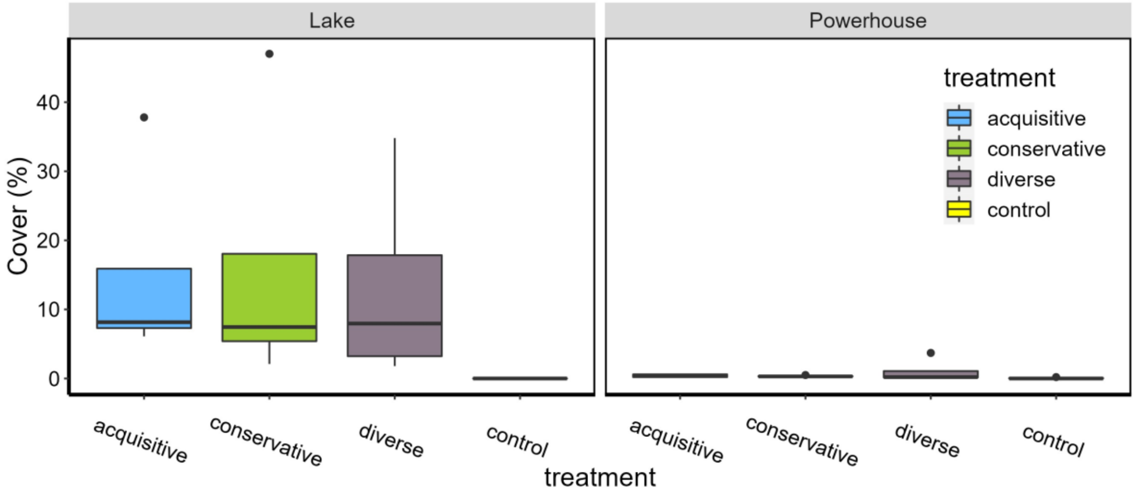

Figure 3.4 Percent cover of planted shrub species across functional strategy planting treatments and time since fire. Colors are different functional strategy planting treatments (blue: conservative, green: acquisitive, gray: diverse, yellow: control). Plantings represent management action one year post fire in the Lake Fire while eight years post-fire in the Powerhouse Fire.

Discussion

This study assessed the role of restoration timing (i.e., planting at different times since fire) and functional community mixes on restoration success in chaparral. We found survival was higher when seedlings were planted sooner after a fire. We found functional community treatment impacted survival only when planted sooner after fire, where conservative treatments had the highest survival one year post-planting. We observed mortality to be greatest after Summer (i.e., during the first Fall and Winter post-planting). We found shrub cover was higher when seedlings were planted sooner after a fire, and planting increased shrub cover regardless of functional community treatment. Together, we demonstrated that trait-based species selection and the timing of restoration can influence restoration success and expand on findings below.

Selecting species palettes based on community functional strategies can be useful in meeting functional restoration goals (Merchant et al. 2022; Gornish et al. 2023). There was a clear positive impact of restoration, where shrub cover was higher in planted treatment plots compared to control plots. Interestingly, we found functional strategy treatment success changed over the first year of restoration, where the acquisitive treatments planted sooner after fire had higher survival during the establishment and Summer drought period, but the conservative treatments had better survival at one year post-planting (Fig. 3.3). This suggests the conservative resource-use strategy is a good option for improving survival in chaparral post-fire restoration, and highlights the transient nature of restoration driving the need for long term monitoring (Shriver et al. 2019), in this case to further assess which community functional treatment promotes long term survival. When restoration site conditions have high invasion pressure and rapid establishment is key to preventing invasion, planting acquisitive species palettes may be the preferred option (Fargione et al. 2003; Funk et al. 2008; Merchant et al. 2022), as we observed high initial establishment in the acquisitive treatment. Our novel use of regeneration traits to inform species palettes has shown using early life stage traits in restoration is beneficial. Regeneration traits are increasingly linked to establishment and survival (Larson et al. 2015; Zirbel and Brudvig 2020; Arend da Silva et al. 2020), but identifying the right trait that influences restoration success (e.g., SLA, root elongation rate, intrinsic water use efficiency) is still needed to improve the efficacy of trait-based restoration.

The restoration context (i.e., where, when, and how restoration is done) creates variability in restoration success (Brudvig et al. 2017). We found the timing of restoration impacts project success where survival and cover were higher when seedlings were planted sooner after a fire. As resources become limited over time since fire (Parker et al. 2016; Hanan et al. 2016; Allen et al. 2018), conditions become less suitable for planting, reducing restoration success like we observed here. When restoration occurs many years post disturbance, more site amelioration (e.g., invasive species removal, soil amendments) or restoration maintenance (e.g., supplemental watering) may be required and are avenues of future research. To better prepare for rapid restoration after a disturbance, utilizing landscape scale tools to identify vulnerable/low recovery areas and higher ecosystem degradation risk can help practitioners quickly prioritize restoration areas (e.g. Post-fire Restoration Prioritization (PReP) tool; Underwood et al. 2022). Additionally, we found restoration timing regulated the impact planting treatments had on survival, where functional community treatments only mattered when planted sooner after fire. Survival was very low when planted later after a fire, suggesting there are greater survival barriers for restoration occurring longer after a disturbance (e.g., lack of available nutrients) that supersedes any resource partitioning dynamics that could occur via the functional community palettes. When restoration took place in natural recruitment conditions sooner after a disturbance, our functional community palettes mimicked selection dynamics that occur during recovery (i.e., resource use strategy impacted survival). This highlights the overall importance of restoring at the right time conducive for plant establishment in the post-disturbance setting.

Identifying vulnerable time points for plants is important to decide on appropriate restoration techniques (Allen et al. 2018). Summer drought is thought to be the largest driver of mortality (Allen et al. 2018), but we observed mortality to be highest after Summer (i.e., the first Fall and Winter post-planting), after plants had successfully established and survived through the Summer dry period. A potential reason for this high mortality is that we might not have captured all of the drought mortality during the early Fall sampling (end of October), especially if lack of precipitation continued beyond the Summer months. The Santa Ana winds, common in the Fall in Southern California, could have further created a prolonged period of drought due to the high evapotranspirative demand plants experience during high wind events (Hanson 1991). Winter temperatures and frost damage could also adversely impact seedling survival, as seedlings are more susceptible to environmental stressors than established adults adapted to their environment (Grubb 1977; Gabler and Siemann 2012). Additionally, the uncertainty of survival of drought deciduous plants in the Summer may have inflated some of the mortality recorded during the last survey, but few species employ this strategy (i.e., *Ribes areum*) and would not fully explain the high mortality observed. Further study is needed to identify the drivers of high mortality after Summer in order to inform future restoration action, such as supplemental watering in Fall or using traits to select more drought-tolerant or frost-tolerant species.

Conclusion

Assessing drivers of restoration success is important to improve efficacy as the need for restoration increases with global change. We found the timing of restoration mediates restoration success post disturbance and can regulate the impact regeneration trait-based methods have on restoration success. Restoration can increase post-fire recovery, but additional strategies are needed to improve restoration outcomes the longer restoration is delayed after disturbance. Together, we demonstrated how restoration timing and trait-based methods influence restoration success in a post-wildfire landscape.

References

Allen, E. B., Williams, K., Beyers, J. L., Phillips, M., Ma, S., & D'Antonio, C. M. (2018). Chaparral Restoration. In E. C. Underwood, H. D. Safford, N. A. Molinari, & J. E. Keeley (Eds.), *Valuing Chaparral: Ecological, Socio-Economic, and Management Perspectives* (pp. 347–384). Springer International Publishing. https://doi.org/10.1007/978-3-319-68303-4_13

Arend da Silva, I., Guido, A., & Müller, S. C. (2020). Predicting plant performance for the ecological restoration of grasslands: the role of regenerative traits. *Restoration Ecology*, *28*(5), 1183–1191. https://doi.org/10.1111/rec.13182

Balachowski, J. A., & Volaire, F. A. (2018). Implications of plant functional traits and drought survival strategies for ecological restoration. *The Journal of Applied Ecology*, *55*(2), 631–640. https://doi.org/10.1111/1365-2664.12979

Bashirzadeh, M., Abedi, M., Shefferson, R. P., & Farzam, M. (2023). Post-Fire Recovery of Plant Biodiversity Changes Depending on Time Intervals since Last Fire in Semiarid Shrublands. *Fire*, *6*(3), 103. https://doi.org/10.3390/fire6030103

Brudvig, L. A. (2011). The restoration of biodiversity: where has research been and where does it need to go? *American Journal of Botany*, *98*(3), 549–558. https://doi.org/10.3732/ajb.1000285

Brudvig, L. A., Barak, R. S., Bauer, J. T., Caughlin, T. T., Laughlin, D. C., Larios, L., Matthews, J. W., Stuble, K. L., Turley, N. E., & Zirbel, C. R. (2017). Interpreting variation to advance predictive restoration science. *Journal of Applied Ecology*, *54*(4), 1018–1027. https://doi.org/10.1111/1365-2664.12938

Burned Area Report Lake Fire. (2020). USFS.

Carlucci, M. B., Brancalion, P. H. S., Rodrigues, R. R., Loyola, R., & Cianciaruso, M. V. (2020). Functional traits and ecosystem services in ecological restoration. *Restoration Ecology*, *28*(6), 1372–1383. https://doi.org/10.1111/rec.13279

Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H., & Silveira, F. A. O. (2018). Ontogenetic shifts in plant ecological strategies. *Functional Ecology*, *32*(12), 2730–2741. https://doi.org/10.1111/1365-2435.13221

Falk, D. A., van Mantgem, P. J., Keeley, J. E., Gregg, R. M., Guiterman, C. H., Tepley, A. J., JN Young, D., & Marshall, L. A. (2022). Mechanisms of forest resilience. *Forest Ecology and Management*, *512*, 120129. https://doi.org/10.1016/j.foreco.2022.120129

Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National*

Academy of Sciences of the United States of America, *100*(15), 8916–8920. https://doi.org/10.1073/pnas.1033107100

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd ed.). Sage.

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution*, *23*(12), 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Funk, J. L., & McDaniel, S. (2010). Altering light availability to restore invaded forest: The predictive role of plant traits. *Restoration Ecology*, *18*(6), 865–872. https://doi.org/10.1111/j.1526-100x.2008.00515.x

Gabler, C. A., & Siemann, E. (2012). Environmental Variability and Ontogenetic Niche Shifts in Exotic Plants May Govern Reinvasion Pressure in Restorations of Invaded Ecosystems. *Restoration Ecology*, *20*(5), 545–550. https://doi.org/10.1111/j.1526-100X.2012.00901.x

Garbowski, M., Johnston, D. B., & Brown, C. S. (2021). Leaf and root traits, but not relationships among traits, vary with ontogeny in seedlings. *Plant and Soil*, *460*(1), 247–261. https://doi.org/10.1007/s11104-020-04790-z

Gornish, E. S., Campbell, C., Svejcar, L., Munson, S. M., Vaughn, K., Spaeth, M. K., Yelenik, S. G., Wolf, A., & Mitchell, R. (2023). Functional traits are used in restoration practice: a response to Merchant et al. (2022). *Restoration Ecology*, *31*(7). https://doi.org/10.1111/rec.13880

Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, *52*(1), 107–145. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-185X.1977.tb01347.x

Hanan, E. J., D’Antonio, C. M., Roberts, D. A., & Schimel, J. P. (2016). Factors Regulating Nitrogen Retention During the Early Stages of Recovery from Fire in Coastal Chaparral Ecosystems. *Ecosystems* , *19*(5), 910–926. https://doi.org/10.1007/s10021-016-9975-0

Hanes, T. L. (1971). Succession after Fire in the Chaparral of Southern California. *Ecological Monographs*, *41*(1), 27–52. https://doi.org/10.2307/1942434

Hanson, R. L. (1991). Evapotranspiration and droughts. *US Geological Survey Water-Supply Paper*, *2375*, 99–104.

Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., & Johnson, C. A. (2001). *Climate change 2001: the scientific basis*. The Press Syndicate of the University of Cambridge. http://cedadocs.ceda.ac.uk/981/8/Chapter_7.pdf

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, *169*(4), 1043–1052. https://doi.org/10.1007/s00442-012-2253-8

Kimball, S., Funk, J. L., Spasojevic, M. J., Suding, K. N., Parker, S., & Goulden, M. L. (2016). Can functional traits predict plant community response to global change? *Ecosphere* , *7*(12), e01602. https://doi.org/10.1002/ecs2.1602

Kimball, S., Lulow, M., Sorenson, Q., Balazs, K., Fang, Y.-C., Davis, S. J., O'Connell, M., & Huxman, T. E. (2015). Cost-effective ecological restoration. *Restoration Ecology*, *23*(6), 800–810. https://doi.org/10.1111/rec.12261

Larson, J. E., & Funk, J. L. (2016). Regeneration: an overlooked aspect of trait-based plant community assembly models. *The Journal of Ecology*, *104*(5), 1284–1298. https://doi.org/10.1111/1365-2745.12613

Larson, J. E., Sheley, R. L., Hardegree, S. P., Doescher, P. S., & James, J. J. (2015). Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. *The Journal of Applied Ecology*, *52*(1), 199–209. https://doi.org/10.1111/1365-2664.12350

Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, *17*(7), 771–784. https://doi.org/10.1111/ele.12288

Lenth, R. V. (2021). *emmeans: Estimated Marginal Means, aka Least-Squares Means* (Version R package version 1.6.3). https://CRAN.R-project.org/package=emmeans

Leverkus, A. B., Lázaro González, A., Andivia, E., Castro, J., Jiménez, M. N., & Navarro, F. B. (2021). Seeding or planting to revegetate the world's degraded land: systematic review and experimentation to address methodological issues. *Restoration Ecology*, *29*(4). https://doi.org/10.1111/rec.13372

Loh, R., Ainsworth, A., & D'Antonio, C. (2009). *Testing native species response to fire – a first step towards building fire resilient native plant communities at Hawai'i Volcanoes National Park*. Technical Report No.167. Pacific Cooperative Studies Unit, University of Hawai`i, Honolulu, Hawai`i. 30 pg. https://scholarspace.manoa.hawaii.edu/handle/10125/50814

Lopes, L. F., Fernandes, P. M., Rego, F. C., & Acácio, V. (2022). Public funding constrains effective postfire emergency restoration in Portugal. *Restoration Ecology*, *31*(3). https://doi.org/10.1111/rec.13769

Mangiafico, S. (2022). *rcompanion: Functions to Support Extension Education Program Evaluation* (Version R package version 2.4.18). https://CRAN.R-project.org/package=rcompanion

Merchant, T. K., Henn, J. J., de Silva, I., Van Cleemput, E., & Suding, K. N. (2022). Four reasons why functional traits are not being used in restoration practice. *Restoration Ecology, 31*(3). https://doi.org/10.1111/rec.13788

Ogle, D. H., Doll, J. C., Wheeler, P., & Dinno, A. (2022). *FSA: Fisheries Stock Analysis* (Version R package version 0.9.3). https://github.com/fishR-Core-Team/FSA

Parker, V. T., Pratt, R. B., & Keeley, J. E. (2016). TWENTY-FOUR. Chaparral. In H. Mooney & E. Zavaleta (Eds.), *Ecosystems of California* (pp. 479–508). University of California Press. https://doi.org/10.1525/9780520962170-028

Park, I. W., & Jenerette, G. D. (2019). Causes and feedbacks to widespread grass invasion into chaparral shrub dominated landscapes. *Landscape Ecology, 34*(3), 459–471. https://doi.org/10.1007/s10980-019-00800-3

Pausas, J. G. (2004). Changes in Fire and Climate in the Eastern Iberian Peninsula (Mediterranean Basin). *Climatic Change, 63*(3), 337–350. https://doi.org/10.1023/B:CLIM.0000018508.94901.9c

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. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany, 61*(3), 167. https://doi.org/10.1071/bt12225

Perring, M. P., Standish, R. J., Price, J. N., Craig, M. D., Erickson, T. E., Ruthrof, K. X., Whiteley, A. S., Valentine, L. E., & Hobbs, R. J. (2015). Advances in restoration ecology: rising to the challenges of the coming decades. *Ecosphere , 6*(8), art131. https://doi.org/10.1890/es15-00121.1

PRISM Climate Group, Oregon State University, https://prism.oregonstate.edu, data created 4 Feb 2014, accessed 30 Oct 2023

R Core Team. (2021). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.* https://www.R-project.org/

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

Shriver, R. K., Andrews, C. M., Arkle, R. S., Barnard, D. M., Duniway, M. C., Germino, M. J., Pilliod, D. S., Pyke, D. A., Welty, J. L., & Bradford, J. B. (2019). Transient population dynamics impede restoration and may promote ecosystem transformation after disturbance. *Ecology Letters*, *22*(9), 1357–1366. https://doi.org/10.1111/ele.13291

Spasojevic, M. J., Yablon, E. A., Oberle, B., & Myers, J. A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* , *5*(10), art129. https://doi.org/10.1890/ES14-000159.1

Staley, D. M., Smoczyk, G. M., & Reeves, R. R. (2013). *Emergency Assessment of Post-Fire Debris-Flow Hazards for the 2013 Powerhouse Fire, Southern California*. U.S. Geological Survey. http://pubs.usgs.gov/of/2013/1248/

Syphard, A. D., Brennan, T. J., Rustigian-Romsos, H., & Keeley, J. E. (2022). Fire-driven vegetation type conversion in Southern California. *Ecological Applications: A Publication of the Ecological Society of America*, *32*(6), e2626. https://doi.org/10.1002/eap.2626

Therneau, T. M. (2023). *A Package for Survival Analysis in R* (Version R package version 3.5-7). https://CRAN.R-project.org/package=survival

Underwood, E. C., Hollander, A. D., Molinari, N. A., Larios, L., & Safford, H. D. (2022). Identifying priorities for post-fire restoration in California chaparral shrublands. *Restoration Ecology*, *30*(3). https://doi.org/10.1111/rec.13513

Van de Water, K. M., & Safford, H. D. (2011). A Summary of Fire Frequency Estimates for California Vegetation before Euro-American Settlement. *Fire Ecology*, *7*(3), 26–58. https://doi.org/10.4996/fireecology.0703026

VinZant, K. (2013). Guidelines for Choosing a Restoration Plant Palette and Collecting Native Plant Materials. *Proceedings from the Chaparral Restoration Workshop*, 85–91.

Weiher, E., & Keddy, P. A. (1995). Assembly Rules, Null Models, and Trait Dispersion: New Questions from Old Patterns. *Oikos* , *74*(1), 159–164. https://doi.org/10.2307/3545686

Zirbel, C. R., & Brudvig, L. A. (2020). Trait–environment interactions affect plant establishment success during restoration. *Ecology*, *101*(3), e02971. https://doi.org/10.1002/ecy.2971

Appendix S3

Table S3.1 Species mean regeneration traits.

Table S3.2 Summary model statistics for an ANOVA on a Cox proportional hazard model assessing survival probability across time since fire and functional strategy planting treatments.

Table S3.3 Summary model statistics for non-parametric Scheirer Ray Hare test assessing how time since fire and functional strategy planting treatment influence shrub cover.

Table S3.1 Species mean regeneration traits. Count is the number of individuals measured, LA: Leaf Area, SLA: Specific Leaf Area, LDMC: Leaf Dry Matter Content. $^+$ indicates values measured at the California Botanic Gardens nursery, all other traits were measured in the field.

Species	Count	LA (cm^2)	SLA (cm^2/g)	LDMC (mg/g)
Acmispon glaber	41	0.236634	114.7804	315.3552
Adenostoma fasciculatum	48	0.187813	107.513	425.0067
Arctostaphylos glandulosa	45	1.285022	91.08262	416.2396
Artemisia californica	7	1.003143	145.5926	384.7066
Atriplex canescens$^+$	12	0.664	84.54845	262.4234
Ceanothus leucodermis	47	1.512255	132.5909	372.5568
Dendromecon rigida	35	10.16574	123.8383	204.6843
Diplacus longiflorus	14	3.491143	127.3561	377.6488
Encelia californica	9	5.856444	154.9939	201.8218
Eriophyllum confertiflorum$^+$	6	0.505667	189.9565	176.6437
Eriodictyon crassifolium	7	31.63457	101.8563	306.4206
Eriogonum fasciculatum	25	0.59465	78.88687	388.2402
Ericameria pinifolia$^+$	9	0.527444	96.08924	278.0761
Hazardia squarossa$^+$	10	1.7675	127.4483	264.3511

Species	Count	LA (cm^2)	SLA (cm^2/g)	LDMC (mg/g)
Keckiella cordifolia[+]	8	1.12975	170.0514	227.1452
Lepidospartum squamatum[+]	15	0.698467	126.1362	218.4904
Lonicera subspicata	22	1.409955	129.2656	356.4018
Malacothamnus fasciculatus[+]	10	9.1606	129.5422	261.6297
Peritoma arborea[+]	10	0.7934	128.0444	193.8589
Rhus ovata	14	3.223071	103.9643	353.8966
Ribes aureum[+]	11	6.862091	219.9888	298.0958
Rosa californica[+]	9	4.989667	150.7829	398.5702
Salvia apiana[+]	10	2.9847	66.49032	319.8885
Salvia mellifera	5	6.049	82.56418	251.4403
Trichostema lanatum[+]	7	0.619571	93.04996	302.9835

Table S3.2 Summary model statistics for an ANOVA on a Cox proportional hazard model assessing survival probability across time since fire and functional strategy planting treatments. Proportion survival was calculated using the surv function in R. Chisq values are presented. Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001).

	Chisq	Pr(>Chisq)
fire	58.3025	2.248e-14***
treatment	12.1121	0.002344**
fire:treatment	9.6094	0.008191**

Table S3.3 Summary model statistics for non-parametric Scheirer Ray Hare test assessing how time since fire and functional strategy planting treatment influence shrub cover. H values are presented with subscript degrees of freedom (variable, residual). Asterisks indicate significance levels (* 0.05, ** 0.01, *** 0.001).

	H value	p-value
fire	$7.0181_{1,24}$	0.00807**
treatment	$15.5850_{3,24}$	0.00138**
fire:treatment	$3.4032_{3,24}$	0.33354

Conclusion

This dissertation highlights how regeneration traits can be used to improve post-disturbance recovery predictions and provides experimental evidence to improve chaparral post-fire restoration outcomes using a trait-based approach. The first chapter demonstrates how different dimensions of regenerations traits scale across ecological processes to improve our understanding of community recovery, where the diversity of regeneration traits is key to increasing shrub recovery and promoting resilience to disturbances. The second chapter highlights the importance of identifying how ontogeny and spatial scales impact traits to improve trait-based approaches in community (re)assembly. The third chapter demonstrates how restoration timing and trait-based methods influence chaparral post-fire restoration success. Overall, these studies elucidate how regeneration traits mediate chaparral post-fire recovery and restoration.