

AN ABSTRACT OF THE DISSERTATION OF

Austin Himes for the degree of Doctor of Philosophy in Forest Ecosystems and Society presented on July 24, 2019.

Title: Impacts of Tree-species Composition and Diversity on Ecosystem Services in Plantations of the Coastal Pacific Northwest: Assessing Values, Trade-offs, and Synergies

Abstract approved:

Klaus J. Puettmann

The objective of this dissertation was to examine trade-offs and synergies between multiple ecosystem services derived from plantation forests in the coastal Pacific Northwest. I accomplished this in five chapters. In the first chapter I provided background information for the study. In the next chapter I set the context for assessing trade-offs and synergies between different ecosystem services by espousing value pluralism based on the recently proposed concept of relational values. Relational values provide a mode of articulating what diverse stakeholders deem important in their own context specific language and should be considered alongside instrumental and intrinsic values when assessing the value of ecosystem services. In the third chapter, I shifted focus to a field study on the relationships between tree species diversity and composition and three measures of ecosystem components in late-rotation, even-aged, intensively managed plantation forests of the Pacific Northwest (35-39 years of age). I observed variable patterns in the different measures' relationships to tree species composition and diversity that could be explained by differences in tree species phenology, shade tolerance, and disease which mediate plant interactions. The results suggested plantation management focused solely on wood production may miss opportunities to provide other ecosystem services. I further tested this hypothesis by integrating the data from the

field study with the relational values framework in the fourth chapter. I derived proxies for nine ecosystem services. I then determine the tree species composition that minimized trade-offs between subsets of the nine ecosystem services representing four different management frameworks. The ecosystem services included in each management framework were based on value priorities and the level of social organization corresponding to the benefits expected from the measured ecosystem services proxies. While most individual ecosystem services were optimized in monocultures, when multiple ecosystem services and values were considered simultaneously diverse mixtures of tree species were best. In the fifth chapter I synthesized results and concluded that within these managed plantations tree species diversity and human values interact to inform management decisions which shape the provisioning ecosystem services. Finally, I suggest future research focused on mechanisms behind ecological responses and connecting multiple levels of social, spatial, and temporal scales. Research that leads to a better understanding of the interrelationship between ecosystem functions, ecosystem services and values is needed to further test ecosystem services cascade theory.

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Impacts of Tree-species Composition and Diversity on Ecosystem Services in
Plantations of the Coastal Pacific Northwest: Assessing Values, Trade-offs, and
Synergies

by
Austin Himes

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Austin Himes, Author

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CONTRIBUTION OF AUTHORS

Dr. Barbara Muraca was involved in the writing and conceptual development of Chapter 1 and assisted with the development of the values matrix in Chapter 3.

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DEDICATION

I wish to dedicate this dissertation to my father, Dean Himes. He spent weeks camping in a tent, trouncing up and down the coast range, installing plots, and helping collect data with a bum hip that was scheduled for replacement surgery. His direct contributions to this research are among the least of what he has done to help shape my success, my character, and my life. He is the best man I know.

IMPACTS OF TREE-SPECIES COMPOSITION AND DIVERSITY ON ECOSYSTEM SERVICES IN PLANTATIONS OF THE COASTAL PACIFIC NORTHWEST: ASSESSING VALUES, TRADE-OFFS, AND SYNERGIES

Chapter 1. Background and Introduction

The objective of this research was to determine the relationship between tree species diversity and ecosystem functions, ecosystem services, and values in the context of production plantations in the Pacific Northwest Coast Range. I also sought to evaluate trade-offs and synergies between ecosystem services as a function of managing stands for different levels of tree species richness and different types of values.

While the terms ecosystem function and ecosystem service have sometimes been used interchangeably I adopt the distinction that ecosystem function refers to biological structures and process important from an ecological perspective (like productivity) and goods or services refer to products or outcomes of ecosystem functions that provide direct benefits to humans (Boyd and Banzhaf, 2007; de Groot et al., 2002). The Millennium Ecosystem Assessment (MEA) is a broadly accepted framework for defining ecosystem services and divides them into four categories: provisioning services like food, clean water, fiber, and fuel; regulating services like climate regulation and flood control; cultural services like recreation, education, and aesthetics; and supporting services like primary production and soil formation (MEA, 2005).

The idea that biodiversity increases ecosystem functions, services, and stability is not new. Charles Darwin was one of the first to suggest the relationship in 1858 (Hector and Hooper, 2002). In the twentieth century, agricultural researchers observed that productivity was greater if two crops were grown together instead of by themselves (Vandermeer, 1992). They hypothesized that reduced competition through complimentary resource use and species facilitating the growth of one another were responsible for the increase in productivity (Vandermeer, 1992). Controlled empirical

studies of the species diversity-growth relationship were scarce until the 1990's when high profile studies in model systems demonstrated a link between the number of species or species functional groups with productivity and nutrient retention (Naeem et al., 1996, 1994; Tilman et al., 1997a, 1997b). However, the higher productivity in these studies could not be affirmatively contributed to species interactions per se (labelled complementary effect), as the higher likelihood that very productive species are included in the higher diversity treatments could also explain the results (labelled selection effect). For example, several studies found that species composition, specifically the traits of the species included in the treatments, was the main determinant of increased productivity (Hooper, 1998; Hooper and Vitousek, 1997). Selection effect is expected to drive the biodiversity ecosystem function relationship when a single resource is the basis of competition (Tilman et al., 1997b). In a large study in European grasslands, selection effects varied from negative to positive, depending on the biomass of the dominant species relative to the community, but was zero on average (Loreau and Hector, 2001). The current understanding is that ecosystems require a plurality of species to function in a steady state and across communities average complementary effects will be positive (Loreau, 2010; Loreau et al., 2001; Loreau and Hector, 2001).

Early studies investigating the relationship between biodiversity and ecosystem functions were extremely insightful but had limitations. Most of the studies focused exclusively on herbaceous species, documented responses over a relatively short time and only measured one or two ecosystem functions (Hooper and Vitousek, 1997; Naeem et al., 1996; Tilman et al., 1997a). More recent studies expanded the focus to trees and investigated biodiversity-productivity relationships in boreal (Grossiord et al., 2013), temperate (Scherer-Lorenzen et al., 2007), and tropical forests (Erskine et al., 2006), and included conifers (Forrester et al., 2013), broadleaves (Jacob et al., 2010), and mixed conifer/broadleaf forests (del Río and Sterba, 2009). Many studies found productivity increased with higher tree species richness but there were also

examples where no relationship was evident, or productivity was negatively correlated with the number of tree species. A meta-analysis found, on average, mixed species stands had no effect on height and a moderate effect on DBH of trees relative to monocultures, but 19 out of 46 species grew slower in mixed stands (Piotto, 2008). In a global meta-analysis of forest biodiversity-productivity studies, species mixtures had nearly 24% more productivity than monocultures, but regression analysis suggested species evenness, heterogeneity of shade tolerance, and stand age explained more of the variation in productivity than species richness (Zhang et al., 2012). According to stress-gradient hypothesis, which is supported by multiple studies, the positive relationship between biodiversity and productivity is likely to increase along a gradient of declining site productivity (Forrester and Bauhus, 2016; Río et al., 2014; Toïgo et al., 2015). Stand density can also impact the size and direction of the biodiversity productivity relationship in forests but the direction and magnitude depend on what resources are limiting and how species interaction affecting those resources are mediated by density (Forrester and Bauhus, 2016).

Many studies suggest that biodiversity is important for maintaining multiple ecosystem services through time and changing environmental conditions (Duffy, 2009; Gamfeldt et al., 2013, 2008; Isbell et al., 2011; Puettmann, 2014). At the same time, trade-offs between the quantity of ecosystem services provided by forests under different management scenarios are well documented (Bradford and D'Amato, 2012; Kline et al., 2016; Nalle et al., 2004). For example, in Oregon, Hairy Woodpecker presence increased three-fold in heavily thinned Douglas-fir stands compared to unthinned stands while Varied Thrush detections decreased by half, suggesting management to maximize the presence of one species could have deleterious effects on the presence of the other (Hayes et al., 2003). Often, trade-offs are not as simple as favoring habitat for one species at the expense of another. There are a multitude of services affected by management action which may interact in complex and unpredictable ways across temporal and spatial scales larger and smaller than the

management action targets (Maass et al., 2005; Rodríguez et al., 2006). In forestry settings, owners typically do not place the same value on all ecosystem services. Instead owners have a ranking that reflects their values, economic needs, environmental attitudes as well as the social and regulatory framework of their operation. Thus, increasing the most valuable services may be more important than increasing total ecosystem services. Furthermore, many ecosystem services are only desirable or relevant at a minimum quantity which creates threshold dynamics. For instance, it may be necessary for revenue to meet or exceed the operating expenses for owners to manage their land. Similarly, wildlife species may require a minimum expanse of suitable habitat to support viable populations. If the quantity of a service falls below these minimum thresholds it no longer provides a benefit.

Plantation forests may need to supply more ecosystem services in the future to provide for the demands of a growing population. However, for practitioners of traditional plantation forestry income maximization is usually the desired outcome and only mixtures that are more productive than the best performing monoculture in terms of net income are likely to be attractive (Schmid et al., 2008). This narrow view assumes stable conditions free of disease or unplanned disturbance and ignores other benefits of mixtures, such as risk reduction, disease resistance, and wood quality that mixed species stands can impart (Knoke et al., 2008; Perry et al., 1992). Maximizing the efficient production of a single ecosystem service also comes at the cost of system resilience (Walker and Salt, 2012). However, with growing emphasis on multiple use forestry and ecosystem services, more forest managers are considering factors in addition to timber value when making decisions. Direct monetization of ecosystem services, like carbon storage, and forest certification schemes promoting multiple ecosystem services incentivize managers to consider a broader range of options (Adams et al., 2011; Auld et al., 2008; Robert and Stenger, 2013).

It is a major challenge to comprehensively evaluate ecosystem services when trade-offs exist and services may not come in commensurate units. Forest managers need tools to assess the value of managing a mixture of species relative to monoculture systems in terms of a full suite of ecosystem services (Christin et al., 2016).

Economic evaluation methods, such as cost benefit analysis are often used to assess trade-offs (Saarikoski et al., 2016), but evaluation schemes that reduce ecosystem services to monetary terms have been criticized because of ethical considerations (Jax et al., 2013). Philosophers and conservationists have argued that nature has intrinsic value and reducing ecosystems to the monetary value of the services they provide suggests a willingness to sell ecosystem functions that may be essential or irreplaceable (O'Neill, 1993; Spash, 2008). Furthermore, commodification of ecosystem services may ignore the complex relationships and power asymmetries among those benefiting from ecosystems (Kosoy and Corbera, 2010). Economic analysis can also be complicated and difficult for land managers to implement (Bradford and D'Amato, 2012). Despite these criticisms, economic valuations of ecosystems services are arguably critical to communicating the importance of ecosystem services to human wellbeing (Costanza et al., 2014). Understanding the benefits and limitations of different evaluation methods applied to real-life managed ecosystems will advance our understanding of ecological processes and help managers make informed decisions.

In this dissertation, I began with a review of value types commonly used to express why nature is important to people and promote the use of relational values as the key to pluralistic valuation of ecosystem services. In this context, relational values may be a solid foundation for assessing trade-offs between incommensurate values. Next, I presented the relationship of different proxies of ecosystem function to tree species composition and diversity from a study in plantation forests of the coastal Pacific Northwest. Then, combining data from the field study, literature and existing models I estimated the relationship of nine potential ecosystem services to tree species

composition and diversity. I compared trade-offs and synergies between individual services and four management frameworks representing a range of relational values and management objectives. Finally, I concluded with thoughts on the interrelationship of tree-species diversity, ecosystem function, ecosystem services, and values as well as suggestions for future research.

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Chapter 2.

RELATIONAL VALUES: THE KEY TO PLURALISTIC VALUATION OF ECOSYSTEM SERVICES

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Abstract

Multiple frameworks have recently been proposed adopting relational values as a new domain of value articulation distinct from the dichotomy of intrinsic and instrumental values that has dominated environmental ethics for decades. In this article, we distinguish between the innate relationality of all evaluative process and relational values as the content of valuation which is a new and fruitful category for expressing the importance of specific relationships people hold with non-human nature. We examine the concept of relational values used in recent frameworks and propose a simple conceptualization with clear distinctions between relational, instrumental, and intrinsic (inherent moral) values. We argue that as a new category of value articulation, relational values provide conceptual and empirical insights that the intrinsic/instrumental value dichotomy fails to deliver. Finally, we draw on theoretical and empirical research to show why a clear distinction between instrumental and non-instrumental relational values is important for environmental conservation, sustainability, and social justice.

Introduction

Since the introduction of the term ‘relational values’ as an analytical framework to assess the ways people articulate the importance of ecosystem services in their specific, socio-culturally embedded language of valuation, the concept has been employed in several theoretical studies and tested empirically. In this paper, we provide a short overview of the term by first distinguishing between the relationality inherent in all valuation processes and the specific articulations of relational values as used in taxonomies (Arias-Arévalo et al., 2018) and classifications (Pascual et al., 2017). We then present and critically discuss how intrinsic, instrumental, and relational values are employed in the literature, and articulate the need for differentiating relational values that are *anthropocentric yet non-instrumental*. We show why this difference is crucial for the way we conceive of and implement value formation. Besides the framework of moral obligations towards non-human entities and merely instrumental benefits of ecosystem services to people, we argue that a more sophisticated consideration of non-instrumental, relational values and a pluralistic approach to value articulation are needed to fully understand how and why people care about non-human nature. We reject the either/or mentality of the intrinsic vs. instrumental value debate and suggest that non-instrumental relational values fill a gap left by inadequacies and ambiguities in the common application of the instrumental/intrinsic paradigm.

Relational Values: a new category of value assessment

Relational values are included in many recent frameworks and hierarchies proposed for the valuation of ecosystem services. Muraca’s (2011) formative contribution proposed the concept of relational values in a theoretical framework aimed at representing normative judgments about nonhuman nature. More recently, the IPBES (Intergovernmental Platform on Biodiversity and Ecosystem Services) has included, in addition to instrumental values, the category of relational values in its conceptual

framework to address nature's benefits to people (Díaz et al., 2015; Díaz et al., 2015; Pascual et al., 2017). IPBES describes relational values as "...imbedded in desirable (sought after) relationships, including those between people and nature..." (Díaz et al., 2015). The IPBES framework embraces relational values as a departure from the economic valuation framework that commonly dominates assessments of ecosystem services and nature's benefits to people (Díaz et al., 2015).

Critics question that relational values can be adequately articulated as distinct from instrumental and intrinsic values (Hahn et al., 2015; Maier and Feest, 2016). For example, against the IPBES framework Mair and Feest (2016) claim that relational value is not an adequate analytical category and serves no purpose, because all values and desires are in principle relational. While we agree that all valuation processes are ultimately relational, we make the case in this paper that relational values are a fruitful category of classification if the contents of valuation that mirror different ways of understanding, articulating or expressing the importance of specific forms of relationships with non-human nature are clearly distinguished from the inherently relational nature of valuation.

Processes of valuation as fundamentally relational vs. relational value as the content of valuation

We make a distinction throughout this paper between the *process of valuation* and the *content of valuation*. The *process of valuation* refers to how it occurs that something we encounter becomes important, significant, or worth our attention. The *content of valuation* is the product of the *process of valuation* and it refers to *what* is valued and how the value is *attributed* and *articulated*. We believe this distinction resolves confusion described by Muradian and Pascual (2018) around use of the term 'relational values,' and the general relational nature of valuation.

With respect to their nature and genesis, all valuations are essentially relational. Valuations are neither entirely produced by the observer nor inherent to the thing but

arise in the space of encounter where the subject and objects originate (Arias-Arévalo et al., 2018; Muraca, 2016a). Thus, the genesis of valuations is not merely subjective nor only objective but rather constitutive of both. Even before we identify ‘things’ and judge them, a vague and non-conscious sense of importance guides and elicits our attention to ‘something that matters’ (Muraca, 2016a). In daily life, we don't first run into an object, then observe it, and then judge it, rather we are already immersed in value-led relationships that evoke what matters and becomes thereby an object for us. A good example is the relationship one has with their native language. We are embedded in a non-neutral relationship with our native language that is independent of our actual preferences about it. It constitutes our identity and the realities we relate to; it thus shapes the horizon of possibility for the expression of our preferences. In a similar way, all processes of valuation are rooted in forms of embeddedness and importance that are constitutive of who we are but are often unexpressed and outside our conscious awareness. In this sense it is possible to talk about relational value with respect to the fundamental and immediate feeling of “importance, worth, or significance that something has for an individual” (Jones et al., 2016; Schroeder, 2013) and that sustains any process of value formation.

In a more specific sense, the orientation of importance towards the world is mediated, influenced, and co-determined by socially shared horizons of meaning that form shared narratives, institutions, norms, and habitualized practices. The way in which we come to consider something as important, is the result of the social processes of value formation and transformation (Irvine et al., 2016; Kenter, 2016; Kenter et al., 2016).

With respect to the content of valuation (*what* is considered important and how this attribution of importance is articulated), relational values enable a space, both forming and eliciting values, in which anthropocentric, yet non-instrumental, relationships to nature can be expressed. Technically speaking, relational values can refer to the articulation of both instrumental and non-instrumental relations (Muraca,

2011, 2016a). Following more recent literature, we employ here the term in a narrower sense with reference to non-instrumental relationships. Such relationships are not reducible to mere means to some humans' end, but constitute who we are as humans. They are deeper and more complex than merely instrumental ones (Moreno-Mateos et al., 2015). Following Chan et al. (2016), relational values refer to “preferences, principles, and virtues associated with relationships, both interpersonal and as articulated by policies and social norms” (Chan et al., 2016:1462). They include action, experiences, and habits associated with the ‘good life’ in the sense of a meaningful, ethically responsible, and overall satisfying life, or what is called eudaimonic values. They do not refer to things but derive from “relationships and responsibilities to them” (Chan et al., 2016:1462). In this second meaning, relational values are an indispensable category of classification that expands the perspective on valuation and enables a more adequate and pluralistic assessment of value (Arias-Arévalo et al., 2018). A pluralistic approach not only captures the variety of ways people express why they value what they call nature (Gómez-Baggethun and Martín-López, 2015; Jacobs et al., 2016), but also enables a multiplicity of perspectives and valuation languages to be employed on their own terms, thus supporting collective and reflexive processes of value formation.

Relational values enable more adequate articulation of values than the intrinsic/instrumental dichotomy.

With respect to the content and not the nature of valuation in recent environmental literature, relational values are generally framed as a third alternative to the traditional intrinsic/instrumental dichotomy that is rooted in environmental ethics and nature conservation debates (Chan et al., 2016; Frankena et al., 1979; Muraca, 2011; Norton, 1991; Rolston, 1988). The Millennium Ecosystem Assessment reinforced the intrinsic/instrumental dichotomy in the context of ecosystem services by invoking the Kantian logic that an entity can have either a *price* or a *dignity* (Alcama and Al, 2003). In environmental valuation and ecosystem service literature, the definition of

instrumental values is generally clear-cut: things that are means to some external end. However, different and contradictory meanings are often conflated with respect to intrinsic value, in order to capture independence from human needs, meanings, and preferences as well as values that are relational but are non-instrumental. The clarification of the concept of relational values to address specifically non-instrumental relations offers a solution to this contradictory use. Following O’Neill (O’Neill, 1993), we claim that we may value something (1) in virtue of its relation to other objects, but independently of human needs, meanings, interests or preferences which corresponds to the common use of intrinsic value, or (2) in virtue of its specific relations to people. Such relationships can refer to either (2a) a constitutive component for flourishing (a good human life, i.e. a life worthy of a human being (Nussbaum, 2001), including moral responsibility and care for the flourishing of other beings and the foundations of our socio-cultural self-understanding,¹ or (2b) in virtue of it being instrumental (means to an end) to satisfy human needs and preferences (O’Neill, 1993:ff14). Accordingly, instrumental values overlap to a certain extent with relational values, as they both refer to human-nature relationships, but do not correspond exactly and one may be present without the other.

IPBES defines intrinsic values as “values inherent to nature, independent of human judgment” (Pascual et al., 2017:9) and as non-anthropocentric (Pascual et al., 2017). This definition is confusing as it conflates three different meanings of intrinsic: a) referring to inherent, non-relational, properties of objects, b) independent of human valuation and judgment, and c) bearers of inherent moral value as ends-in-themselves and subjects with their own good (O’Neill, 1993). We have to draw an important distinction between *epistemic anthropocentrism*, which means that knowledge and judgments are always human-centered and that valuations must come from a human perspective, and *moral anthropocentrism*, which states only humans are bearer of

¹ This is close to the meaning of non-instrumental relational values as I use it here.

values and worthy of direct moral consideration. According to Batavia and Nelson (Batavia and Nelson, 2017), morally non-anthropocentric, intrinsic values (non-human entities deserving direct moral consideration for their own sake) are essential for nature conservation and reflect the motivation of environmental activists and scientists. This is supported by empirical evidence (Admiraal et al., 2017; Arias-Arévalo et al., 2017; Moreno-Mateos et al., 2015) and theoretical analyses (Jax et al., 2013; Muraca, 2011, 2016a). By this definition, intrinsic values are a powerful motivator for conservation on moral grounds but are outside the scope of evaluation of nature's contribution to people or ecosystem services (Piccolo, 2017).

It is difficult to imagine non-anthropocentric values in the epistemic sense. IPBES uses the term intrinsic value to address ecological functions as they are described by scientific research. Now, how can ecological processes – defined as inherent to nature – be independent of human judgment or of “any human consideration of its worth and importance” (Diaz et al., 2015:4), if they are articulated via scientific research, i.e. human research that assesses its ecological importance? It is likely that the intention of Diaz et al. (2015) is to highlight the distinction between values that are independent of expressed human interests or preferences (but not judgment!) and those that refer to direct benefits to people, both in the sense of means – goods and services (instrumental) – and in the sense of constituents of a good life (relational). To avoid confusion, we plead to reserve the use of the term intrinsic values to the attribution of inherent moral value to entities that can be legitimately considered as subjects-of-a-life or ends in themselves in a moral sense.

Instrumental, intrinsic, and non-instrumental relational values are distinct and not commensurable, but they are connected and can be simultaneously present in a common framework that embodies the complexity of how people articulate how and why non-human nature matters to them. Excluding one form of value articulation or reducing all to one type result in negatively biased assessment of value (see Figure 2.1) (Arias-Arévalo et al., 2018; Martinez-Alier et al., 1998). Arias-Arévalo et al.

(2018, 2017) classify between three different narratives that cannot be aggregated into synthesis assessments and corresponds to the three value typologies: gaining from nature (instrumental), living for nature (intrinsic in the sense of the direct moral consideration of nonhuman subjects of a life), and living in nature (relational). In recent environmental literature relational values are associated with embeddedness, collective meaning, flourishing, heritage, beauty, self-transformation, sense of place, spirituality, livelihoods, justice, conviviality, care, and kinship (Admiraal et al., 2017; Arias-Arévalo et al., 2017; Cundill et al., 2017; Gould et al., 2015; Gould and Lincoln, 2017; Jackson and Palmer, 2015; Singh, 2015).

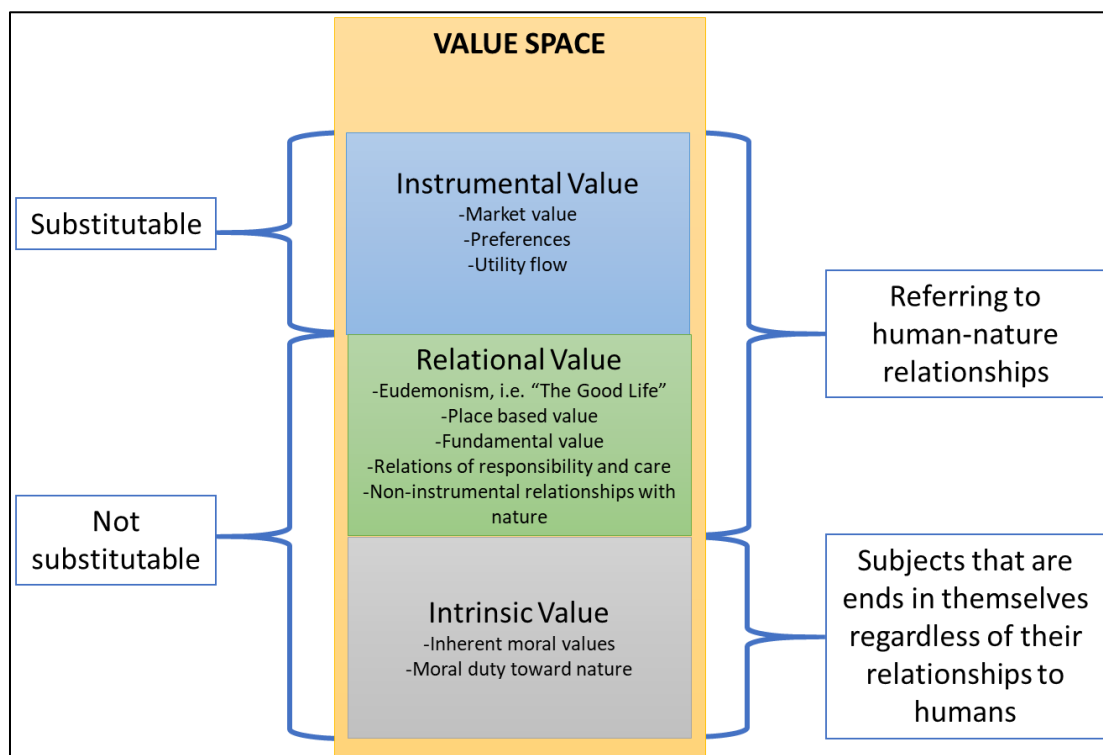


Figure 2.1 Distinction between instrumental, relational, and intrinsic values of nature. Both instrumental and relational values are fundamentally rooted in the relationships people have with nature and each other while intrinsic values are independent of a specific relation to human interests, needs, preferences, and

meanings. Instrumental values are substitutable while relational and intrinsic values are not. Finally, the value space is not completely occupied by these three typologies leaving open the possibility that other distinct value domains to exist.

Empirical studies show that eudaimonic values, including aesthetic and spiritual values, play a key role for the motivation to act for biodiversity and nature conservation (Admiraal et al., 2017; Cooper et al., 2016; Moreno-Mateos et al., 2015). Relational values are important components of wellbeing and a meaningful life. Gould et al. (2015) showed that relational values, such as kinship with nonhuman entities and social relationships, were commonly expressed during interviews designed to understand cultural ecosystem services in two very different communities. Dawson and Martin (2015) found that Rwandans of different cultural and historical backgrounds varied in the way they valued provisioning ecosystem services. Relational values such as connectedness, place attachment, and components of 'living a good life' all ranked highly among reasons Europeans were motivated to care about biodiversity (Admiraal et al., 2017). Kaltenborn et al. (2017) found that people in the fishing community of Röst Norway derived benefits from ecosystem services that went beyond satisfied preferences and material acquisition and included relational values essential to "living a good life in Röst," including struggle, hardships, and capabilities that tied people to their environment and the challenge of their work. The relational benefits identified as essential to the "good life in Röst," were important to community and individual identities. Relational values are relevant to broad groups of people and are held distinct from both instrumental and intrinsic values (Klain et al., 2017).

Finally, relational values are essential to adequately represent non-Western languages of valuation. An example is the web of relationships that constitute the living territory of Indigenous people inhabited and shared by human and nonhuman beings (Jackson and Palmer, 2015). Different names are used to address this constitutive web of relationships, such as earth, country, or Pachamama (Mother Earth). The protection or

conservation of ‘nature’ independently of humans makes little sense in the context of this web: “relations between people, animals, physical objects, and indeed spiritual entities simply ‘happen, they carry on, they are their stories’” (Ingold, 2011:175). They and their relations are in this way forever ‘alive’ and dynamic, continuously woven together into the fabric of the world” (Jackson and Palmer, 2015:124).

Instrumental versus non-instrumental relations: A difference that makes a difference

There is no inherent characteristic of an entity that in and of itself can justify the attribution of instrumental or non-instrumental value to it. Thus, in principle, any content of valuation can be framed in terms of instrumental or non-instrumental relationships (Arias-Arévalo et al., 2017; Muraca, 2016a), depending on the context of reference. However, the way in which values are articulated and assigned bears on significant differences with respect to the space of possible action (Gorddard et al., 2016), including policies, individual and collective behavior, motivation settings of social actors, and implications of social, environmental, and epistemic (in)justice.

The process of value formation is reflexive (Popa and Guillermin, 2017), i.e. it operates through critical reconsiderations and transformations in the social realm. As empirical studies suggest (Jacobs et al., 2017), valuation methods operate as *value articulating institutions*, which influence value formation and co-determine value themselves (Kenter et al., 2016), instead of just eliciting pre-existing values (Gómez-Baggethun and Martín-López, 2015; Vatn, 2005). For example, assessments that neglect the reflexivity in the process of value formation and claim to take manifested preferences as unquestionably given de facto performatively contribute to form values that exclude collective processes or institutional settings through which values are typically discussed, questioned, and transformed (Stagl, 2012; Vatn, 2017).

Instrumental language masks alternative modes of relating to nature. Value articulation frameworks that do not consider relational values ignore historic power

imbalances between different cultural views of human nature relationships, hiding underlying social power relations (Berbés-Blázquez et al., 2016). For example, articulating the value of Pacific salmon in terms of only instrumental values silences the specific languages through which Indigenous People express their deep and multifaceted relationship with salmon and their relational web. Ignoring this specific language of valuation perpetuates the forced assimilation to the settler's narrative. Under these circumstances, merely offering a monetary compensation for the loss of their fisheries leads to the perverse use of market logic to justify or veil modern echoes of past colonial atrocities. Policy guided by merely instrumental metrics can appear successful but have severely negative impacts on the wellbeing of local communities who are most affected if relational values are neglected (Woodhouse et al., 2015) and heterogeneous languages of valuation are forced into an instrumental framework.

Values associated with cultural ecosystem services or with aesthetic and spiritual meanings often refer to non-substitutable components of a good human life. Forcing these languages of valuation into an instrumental framework leaves them ill-defined and neglects the complexity and specificity of relations articulated by the people in their own terms (Hirons et al., 2016). In fact, directly implied by the definition of instrumental values is that objects, in so far as they are means to ends, are substitutable. Any combination of objects that achieves the same desired ends would have equivalent value if only their instrumental contributions to wellbeing are considered. Instrumental consideration enables the abstraction from the specific context of reference and from the qualitative, often unrepeatable, characteristics of particular relationships with nature. Moreover, because money operates as the universal equivalent of any exchange value, instrumental consideration provides a gateway to commodification and marketization of nature (Kosoy and Corbera, 2010). Through the market logic the qualitative and context-specific characteristics of relationships (in this case with non-human nature) are concealed behind the fetishized

value of a commodity (Kosoy and Corbera, 2010). As a value articulating institution, the market acts as a performative space through which human-nature relationships are (re)constructed in instrumental terms (Kolinjivadi et al., 2017).

Finally, instrumental language implies one-directional flow of benefits and masks not only the reciprocity of human-nature relationships in terms of care or *services to the ecosystems* (Comberti et al., 2015; Jackson and Palmer, 2015; Singh, 2015), but also the mediation and co-construction of ecosystem services via human material and cultural activity (Fish et al., 2016; Martínez-Alier, 2003). West et al. (2018) assert that approaches to environmental sustainability myopically focused on market-based instrumental values ignore the relational value of care which reciprocates and nurtures wellbeing between humans and non-human nature. Means to an end logic of instrumental language precludes the possibility that the means themselves may be important. Jax et al. (2018) further articulate the reciprocity of human-nature relationships through feminist theory, positing that caring *for* nature is constitutive of part of a living a good human life.

Conclusion

Existing frameworks and typologies of relational values vary, but we believe the framework presented in this paper unifies common key components and provides clear defining principles that will facilitate future discussion and streamline operationalization of relational values into frameworks for ecosystem services and nature's benefits to people. The framing of relational values in this article addresses the criticism that relational values are not a distinct or useful categorization of value, and it fills a void in value articulation left by the inadequacies and inconsistency of the instrumental/intrinsic value dichotomy. Empirical research supports that relational values are important to people and considered distinct from both intrinsic and instrumental values. The inclusion of relational values in pluralistic methods of valuation enables greater epistemic justice, makes power asymmetries visible, and

offers a framework for the articulation of human-nature relationships that challenges the Western dichotomic model of either conserving nature for its own sake (wilderness) or securing the utility flow of natural capital (instrumentality, eco-efficiency) (Martínez-Alier, 2003; Muraca, 2016b).

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Chapter 3

TREE SPECIES DIVERSITY AND COMPOSITION RELATIONSHIP TO
BIOMASS, UNDERSTORY COMMUNITY AND CROWN ARCHITECTURE IN
INTENSIVELY MANAGED PLANTATIONS OF THE COASTAL PACIFIC
NORTHWEST, USA

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Abstract

Trends in landcover and demand for ecosystem services suggest plantation forests will be expected to provide a larger quantity and diversity of ecosystem services in the future. I identified three measures that can be indicative of the potential provision of ecosystem services (above ground biomass, understory biodiversity, and crown length) and compared their relationship to tree species composition and diversity in intensively managed forest plantations in the Coast Range of the US Pacific Northwest. This was a point-in-time study conducted in similarly aged stands of western hemlock, Douglas-fir, red alder, and mixtures of the three species. I focused on late rotation stands (35-39 years-old) to allow the longest period of species interactions within the management regime. In this operational setting I did not observe the positive relationship between species diversity and productivity as indicated by above ground biomass of trees, which has been observed in other studies. I attributed the lack of positive relationship between species diversity and productivity on management practices aimed at minimizing tree-tree interaction, and thus interspecific interaction, during most of the rotation. However, crown length and understory species diversity were greater in areas with mixtures of tree species compared to monocultures. When multiple ecosystem components were considered simultaneously, intimate mixtures of multiple tree species out-performed monocultures. The observed relationships between above ground biomass, understory biodiversity, and crown length to tree species composition and diversity are likely explained by differences in tree phenology, shade tolerance, and disease susceptibility of the tree species in mixture. These mechanisms likely interacted with management actions to mediate plant competition and facilitation. Based on the results, intensive management solely fixated on wood production homogeneously throughout the plantation may miss opportunities to provide other ecosystem services and support more diverse and growing demands of society for nature's benefits.

Introduction

Demand for ecosystem services provided by forests (e.g., genetic resources, wood production, habitat for terrestrial biota and fauna) is projected to increase dramatically in coming decades (Alcamo et al., 2005). Rapid human population growth and increased pressures on natural resources over the last century have led to more native forests becoming degraded, with an associated decline in their provision of various ecosystem services (Millennial Ecosystem Assessment (MEA), 2005). In contrast, the area in forest plantations increased by more than 100 M ha since 1990 and consequently these forest types provide an expanding quantity of selected ecosystem services (Payn et al., 2015). Given the historical and ongoing trends in forest cover specified above coupled with the projected increase in demand for ecosystem services from forests, the role of plantation forests in providing a diversity of ecosystem services is likely to increase in the future.

In the 20th and 21st centuries, plantation forests in the European and Euro-American tradition have been managed primarily for provisioning wood fiber with the assumption that most other services benefit from “good” timber management, an idea called ‘Kielwassertheorie’ or ‘wake theory’ (Schuler, 1998). Ecosystem services that did not benefit from timber production were often viewed as constraints. However, increased societal demand for a wider array of goods and services has led to incentives for managers to focus on benefits besides timber (Robert and Stenger, 2013). For example, carbon markets, wetland mitigation banking, water quality trading and conservations easements have the potential to offset the opportunity costs of management decisions that result in suboptimal timber production but cultivate or protect other values (Deal et al., 2012). Regulations and voluntary certification programs like FSC and PEFC also require explicit consideration of non-timber services (Fernholz et al., 2011). However, the demand for services beyond the provisioning of wood fiber often results in trade-offs and the need for forest managers to balance the outflow of multiple ecosystem services (Bauhus et al., 2010).

Increasing tree species diversity in plantations established for timber production has been suggested as one way to increase the potential provision of ecosystem services (Verheyen et al., 2016). Ecosystem processes and structures related to the provisioning of ecosystem services can vary between mixed stands and monocultures. Notably studies in many systems have found that mixtures of plant species can be more productive than expected when compared with monocultures, a phenomena known asoveryielding (Hector, 2006). Experimental studies of productivity (measured as biomass or harvestable wood accumulation over time) that compare intensively managed plantation forests with a mixture of species to those with monospecific monocultures have had mixed results. In temperate plantations Amoroso and Turnblom (2006) found that stand density mediates the impact that mixing tree species has on stand productivity. In tropical plantations Bouillet et al., (2008) found that mixtures of species were more productive than monocultures on some sites but not on others which they attributed to facilitation (interactions between plants species where at least one species benefits and neither is harmed) and stress-gradient hypothesis which states that facilitation is more likely under high abiotic stress conditions (see Forrester and Bauhus, 2016 for detailed discussion and further references on mechanisms affecting species mixing effects on productivity in forests).

Mixing species in plantations can affect trees and associated vegetation relative to monocultures. For example, differences between mixed species and monoculture stands have been found in the height of crown base in trees (Grotta et al., 2004), total tree height, the length of crown (Bauhus et al., 2004), and allometry of trees (Forrester et al., 2017). Understory plant diversity is also influenced by trees species composition because of variation in light infiltration, water, and soil chemistry (Barbier et al., 2008). Few studies in mixed-species plantations consider multiple responses or more than two tree species, even though high plant diversity is needed to support multiple ecosystem services (Isbell et al., 2011). Multiple ecosystem services may increase in mixed-species forests compared to monocultures generally, but the

specific species mixture and biogeographical context are important for assessing trade-offs justifying regional studies of biophysical responses to tree species composition and diversity in production forest (Felton et al., 2016).

I conducted an exploratory study in even aged, intensively managed plantations in the Coastal Pacific Northwest, USA to investigate how above ground biomass of trees, the average length of live tree crowns, and the diversity of understory species respond to tree species composition. I also investigated what tradeoffs existed between these measures of ecosystem components in operational settings. Exploratories are an efficient hybrid of planted experiments and inventory studies for analyzing ecosystem properties in tree species mixtures and comparing them to monocultures in which existing mature stands with comparable environmental conditions and management regimes are explicitly selected to represent a gradient of tree species diversity (Bauhus et al., 2017). The plantations I focused on were 35-39 years-old, regenerated from clear-cut harvest, and included monocultures and all species combinations of western hemlock (WH), Douglas-fir (DF) and red alder (RA). I focused on above ground biomass of trees, the average length of live tree crowns, and the diversity of understory species because these measures are responsive to growing conditions and can be viewed as proxies related to several ecosystem services. Also, these ecosystem measures can be derived from forest inventory data commonly collected by plantation forest managers. As such, they can be used by managers to make practical assessments of potential ecosystem service response to management decisions. Furthermore, because the stands in this study were managed as working plantation the results may be more representative of real-world operational conditions than planted experiments.

Above ground biomass of trees (AGB) was selected because it is representative of the cumulative productivity of the trees and is integral to multiple ecosystem services like the provisioning of wood fiber and forest carbon storage (Chojnacky et al., 2014). Diversity of understory plant species was selected as a variable because many

ecosystem functions and services are mediated by non-tree species (Gamfeldt et al., 2013). For example, the understory plant community provides critical habitat and forage for a wide variety of animal species and can directly contribute to numerous cultural and provisioning ecosystem services derived from medicinal and edible species (Whigham, 2004). Furthermore, the cover of understory species with functional traits like drought and heat tolerance may increase the stability and resilience of understories, as well as the services they provide (Neill and Puettmann, 2013). Also, biodiversity itself is considered an ecosystem service, and the understory plant community represents a large portion of the overall biodiversity of forest systems (Duguid and Ashton, 2013). I selected live crown length as a variable because it has many attributes that make it an attractive and feasible indicator of multiple potential ecosystem services. It is already widely used in silviculture because it is easy to measure in the field (Maguire and Kanaskie, 2002). It is a predictor of tree growth, leaf area, and tree photosynthetic capacity (Gilmore et al., 1996; Maguire and Bennett, 1996; Wykoff, 1990). Length of the live crown is also a surrogate for the distribution of branch biomass which correlates to arthropod abundance (Halaj et al., 2000) an important requirement for wildlife that feed on insects (Kalcounis et al., 1999). Larger crowns also provide more area for some species of birds to nest and forage (Hayes et al., 1997). Therefore, live crown length is a suitable proxy for multiple aspects of the ecosystem (future growth potential, foundational trophic level, and critical structures) and the potential services that they support (wildlife habitat and potential future wood production or carbon capture).

My objectives were to determine: 1.) if the above ground biomass of trees, average live crown lengths, and vascular plant species diversity of the understory individually have positive relationships with tree species diversity, 2.) if above ground biomass of trees, average live crown lengths, and vascular plant species diversity of the understory increase or decrease with one another as there are changes in tree species diversity and composition, and 3.) if mixed-species stands are related to higher levels

of all three measures simultaneously compared to monocultures. I collected field data to estimate the three measures, and then assessed their relationship to tree species composition and diversity using a surface response model.

Material and methods

Study area description

The study was located within the Lewis and Clark Timberlands, a 70,000 ha industrial plantation forest in the Coast Range of northern Oregon and southern Washington, USA near the mouth of the Columbia River. The area is mountainous with elevation ranging from sea level to a high point just over 1000 m. The forests are part of the *Thuja plicata* zone near the coast and transition into the *Tsuga heterophylla* zone east into the mountains (Franklin and Dyrness, 1973). The mean annual rainfall is 180-320 cm year⁻¹, but summers can be dry. Mean annual temperatures are 7-11 °C and daily low temperatures frequently fall below freezing in the winter. The soils are igneous and sedimentary in origin and tend to be very well drained with very high water holding potential (“Web Soil Survey,” n.d.). The area is characterized as having the most productive temperate forests in the world (Franklin and Dyrness, 1973).

Most of the property has been managed for commercial timber production for at least two rotations. Because the ownership of the property has changed multiple times in recent decades, precise management records for all study stands were not available. However, based on typical management practices I can assume all study stands were planted within two years of harvest with 890-1075 trees ha⁻¹. Planted species included western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*). Both monocultures and mixed conifer stands were planted. Vegetative competition was typically controlled chemically within the first two years following harvesting. Based on current spacings, it is likely all stands were pre-commercially thinned around age 15 to maintain the 890-1075 trees ha⁻¹ following

natural regeneration of western hemlock and red alder (*Alnus rubra*) from windblown seed. During pre-commercial thinning the largest defect-free trees were retained regardless of species. Thus, naturally regenerated trees may have been retained at pre-commercial thinning if they were able to achieve dominant or co-dominant positions in the canopy.

As a result of past management, the landscape is a mosaic of even aged stands with similar stocking but species compositions that range from monocultures to mixtures of multiple tree species. For this study, I selected the three predominant species in abundance and economic importance: western hemlock, Douglas-fir, and red alder. Limiting the study to only three tree species was necessary because inventory data indicated that mixtures of four tree species or more were rare. These three species also provide the greatest functional contrast by including deciduous red alder, shade tolerant conifer western hemlock, and the shade intolerant conifer Douglas-fir. All three species are native to the area, they grow on the same sites, sample stands had all three species within a single canopy layers, they can be commercially harvested on the same rotation lengths, and the harvest costs and market opportunities in the region are similar. Western hemlock likely regenerated through a combination of planting and naturally seeded trees, Douglas-fir were likely all planted, and all red-alder seeded in naturally. Micro-site factors may have contributed to where naturally seeded trees established and persisted, the most significant factor being seed bed conditions. Specifically, western hemlock is more likely to establish in duff or on woody debris while red alder is more likely to establish on exposed mineral soil (Gray and Spies, 1997; Harrington et al., 1994). The conditions of the forest floor at the time of establishment were likely influenced by previous harvest. For example, skid trails, landings, burns and areas where trees were dragged may expose mineral soil while areas not impacted by equipment or log skidding are likely to retain intact forest litter and residual rotting wood. The result of standard harvest practices in the area is a mosaic of exposed mineral soil, down woody debris, and intact forest floor.

All three species are well adapted to the conditions throughout the study area and are known to commonly grow in mixture with each other (Harrington et al., 1994). Another factor potentially affecting natural seeding of red alder is spots where herbicide was not applied during site preparation, which would have also retained “competing” non-tree vegetation.

Management objectives may have influenced where foresters planted Douglas-fir or western hemlock. For example, Douglas-fir tends to be impacted on the plantations by the endemic pathogen *Phaeocryptopus gaeumannii*, which causes Swiss needle cast and reduces growth. Swiss needle cast is more severe today than it was when the study stands were established. The pathogen is most severe close to the coast, and today many managers avoid planting Douglas-fir near the coast line. However, many of stands with Douglas-fir selected for this study were very close to the coast-line. Douglas-fir foliage was sampled from 21 of the 24 plots by felling three trees and collecting branches from the whorl closest to the mid-point of the live crown. In all cases, visual estimates indicated average needle retention was less than three years and *Phaeocryptopus gaeumannii* presence was confirmed by DNA sequencing using PCR confirming that Swiss needle cast disease was ubiquitous within the study (Shaw et al., 2011).

Study Design

The study approximates a replacement series design with all combinations of three tree species, including monocultures. Replacement series biodiversity experiments, sometimes called substitutive, retain the same level of individual density in plots with all levels of plant species diversity (Jolliffe, 2000). Thus, the operational reality of this industrial plantations approximates a replacement design because density is carefully managed but species composition varies. The study design required identifying multiple plots that represent seven different species compositions and cover the study area. Since the study was conducted in existing mature stands instead

of planted experimental plots, the species composition reflects a combination of management choices and environmental conditions that allowed for the establishment and persistence of the tree species present. The target species compositions represented all possible combinations of three selected tree species and their monocultures as described in table 3.1. The target species compositions also represented the vertices, midpoints, and centroid of a three-dimensional simplex, facilitating response surface analysis (Cornell, 2011).

Table 3.1 Description of species composition criteria for field selection of plots with proportions based on stem counts.

	WH	DF	RA	WHDF	WHRA	DFRA	WHDFRA
Tree species in plot	Western hemlock	Douglas-fir	Red alder	Western hemlock and Douglas-fir	Western hemlock and red alder	Douglas-fir and red alder	Western hemlock, Douglas-fir, and red alder
Maximum proportion of a single species	1.00	1.00	1.00	0.70	0.70	0.70	0.50
Minimum proportion of a single species	NA	NA	NA	0.30	0.30	0.30	0.25

Plots were considered monoculture if the proportion of all trees (by stem number) belonging to a single species was at least 0.90. Both target species in the two-species plots needed to be at least 0.30 and could not exceed 0.70 of the tree stems and a proportion no larger than 0.05 of trees were permitted to be non-target species. Three species mixtures had to have between 0.25-0.50 of each target species and no more than 0.05 of the tree stems in the plot could be other species. Only trees with diameter at breast height (DBH) greater than 10 cm were counted. Plots were selected to contain similar overstory densities, around 800 trees ha⁻¹ (range from 700-987 trees

ha⁻¹). Plots were all in stands with similar stand history and age (35-39 years). This age range was selected because it was close to final rotation age and therefore allowed the maximum time for tree and species interactions within intensively managed plantations.

I identified candidate stands likely to meet the composition, density, and age specifications from inventory data. The latitude, longitude, average elevation, average slope, average aspect, and when available 50-year site index of candidate stands were also retrieved from the database. I calculated the potential annual direct incident radiation (PDIR) and heat load index for each candidate stand as indicators of environmental variability. Heat load index and PDIR were calculated using latitude, slope, and aspect data (McCune et al., 2002). Potential annual direct incident radiation is the amount of solar radiation energy received on a given surface over a year and is the maximum energy that plants could intercepted for photosynthesis. Heat load varies from PDIR because energy intercepted in the afternoon will have a larger effect on heating than energy intercepted in the morning and consequently a different potential rate of photosynthesis. A final subset of 142 candidate stands was selected to maximize the range of PDIR, heat load, elevation, and site index across all target species compositions. The final subset of stands was investigated in the field, and 43 plots were installed in 25 stands where conditions fell within the target density range and species composition. No two plots with the same species composition were included in the same stand in order to avoid pseudo replication. Within stands, plot centers were selected to meet density and species composition parameters. Average, minimum and maximum of PDIR, heat load, elevation, TPA, and site index for plots of each species composition are shown in table 3.2.

Plots were circular with 10-meter radii (314m²). This plot size choice was guided by previous studies on tree species interaction in the Pacific Northwest (Canham et al., 2004; D'Amato and Puettmann, 2004). Plots were buffered by at least 10 meters from openings, roads, or streams.

Table 3.2. Average (min-max) PDIR, heat load, manager reported 50-year site index, elevation, and trees ha⁻¹ of plots with different species composition.

	PRID	Heat Load	Site Index	Elevation (m)	Trees ha⁻¹
WH	0.82 (0.56-0.93)	0.85 (0.67-0.95)	134 (120-148)	177 (37-392)	844 (732-987)
DF	0.90 (0.87-0.95)	0.86 (0.71-0.92)	128 (107-154)	251 (70-459)	759 (700-828)
RA	0.85 (0.65-0.95)	0.82 (0.71-0.92)	136 (115-154)	296 (235-459)	878 (764-955)
WHDF	0.78 (0.60-0.91)	0.76 (0.60-0.91)	118 (108-125)	257 (76-443)	817 (732-891)
WHRA	0.81 (0.56-0.92)	0.85 (0.70-0.92)	134 (119-154)	199 (37-459)	822 (732-891)
DFRA	0.84 (0.56-0.95)	0.83 (0.71-0.92)	146 (126-154)	253 (37-459)	822 (732-923)
WHDFRA	0.77 (0.56-0.90)	0.77 (0.60-0.91)	127 (108-152)	266 (45-443)	891 (859-923)

Data collection

Field data was collected during the summer of 2017. Diameter at breast height (DBH) of all trees in the plot greater than 10 cm DBH were measured. I also measured total tree height and height to live crown for the three trees of each target species closest to the plot center. Height to live crown was defined as the vertical distance between the bottom of the crown and the top of the crown. The bottom of the crown was defined as the lowest point of live green branches that comprised one-third or greater of the bole's projected circumference and was measured from the point those branches attached to the bole of the tree. The top of the crown was defined as the top of the terminal leader or highest point of the tree (FIA, 2018). Measurements were taken with an Haglof Vertex IV hypsometer. Understory species were defined as all vascular plant species less than 3m in height. All vascular plants observed in the study were either trees or understory plants. Intermediate canopy plants are not typical in managed plantations of the region. Understory species were surveyed in four 1m² sampling frames located at 2m and 6m from the plot center in both directions along a transect running uphill/downhill. The identity, total height and percent cover of all vascular plant species in the sampling frame were recorded.

Response variable estimation

Above ground biomass was estimated using species specific allometric equations for each tree and summing the individual tree AGB for each plot (Chojnacky et al., 2014). Since mixture-specific allometric equations were not available for the study stands and destructive sampling of all the plots was not feasible in the operational setting, I had to assume that the generic equations applied to trees on my study sites and deviations due to genetics, stand history, site quality, or species mixtures were minor within the scope of this study (Forrester et al., 2017).

The diversity of understory plants (DUP) for each plot was estimated with Shannon's index based on the average percent cover in subplots as shown in equation 1 (Shannon, 1948). Shannon's diversity index is one of the most widely used indices of species diversity (Spellerberg and Fedor, 2003).

Equation 3.1. Shannon Diversity Index

$$SI = - \sum_i \left(\frac{n_i}{N} * \ln \left(\frac{n_i}{N} \right) \right)$$

SI is Shannon's Index, n_i was the relative abundance of species i based on cover in all understory sampling frames within a plot and all n_i sum to $N=1$.

I defined the live crown length (LCL) for the plot as the average live crown length (difference between total tree height and height to live crown) of three trees of each target species closest to the plot center (3-9 trees in total).

Above ground biomass, understory plant diversity, and live crown length were the response variables in the analytical model described in the following section.

However, this was not a planted experiment where all potentially confounding factors were controlled and thus identified relationships between the response variables and tree species composition should be considered corollary and not necessarily causal.

Analytical approach

Substitutive or replacement series designs are similar to mixture experiments where the response is a function of the proportion of multiple components that sum to one. Thus, I analyzed the data using response surface methodology described for mixtures (Myers and Montgomery, 1995). My study design approximates a simplex centroid design (Cornell, 2011), so I used a special cubic mixture model, i.e., a polynomial model that fits a response surface to three component mixtures with a centroid (Scheffe, 1963).

Equation 3.2. Special Cubic Model

$$Y_k = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{12} x_1 x_2 + \beta_{13} x_1 x_3 + \beta_{23} x_2 x_3 + \beta_{123} x_1 x_2 x_3 + \varepsilon_k$$

where

Y_k	Is the estimated ecosystem function from the k th plot, $k=1-43$
β_1	parameter for the x_1 pure mixture
β_2	parameter for the x_2 pure mixture
β_3	parameter for the x_3 pure mixture
β_{12}	parameter for the mixture of x_1 and x_2
β_{13}	parameter for the mixture of x_1 and x_3
β_{23}	parameter for the mixture of x_2 and x_3
β_{123}	parameter for the mixture of x_1 , x_2 and x_3
x_1	proportion of western hemlock in mixture
x_2	proportion of Douglas-fir in mixture
x_3	proportion of red alder in mixture
ε_k	random error of the k^{th} plot, $\varepsilon_t \sim N(0, \sigma_r^2)$

The sum of x_1 , x_2 , and x_3 must always equal to 1. The model assumes residuals are independent, normally distributed, and have constant variance.

For the analysis, mixture proportions were quantified based on AGB. Aboveground biomass was chosen because of its simplicity and its suggested indication of the ability of each species to access resources (Pretzsch and Forrester, 2017). There were tree species not included in the study design found in some of the plots. Specifically, Sitka spruce or western red cedar occurred in nine of the plots but represented a proportion of less than 0.10 of the total biomass, and in most cases less than 0.02. Sitka spruce and western red cedar were lumped with the most functionally similar study species, western hemlock. The species proportions and total AGB of all 43 plots are depicted in figure 3.1. These proportions vary from the plot selection criteria in table 3.1 because the table 3.1 criteria used stem count instead of biomass to estimate species proportion. Biomass estimates of species were not available *a priori*, and stem counts were a feasible alternative for plot selection in the field.

The special cubic model was fit in R statistical software using the package *mixexp* (Lawson and Willden, 2016). Visual inspection of residuals plots indicated that model assumptions were adequately met. Results were considered statistically significant if the average of monocultures, weighted by their respective proportion in a mixture was not included in the 95% confidence interval of the response surface.

Procedure for optimizing several responses simultaneously

The species composition that supported the highest levels of each of the three response variables described in response variable estimation was determined using a procedure for optimizing several responses simultaneously in mixture experiments (Cornell, 2011). The area of the response surface for each response variable representing species compositions that equaled or exceeded the best performing monoculture were graphed and overlaid upon one another. If there was no overlap of species composition that simultaneously performed as well or better than the best

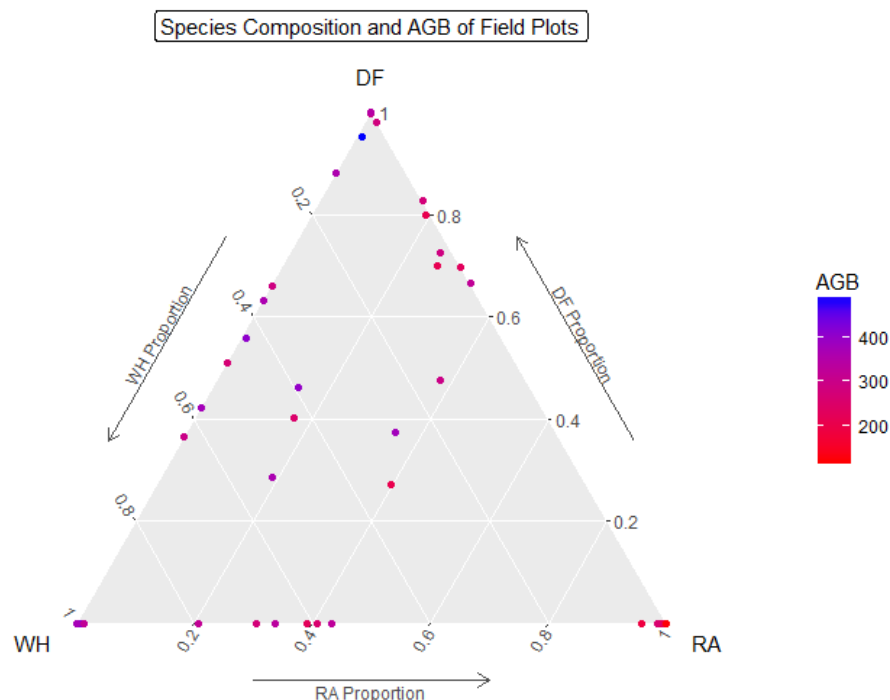


Figure 3.1. Species mixture based on above ground biomass (AGB) of 43 field plots. Total plot AGB represented by shading is in Mg/ha. Each corner for the tertiary plots represents a monoculture (DF=Douglas-fir, WH=western hemlock, RA=red alder), the edges of the plots represent two species mixtures and the interior of the triangle represents all three species mixtures. The proportion of each species can be determined at any point by the corresponding value on each of the three axes.

monoculture for each response variable, then the process was repeated with species compositions that equaled or exceeded 99% of the best performing monocultures. This process was repeated iteratively in increments of 1% until all three response surfaces overlapped one another. Once there was overlap representing species composition that achieved relatively equal levels of all three response variables (within the same percentile relative to the respective best performing monoculture), one response variable at a time would be increased by increments of 1% while keeping the other two constant until the three response surfaces no longer overlapped.

In this way, I estimated the species composition that predicted the greatest levels, relative to each respective best performing monoculture, of each response variable without causing either of the other two to decrease.

Results

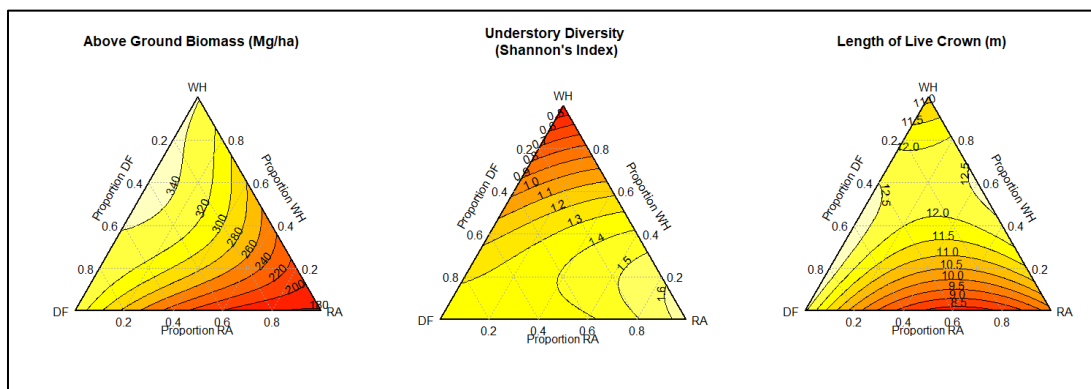


Figure 3.2. Response surfaces of above ground biomass, understory plant species diversity, and live crown length to mixtures of Douglas-fir, western hemlock, and red alder (Corrected Multiple $R^2 = 0.51, 0.66,$ and 0.27 respectively). Triangle layout is as described in figure 3.1. DF=Douglas-fir, WH=western hemlock, RA=red alder. The isolines are at intervals of 20 Mg/ha, 0.1 Shannon's diversity index, and 0.5 m for above ground biomass, understory plant species diversity, and live crown length surfaces, respectively. Color indicates surface values from low (dark red) to high (light yellow).

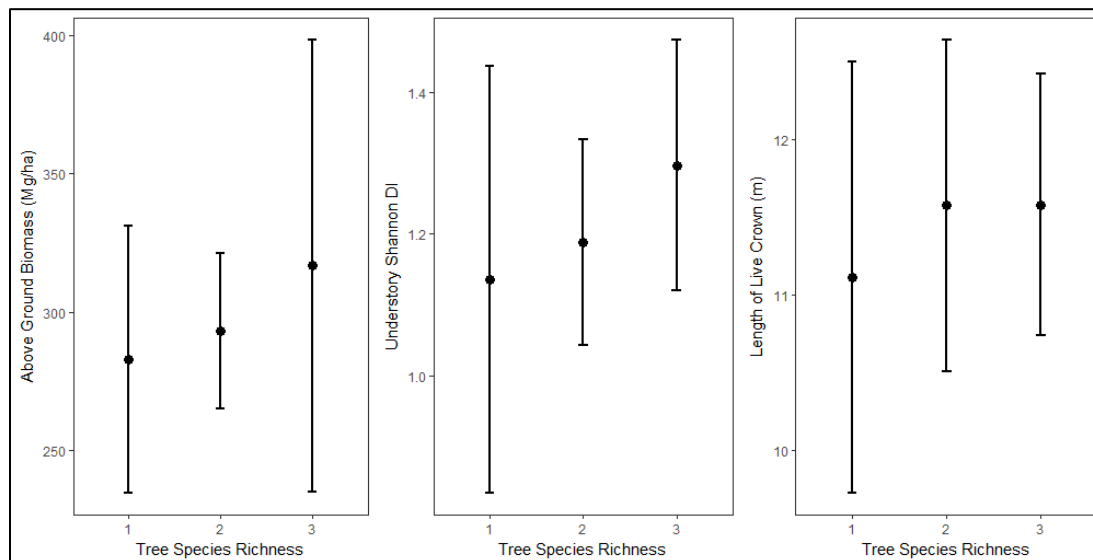


Figure 3.3. The average above ground biomass of trees, understory diversity, and live crown length with 95% confidence interval for plots with 1, 2, and 3 tree species.

Aboveground biomass

The western hemlock (WH) monoculture had the greatest above ground biomass (AGB), followed closely by Douglas-fir (DF), while red alder (RA) had much less AGB (see figure 3.2). As the number of tree species in mixture increased from 1 to 2 to 3, the average plot AGB also increased, but the increase was not statistically significant (see figure 3.3). As highlighted in figure 3.4, the weighted average of the monocultures was viewed as a reference level for the biomass of two-species mixtures, i.e. the sum of each respective monoculture multiplied by its proportion in mixture. The total biomass of the WHDF mixture was similar to the weighted average of the two monocultures, and the biomass of each species in mixed plots was proportional to their respective monoculture. The AGB in RAWH mixtures was also similar to the weighted average of the monocultures at the plot level, but RA AGB tended to be greater in mixture than in monoculture which was offset by WH AGB which was lower in the mixture. In the DFRA mixture AGB was less than the

weighted average of the monocultures, but not statistically significantly so. In the DFRA mix, like the WHRA mix, RA had consistently higher than expected AGB based on the monoculture performance and DF consistently lower, with the effect of DF outweighing the RA.

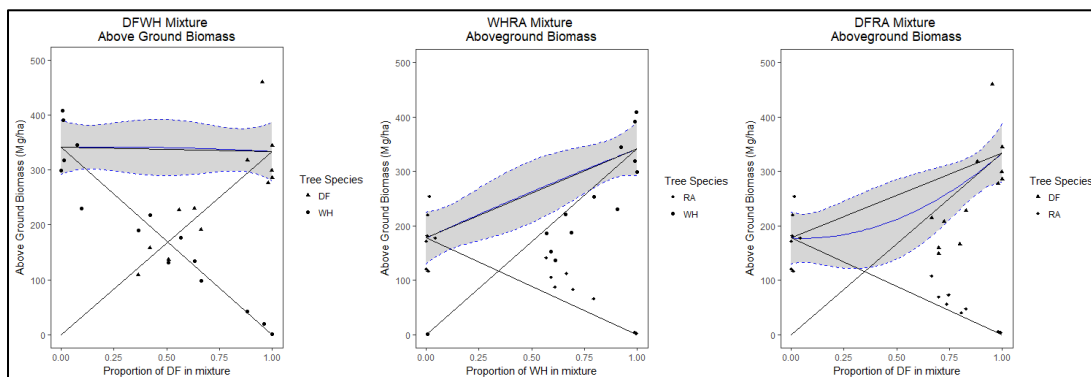


Figure 3.4. Cross plots of two species mixtures. Cross plots show the expected above ground biomass of two-species mixed plots (blue line with shaded 95% CI) with the weighted average of the monocultures as a reference (top black line). Points indicate the biomass of each species estimated in the actual plots. The crossed black lines represent the estimated above ground biomass of each component species at a given proportion based on the performance of its monoculture. Proportions where the blue line is above the top black line or below it are predicted to overyield or underyield, respectively. The distribution of the points representing each species around the corresponding crossed line indicate if individual species performed better (above the line), worse (below the line), or the same (on the line) in mixture as in monoculture.

Weighted average AGBs of monocultures and species mixtures did not differ significantly suggesting that overyielding, the phenomena of species mixtures producing more than the proportionally weighted average of their component species grown in monocultures, did not occur or I was unable to detect it in this study. The response surface predicted greatest above ground biomass with mixture of mostly DF

and WH and a small component of RA. The greatest AGB was predicted to be 342.7 Mg/ha with proportions of 0.61 WH, 0.35 DF, and 0.04 RA but it was not statistically or substantively different from the weighted average of the monocultures (overyielding) or the best performing monoculture (transgressive overyielding) as shown in table 3.3.

Table 3.3. Predicted above ground biomass of monocultures and species mixtures of western hemlock, Douglas-fir, and red alder with 95% confidence intervals and the weighted (based on species proportions) average aboveground biomass of the respective monocultures.

Species Composition	Predicted AGB	95% CI	Average of Monocultures
WH Monoculture	341.6	292.1-391.2	NA
DF Monoculture	334.1	280.3-387.9	NA
RA Monoculture	177.7	130.0-225.3	NA
WH and DF in 0.5:0.5 mixture	341.1	289.9-392.3	337.9
WH and RA in 0.5:0.5 mixture	262.8	205.9-319.7	259.7
DF and RA in 0.5:0.5 mixture	212	139.1-285.0	255.9
WH, DF, and RA in 0.33:0.33:0.33 mixture	309.9	248.7-371.0	284.5

Understory plant species diversity

Forty-one total understory vascular plant species were identified, and plot understory species richness ranged from 1-14. Average diversity of understory plants (DUP) of plots with 1, 2, or 3 tree species did not differ significant ($\alpha=0.05$), however the mean DUP did increase from 1 to 2 and from 2 to 3 (figure 3.3). Understory plant species diversity, as estimated by Shannon's index was greatest under RA monocultures with an average 1.65 and least under WH monocultures with an average of 0.40 (figure 3.2). Understory diversity was projected to be higher than the weighted monoculture averages in all mixtures containing WH, and statistically significantly so for selected mixtures of WH and RA as well as mixtures of all three species (figure 3.5). These

results show that including other tree species with WH was related to higher DUP more than would be expected from the weighted average of the species monocultures.

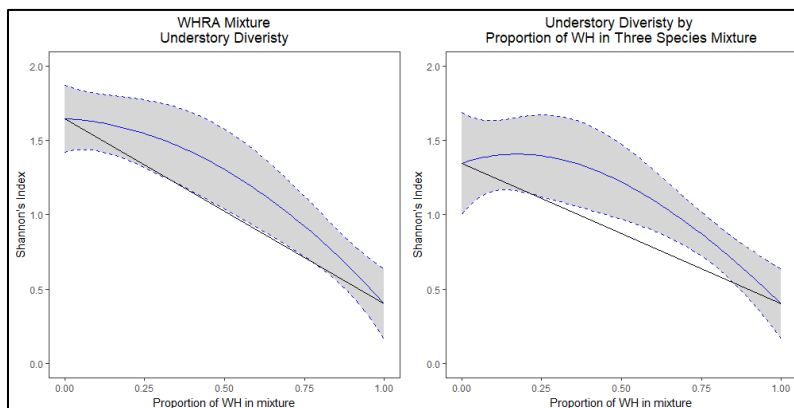


Figure 3.5. Relationship of understory diversity to the proportion of WH in mixture with RA (left) and RA and DF maintained in equal proportion (right).

The straight black line represents the expected value based on the weighted average of the monocultures, the solid curved blue line is the predicted value, and the shaded area within the dotted blue lines is the 95% confidence interval of the predicted values. Where the shaded region is above the solid straight black line, the predicted value is significantly more than the weighted average of the monocultures ($\alpha=0.05$).

Live crown length

Trees in DF monoculture had the longest average live crowns at 12.6m. However, even mixtures of both WHRA and WHDF had equal or greater live crown length (LCL) as the DF monoculture at 12.6m and 12.7m respectively. RA had the smallest LCL of all the monocultures at 9.7m, but the mix of DF and RA had the lowest overall LCL at 8.4m (figure 3.2). Mean LCL was greater on average in plots with 2 species than monocultures but was the same for plots with 2 and 3 species. The difference between plots with 1 and 2 or 3 species was not statistically significant at $\alpha=0.05$ (figure 3.3). In species mixtures with WH, predicted LCL tended to be longer than the weighted average of monocultures. The trend was driven by increased WH

LCL in mixtures compared to WH monoculture. However, not all mixtures showed positive mixing effects of LCL. The response surface indicates DFRA mixtures have less LCL than the weighted average of the monocultures driven by reductions of LCL in both species (figure 3.6).

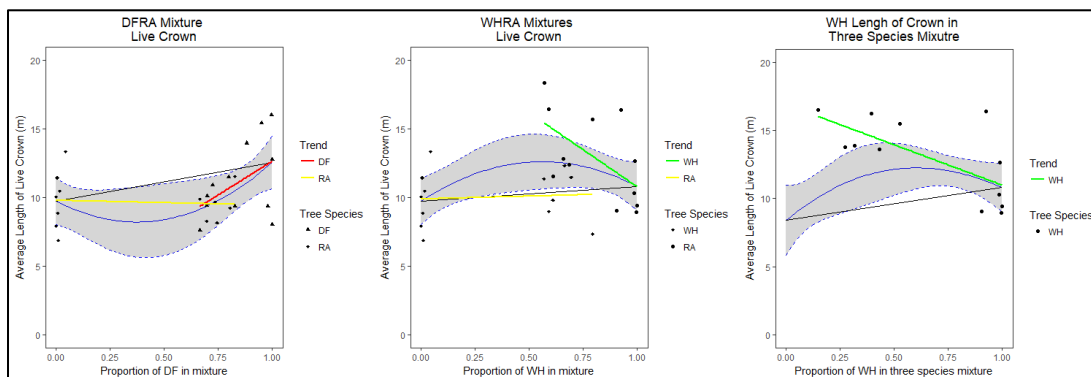


Figure 3.6. Relationship of live crown length to the proportion of DF in mixture with RA (left), proportion of WH in mixture with RA (center), and proportion of WH in mixture with DF and RA held in constant ratio (right). Straight black lines indicate expected values based on weighted average of monocultures, the points are species means from each plot, the blue curved line is the predicted values and corresponding shaded area is the 95% CI. Colored lines are simple trend lines fitted to each species.

Optimal conditions for a combination of the three response variables

The best performing monoculture was different for each of the three response variables. The gradient of AGB and DUP were almost directly opposed along the mixture gradient, i.e., AGB was highest in mixtures composed predominantly of WH with little or no RA while DUP was highest for pure RA plots and lowest for WH monoculture. In contrast, LCL was high for DF monocultures, but also relatively high in even mixtures of WHDF, WHRA, and the three species mixtures. Consequently, no species mixture results in as much or more of all three variables as the respective best performing monocultures. The “optimal” level of all three ecosystem variables

results in 86, 85, and 89 % of AGB, DUP, and LCL, respectively, of the best performing monocultures and was achieved with roughly equal mixture proportions of all three species (0.30 WH, 0.29 DF, and 0.41 RA) (figure 3.7).

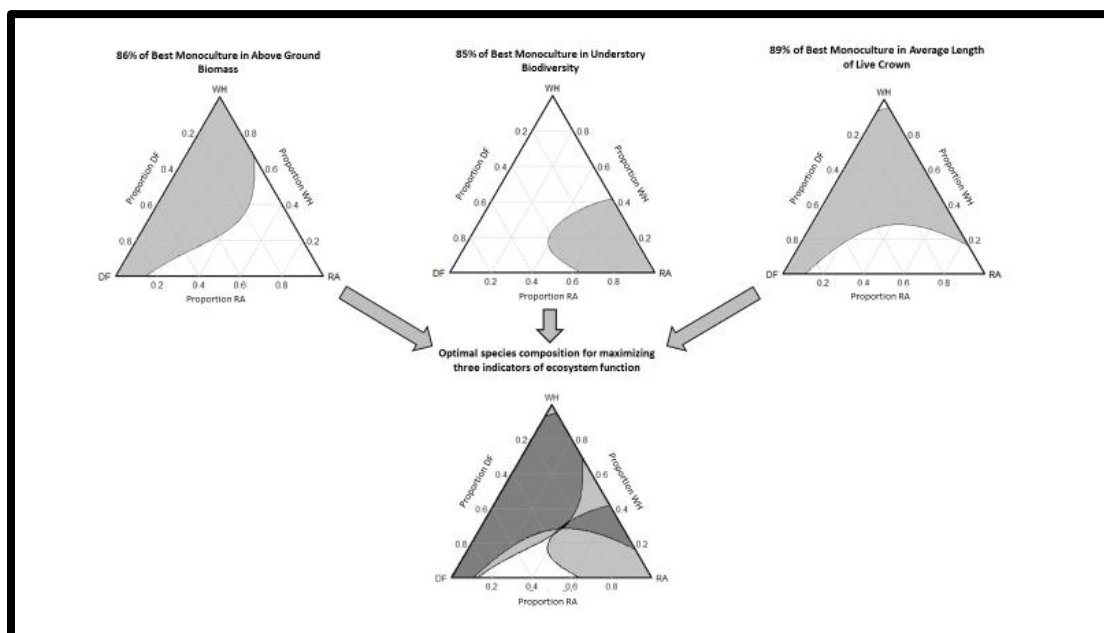


Figure 3.7. Overlapped response surfaces areas representing tree species mixtures that are equal to 86%, 85% and 89% of the best performing monocultures in terms of above ground biomass, understory diversity, and average live crown length, respectively. The overlap of the shaded regions has been minimized and shows the species composition that achieves the greatest levels predicted of all three response variables while minimizing reductions to the others.

Discussion

Correlations between tree species composition and diversity differed for the three ecosystem measures considered in this study. The variation in relationships suggest that multiple mechanisms were likely behind the observed patterns, and some of those mechanisms may play out differently in intensively managed systems compared to typical research installations. Those responses may provide insight relevant to

plantation managers interested in increasing or maintaining high levels of ecosystem functions.

The lack of statistically significant overyielding in my study, as evident by the fact that mixtures did not produce more AGB than was expected from their constitutive monocultures, may be partially due to past management actions (Schulze et al., 2018). For example, managers commonly employ techniques intended to reduce tree and thus species interactions, such as planting at relatively low densities and pre-commercial thinning. These practices were designed to minimize competition, but they also reduce opportunities for facilitation. By maintaining relatively low stand densities through planting and pre-commercial thinning in the study stands tree-to-tree and thus species interactions were minimized for much of the trees' juvenile growth phase, influencing crown, tree and stand level growth trajectories (Garber and Maguire, 2004). Furthermore, when managed at lower densities the stand canopy may not have an opportunity to stratify, which is one of the primary mechanisms of overyielding in mixed species forests (Kelty, 2006). Thus, my results suggest that typical experimental studies which tend to be established at higher density to encourage species interactions (e.g., Boyden et al., 2008) may overestimate impacts of species interactions found in intensively managed landscapes. Similarly, the inclusion of nitrogen fixing species has previously been shown to contribute to overyielding (Piotto, 2008), but I did not observe overyielding in species mixtures with red alder. However, the potential benefit of including nitrogen fixing species in mixtures needs to be viewed in the context of N availability. Specifically, red alder/Douglas-fir mixtures have been shown to overyield on poor N sites (Tarrant, 1961), but were less productive on high N sites typical of my study area (Binkley, 2003). The hypothesis that past management aimed at minimizing competitive impacts on tree and stand productivity was at least partially responsible for my AGB results is also supported by the fact that other ecosystem measures not directly considered in past management of the study stands (i.e., understory diversity and live

crown) were greater in mixed stands than expected from respective monocultures. Thus, my results suggest that management opportunities not commonly utilized in production plantations, like cultivating mixed species stands, may help meet more diverse objectives in terms ecosystem services (Puettmann et al., 2009).

There is general agreement that species identity (as defined by their functional traits) may be useful for identifying underlying mechanisms for performance of species mixtures (Lorentzen et al., 2008). My AGB results appear to be at least partially driven by light competition, canopy shape and relative shade-tolerance differences among species. For example, in the WHRA mixture, WH LCL combined with the higher WH shade-tolerance likely facilitates maintenance of WH growth comparable to monocultures when competing with the deciduous canopies of RA. This was similar to many studies of mixed evergreen/deciduous species that show complementary resource use when deciduous shade intolerant species achieve dominant canopy position over more shade tolerant evergreen trees (Kelty, 2006; Puettmann and Hibbs, 1996). The DFRA mixture showed a contrary pattern with shorter live crown than either respective monoculture and predicted AGB was less than expected from weighted average of the monocultures, with the reduction carried primarily by DF. The impact of Swiss needle cast on DF leaf area (Zhao et al., 2014) may have reduced the contrast in shade tolerance between the species and the potential for complementary light use (Lu et al., 2016). The greater RA AGB in mixtures with both conifers suggests that the canopy architecture of the conifers and deciduous RA may have been complimentary, which has been observed in other forest communities (Pretzsch, 2014). In the case of the two conifers mixing, the AGB of each component species was very similar to its respective monoculture, likely because of the low contrast in functional traits between the two species. Other studies of species mixtures with low contrasting functional traits (deciduous/deciduous mixtures) also did not show overyielding (e.g., Lu et al., 2016).

Tree species identity may also have influenced diversity in understory vegetation. For example, my results suggest that plots where shade intolerant tree species were mixed with very shade tolerant ones, like WH, may be related to greater DUP than would be expected from the average of the respective monocultures. This is because understory species diversity can be affected by light infiltration (Hill, 1979; Jennings, 1999) and very shade tolerant tree species tend to allow less light infiltration than intermediate shade tolerant ones (Canham et al., 1994). Conversely, shade intolerant deciduous species, like RA, allow greater light infiltration when leaves are on, and in addition allow full light penetration in early spring and late fall (Moore et al., 2011). The high levels of understory diversity associated with RA suggest that the understory vegetation may have benefited from the same conditions that allowed RA to become established (e.g., herbicide skips, skid trails, etc.) Also, the understory may have benefited from the impact of RA nitrogen fixation (Hanley et al., 2006). The DUP results in this study generally align with previous research with other species in other systems which support the hypothesis that shade intolerant deciduous tree species support higher levels of understory species diversity than mixed species stands (Berger and Puettmann, 2000). Generally, understory diversity tends to be greatest under deciduous monocultures while conifer species tend to support lower understory diversity, and diversity of vascular plants in the understory is positively related to tree species diversity in mixed stands (Barbier et al., 2008). The exception to this pattern in my study was DF, which supported a surprisingly high level of understory diversity in monoculture, presumably because of the presence of Swiss needle cast, which reduces DF leaf area thus permitted more light infiltration to support understory species (Hansen et al., 2000). This exemplifies how factors exogenous of species identity and diversity *per se*, such as disease and management, can modify species interactions.

In addition to the mechanisms described above, other factors complicate the interpretation of the study results. For example, micro-site edaphic factors may have

influenced where naturally seeding western hemlock and red alder occurred as well as the composition of the understory plant community. Similarly, areas missed by herbicide spray or areas where different herbicides were used may affect the likelihood of hemlock or red alder naturally seeding into an area as well as tree growth and understory plant composition. Because this was an exploratory study and not a planted experiment, I was only able to control for these factors indirectly by choosing stands of similar age and management history from a representative range of environmental factors known to be related to soils and plant growth (elevation, aspect, site index, etc.). My results provide information on whether small scale, highly controlled experiments also reflect outcomes in operational settings.

With regard to the first objective of the study, I found no statistically significant positive relationship between biomass of trees and tree species diversity but vascular plant species diversity and average live crown length both had higher values in some mixtures than expected based on the performance of monocultures. With regard to objective two of the study, I identified trade-offs between different ecosystem responses as a results of tree species composition, namely above ground biomass of trees and diversity of understory plants showed opposite trends along a gradient of western hemlock/red alder mixtures. With regard to the third objective of the study, I found that if high levels of multiple ecosystem functions as represented by above ground biomass of trees, diversity of understory plants, and live crown length, are desired then a near even mixture of all three species was preferable to any monoculture alternative. This supported the theory that complementary effects are generally greatest in mixtures with relatively even proportions of species as each individual is more likely to directly interact with individuals of a different species (Forrester and Bauhus, 2016). My results also supported the theory that greater tree species diversity supports high levels of multiple ecosystem functions, even though monocultures produced higher levels of single functions (Gamfeldt et al., 2008; Isbell et al., 2011; Plas et al., 2016).

My results suggested that within intensively managed plantations, individual ecosystem responses may not be positively related to tree species diversity. However, when multiple indicators of ecosystem function were considered simultaneously mixed stands performed better than monocultures.

In determining the species composition that optimized all three ecosystem responses, each was considered equally desirable. In operational settings it is much more likely the case that one or more ecosystem services will be important to specific managers based on their objectives. Managers can easily apply different weighting schemes to reflect their own preferences and objectives. For example, investment-based managers will prioritize economic returns while public land managers are more likely to consider a wider range of objectives. Furthermore, some ecosystem functions and services may have important thresholds such that reductions beyond a certain point are unacceptable to managers. In the case of thresholds, minimum values can be used to constrain the range of species composition that is acceptable. For example, investment-based managers may need to achieve positive cash flow or a minimum rate of return. None-the-less, it is important to recognize trade-offs implicit in managing to a single objective because myopic focus on the efficient provisioning of a single ecosystem service, like timber, has the potential for undesired outcomes (Messier and Puettmann, 2011). As society looks toward production plantations to provide a broader suite of ecosystem services, management strategies, like mixing tree species that support multiple ecosystem functions are likely to become more important (Bauhus et al., 2010; Bauhus and Schmerbeck, 2010), particularly in the face of uncertain future conditions (Messier et al., 2019). One size likely does not fit all for forest management, and the ‘Kielwassertheorie’ (‘wake theory’) that assumes all the social functions of forests are automatically provided in the wake of production management is clearly up for question (Schuler, 1998).

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Chapter 4

TRADE-OFFS BETWEEN ECOSYSTEM SERVICES ALONG GRADIENTS OF TREE SPECIES DIVERSITY AND VALUES

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Abstract

Trade-offs between incommensurate services are a core challenge to the implementation of the ecosystem services framework. Integral to the challenge of ecosystem service trade-offs is how to incorporate multiple types of value in ecosystem service assessments. The International Platform of Biodiversity and Ecosystem Services (IPBES) recommends pluralistic valuations of ecosystem services that include intrinsic, instrumental, and relational values to better communicate to decision makers the different ways people value ecosystem services. In order to understand how value pluralism may effect trade-offs between ecosystem services, I conducted a study quantifying ecosystem service proxies along a tree species diversity gradient in similarly aged intensively managed plantation forests of coastal Pacific Northwest, USA. My objective was to determine what tree species composition and diversity minimized trade-offs between nine ecosystem services. Further, I developed four management frameworks emphasizing different bundles of the nine ecosystem services based on how those services clumped within a matrix of value types and the level of social organization at which benefits are likely to accrue. I then determined tree species compositions that optimized priority ecosystem services under the four frameworks. Some ecosystem services responded in sync, but I found trade-offs between provisioning ecosystem services with primarily instrumental value and cultural ecosystem services with relational values. Most individual ecosystem services were maximized by monocultures. I also found that high levels of tree species diversity supported the largest plurality of value types and hypothesize that biodiversity may be important not just for increasing ecosystem functions and services, but also increasing the diversity of values supported by ecosystem services.

Introduction

Ecosystem services (ES), or the benefits people receive from nature, can be a useful conceptual framework for policy makers, natural resource managers, and conservationists (Chan et al., 2017; Daily, 1997). The ES framework is often used to support resource management decisions and to communicate the importance of the natural world. However, management actions often result in trade-offs between different ecosystem services (Bradford and D'Amato, 2012; Langner et al., 2017). While the values of many ecosystem services are clearly commensurable (reducible to a single common measure, e.g. commodity goods like timber or grain production), others may be only weakly comparable (comparable without reducing to a single type of value) and are best assessed using multiple criteria (Martinez-Alier et al., 1998; O'Neill, 1993). Navigating trade-offs between incommensurate services in a way that is helpful for decision makers and stake holders with diverse objectives, priorities, and perspectives is a core challenge to the implementation of the ES framework (Rodríguez et al., 2006).

Within the context of forests more and more ecosystem services are being demanded from plantations. Increasing the tree species diversity of plantations has been proposed as a way to meet the growing demand for different ES from these systems that have traditionally been managed almost exclusively to produce wood fiber (Verheyen et al., 2013). Since wood fiber is strongly commensurable with other commodities via common monetary units, trade-offs with other ecosystem services are easily monetized as opportunity costs without consideration for the commensurability of the ES. Because of this, non-monetary values of ES produced from plantations are at a heightened risk of being ignored, and benefits of managing for species compositions other than monocultures may be missed or undervalued.

However, incorporating multiple domains of value articulation in ES assessments is integral to navigating trade-offs (Martín-López et al., 2014). The recent International

Platform on Biodiversity and Ecosystem Services (IPBES) conceptual framework recognized that the benefits people receive from nature and the relative importance of the benefits are context specific and vary with different cultural and institutional settings (Diaz et al., 2015; Pascual et al., 2017). The IPBES recommended pluralistic valuations of ecosystem services that include intrinsic, instrumental, and relational values to better communicate to decision makers the complex ways the value of ES are understood. Many ES valuations are criticized for over dependence on monetary methods (mostly eliciting/capturing instrumental values) which tend to ignore non-instrumental languages of valuation and neglect power asymmetries, thus failing to acknowledge and address issues of epistemic as well as environmental injustice (Jax et al., 2013). This is not only ethically questionable, but also problematic as a basis for policy interventions, as it does not adequately represent the social-ecological complexity of a case (TEEB, 2010). Pluralistic valuation methods are a more holistic way of assessing ES and help resolve these criticisms (Berbés-Blázquez et al., 2016). Pluralistic valuations of ES that include relational values increase the transparency of trade-offs between ES (Cundill et al., 2017; Himes and Muraca, 2018).

In this paper I use a case study to identify ranges of tree species composition and diversity that minimize ES trade-offs while optimizing priority ES under four management frameworks in plantations in the coastal Pacific Northwest of the USA. I selected the ES for each framework to emphasize different value domains by plotting the ES in a values matrix depicting relevant social scale and value types. The methodology I used highlights the ways that interactions between management priorities, values, and biodiversity can change the co-production of ecosystem services.

The aim of my study was to explore four key question. 1.) What trade-offs exist between ecosystem services in relation to tree species composition and diversity? 2.) Do more diverse mixtures of tree species relate to higher levels of multiple ecosystem

services? 3.) Is there a relationship between biodiversity and value domains? 4.) Does monistic value articulation increase trade-offs between ES?

Materials and Methods

Field Study

The study was conducted in Lewis and Clark Timberlands, approximately 70,000 ha of industrial plantation forest in the Coast Range of Northern Oregon and Southern Washington, USA near the mouth of the Columbia River. I sampled forest conditions in multiple plantations of even-aged trees between 35 and 39 years in age. All plantations were established and managed similarly. Across the sampling area 43 ten-meter radius plots were established with the intent of replicating all combinations of Douglas-fir (*Pseudotsuga menziesii*), red alder (*Alnus rubra*) and western hemlock (*Tsuga heterophylla*) in roughly even mixtures. Western hemlock (WH), Douglas-fir (DF) and red alder (RA) were selected because they have similar harvest costs and market opportunities in the region and their growth in the first forty years is comparable (Himes&Puettmann, *in review*). Efforts were made to sample plots of each species composition evenly across the range of known environmental variation, and plots were placed in areas at least 10m from openings where stem density ranged from 700-987 trees/ha (Himes&Puettmann, *in review*). I established six plots of each of the species compositions shown in table 4.1, plus one extra plot of red alder monoculture. Diameter at breast height (DBH) of all trees larger than 10cm in each plot was measured and a subset of three trees of each species were measured for total height, height to live crown, and stem diameter at 25-35% of the total tree height. Damage was also noted for the bottom, middle, and top third of all trees in every plot with a code describing the type and severity of damage following Arney (2015). Understory vascular plant species composition and cover were also sampled in four subplots in each plot. Details on the study area, plot selection, plot installation, tree

measurements, and understory sampling were further described in Himes & Puettmann (*in review*).

Table 4.1. Description of species composition criteria (from Himes & Puettmann *in review*).

	WH	DF	RA	WHDF	WHRA	DFRA	WHDFRA
Tree species in plot	Western hemlock	Douglas-fir	Red alder	Western hemlock and Douglas-fir	Western hemlock and red alder	Douglas-fir and red alder	Western hemlock, Douglas-fir, and red alder
Maximum proportion of a single species	1.00	1.00	1.00	0.70	0.70	0.70	0.50
Minimum proportion of a single species	NA	NA	NA	0.30	0.30	0.30	0.25

In addition to tree and understory data collection, digital photographs of each plot were taken with an i-phone 6s using the True Horizon ap. The following controls were used to ensure unbiased representation of the scenery: Photographs were taken from two locations on opposite sides of the plot boundary looking into the plot center and perpendicular to the predominant slope in landscape. Gridline and bubble level display in the True Horizon ap ensured photographs were consistently taken on level with the plot centered horizontally at the bottom third of the display. The same individual took all photographs while holding the i-phone 6s at eye height. All photographs were taken during full light, avoiding dusk or dawn light conditions, furthermore since all plots were taken under forest canopy and buffered from large openings, the images had relatively consistent diffuse lighting.

Selecting and Calculating Ecosystem Service Proxies

Provisioning of nine ecosystem service proxies was quantified based on the field data (table 4.2). I selected services based on the availability of relevant field data and to

cover a broad spectrum of ecosystem services representing all four categories specified in the Millennium Ecosystem Assessment (MEA, 2005).

I estimated merchantable wood as the net volume of merchantable wood using the Forest Projection and Planning System™ (FPS). FPS is a commercially available fully integrated software and database system for managing working forests. It is commonly used by industrial forest managers to simulate the volume and grade of logs that can be cut from trees based on measurements including diameter at breast height, tree height, and stem taper. Details on FPS are available in Arney (2015), but specific equations used by FPS are proprietary. FPS input data included a measure of potential tree productivity, i.e., site index (King, 1966), defect for the bottom, middle, and top third of all trees (0% ,5% ,10% ,20%, and 30% corresponding to damage severity ratings 0-4), DBH of all trees, and the height and taper (stem shape) of a subset of the trees. I set other FPS parameters to estimate merchantable volume and log grade of every tree in every plot. I used the sum of FPS net merchantable volume (total merchantable volume deducted for defect) of all trees in each plot as the response variable for the Merchantable Wood ES proxy. This proxy was an estimate of the volume of wood fiber that would be commercially utilized from each plot following a clear-cut harvest.

I calculated gross timber revenue by multiplying the FPS output merchantable volume in each log grade by the corresponding average log price delivered to the mill for that grade and species as reported for western Washington by the Washington Department of Natural Resources (WDNR) between 2014 and 2018 (“Timber Sale Query/Log Prices | WA - DNR,” n.d.). I summed the delivered log revenue for each plot. The WDNR prices were used because they were publicly available and overlapped with the sales region of the property. I selected gross timber revenue rather than net cash flow or net present value of timber as the ES proxy because the property managers indicated that there were not substantially different costs associated with the different species and the silvicultural system was even-aged

management with approximately the same rotation length for all three species. Therefore, gross revenue was assumed to be proportional to net cash flow or net present value. Since monetary valuation was not the objective of the study and the property owner's operating costs were proprietary, gross revenue was the most reasonable proxy for commercial value.

Carbon stock was estimated as the carbon content of the above-ground portion of the trees following International Panel on Climate Change (IPCC) Good Practice Guidance for Land Use, Land-Use Change and Forestry (Penman et al., 2003). First, I estimated the total above ground biomass in the trees of each plot using species specific allometric equations (Chojnacky et al., 2014). Next, I estimated the carbon content as the biomass multiplied by a factor of 0.5 (Ross, 2010).

I derived pollinator Supporting Understory, Fire Re-sprouting Understory, Climate Change Resistant Understory, and Herbivore Forage ES proxies from functional traits of understory species as categorized by Neill and Puettmann (2013). Herbivore forage included fruit bearing understory plants and those with moderate or high palatability. Pollinator supporting understory included all insect pollinated plant species. Fire re-sprouting understory species were those with moderate or high fire tolerance. Climate change resistant understory were all plant species that had moderate or high rates for drought tolerance or heat tolerance. I used the average cover (m^2/m^2) of species in each category as an ES proxy.

I determined understory species with human uses including medicinal, edible, and decorative application based on description in Pojar & MacKinnon (2004) or their inclusion in the U.S. Department of Agriculture (USDA) list of Special Forest Products for the Pacific Northwest (Vance et al., 2001). If a plant species appeared in the USDA list or the entry for a species in Pojar & MacKinnon specified that the plant was or had been used for medicine, food, or in the preparation of food I

categorized it as an Edible/Medicinal/Decorative plant. The plot average of the sum cover (m^2/m^2) of all Edible/Medicinal/Decorative plants was used as the ES proxy.

Using a survey instrument, I estimated scenic beauty as perceived by recreation permit holders, i.e., people who registered online for a free recreation permit which was required prior to entering the study area by the land managers. Recreation permit holders use the property for hunting, hiking, running, dog walking, mountain biking, fishing, and other forms of non-motorized recreation. The survey instrument was an online Qualtrics survey that displayed plot photographs and asked respondents to rate the images. The two pictures of each plot were used, except for 9 of the 43 plots in which one of the pictures was out of focus, flagging or a person were prominent in the background, or there was substantial brush in the foreground blocking the view which may have influenced viewers' interpretations of the photographs. In total there were 11 photographs of each species composition. A similar number of photographs was deemed to be a large enough sample to provide reasonable reliability in similar forest ecosystems (Ribe, 2009). The order of the photographs in the survey instrument was randomly assigned. The survey instrument asked respondents to rate the images on a scale of -5 to +5 where -5 indicated very ugly, +5 indicated very beautiful, and 0 indicated neither ugly nor beautiful following Ribe (2009). A link to the survey instrument was sent out by e-mail to 3,487 people who signed up for a free recreation permit for Lewis and Clark Timberlands. Partially finished surveys were not used for analysis. In total, there were 331 complete responses (9.5% response rate). Responses were shifted to a 1-11 scale and the average of the 331 responses to each photograph was calculated and used to represent the population response to the scene. Often this type of psychophysical scaling uses some form of rating protocol like the scenic beauty estimation method (SBE) to standardize the dispersion, skewness and central tendency of various respondents' scenic beauty ratings to a common interval scale (Daniel and Boster, 1976; Ribe, 2009). However, results using SBE have been shown to correlate with direct use of semantic differential scale, like the one used here, at the

0.99 level (Stamps III, 1999). The average response for each plot was used as the Scenic Beauty ES proxy.

Categorizing Ecosystem Services Within a Matrix of Values and Complexity

The nine ES proxies were placed in a values matrix shown in figure 4.1. Arranging the ES in this matrix facilitated the logical grouping of ES into different frameworks and made more transparent some of the assumptions inherent in the ES proxies considered.

Intentionally absent from the matrix were intrinsic values. Intrinsic values, in the sense of inherent moral values, could have been included as a third axis to the matrix scaling deontological justifications for value (similar to Muraca, 2011). Inherent moral values refer to the attribution of rights or dignity (Callicott, 2003; Regan, 2004; Taylor, 1986) to nonhuman entities and include direct moral obligations towards them as ends in themselves (this language of valuation can be used, for example, to argue for the protection of polar bears or wales and can be articulated regardless of its relationship to human interests, needs, or preferences). Intrinsic values are important for biodiversity conservation and often reflect people's motivations when addressing the importance of nonhuman entities as ends in themselves (Batavia and Nelson, 2017). However, I decided to leave out the category of intrinsic values because it was difficult to represent within an ES-based study design. Given the framework analysis proposed here, I believe inclusion of an intrinsic dimension would not substantively change the grouping of the selected ES. Moreover, eliciting intrinsic values in the sense of inherent moral values would require additional methods for data collection that could not be included in this study. The placement of the ES on the proposed matrix resulted from the interpretation above. I believe the nine ES considered would logically cluster into three groups even if individual ES were shifted. The language of valuation (instrumental, relational or intrinsic) mirrors the significance attributed to specific human-nature-relationships. There is nothing inherent in a thing considered

valuable that, in and of itself, justifies an instrumental or relational valuation (Himes and Muraca, 2018). However, forcing heterogeneous languages of valuation, especially non-instrumental ones, into an instrumental framework “leaves them ill-defined and neglects the complexity and specificity of relations articulated by the people in their own terms” (Himes and Muraca, 2018:5). In my matrix I attempted to represent diverse languages of valuation in their own terms, while also acknowledging gradients across different languages of valuations. Furthermore, by specifying the relevant social level at which the ES that were quantified in this study benefit people I hoped to increase the transparency of benefit distribution (i.e. who receives benefits from ecosystem services and if benefits can be transferred away from the place they were generated). Including the relevant social level of benefits with value type in a single matrix also enabled the investigation of interactions between distribution of benefits and value articulation as both can shape the management decisions of different stakeholders.

Relational values help articulate value of those human-nature relationships that would be misrepresented if reduced to a merely instrumental language. They refer to “preferences, principles, and virtues associated with relationships, both interpersonal and as articulated by policies and social norms” (Chan et al., 2016: 1462). In my matrix they encompassed constitutive/eudemonic and fundamental relationships. The former refers to relationships that are essential components of someone’s identity (as individuals or as community) or of a life of flourishing and dignity, i.e. a good human life (Muraca, 2016, 2011; Nussbaum, 2009). The latter refer to necessary, basic conditions for life in general. Framing such conditions merely in terms of means to human ends would have neglected the relationship of fundamental dependence upon them for human life.

The first group of ES I identified was Scenic Beauty, Edible/Medicinal/Decorative Plants, and Herbivore Forage. These ES were best represented by constitutive/eudemonic relational values but may also have instrumental value. Both

Edible/Medicinal/Decorative Plants and Herbivore forage have aspects of instrumental value, but the multi-faceted ways that these types of activities can contribute to a good life constitute more than merely instrumental benefits of the goods foraged, or meat acquired (Kaltenborn et al., 2017). As a result, I categorized the primary (but not sole) value of these ES as eudemonic/constitutive relational (Chan et al., 2018). Similarly, scenic beauty is widely accepted as an aesthetic value that belongs in the relational domain because of its contribution to a good quality of life (Arias-Arévalo et al., 2017). They were all also categorized as cultural ecosystem services.

All three of these values were positioned lower on the y-axis because the benefits of these service were likely to accrue at the level of individuals or groups. For example, scenic beauty was quantified as the average of individual responses to photographs inside of forest stands and the pool of survey participants consisted of individuals who have experience or are interested in being on the property where the research was conducted as evident by their participation in the free permit program. Thus, the scenic beauty response variable I have quantified is likely to reflect the benefits to individuals or groups that visit or intend to visit the study area. Other measures of scenic beauty, like responses of the general populations to landscape views of the Oregon Coast Range may represent the same type of service (scenic beauty), but the benefits would be accrued at a higher level of social organization (all people visiting the Oregon Coast). Scenic beauty accrued to the individual or group in a local context is likely to be more important for the current land managers, while scenic beauty accrued to higher levels of social organization may be more relevant to state wide or national level policy makers.

The second group included Timber Revenue and Merchantable Wood. These two ES proxies were commodities. They were easily substitutable and were means to other ends, i.e. building shelter or buying shelter, thus clearly their value was primarily instrumental (Himes and Muraca, 2018). As commodities, (quantified as the volume

of wood and dollar value of that wood) the benefits of these ES were largely determined by markets, accrued to international investors and traded globally, hence they were positioned high on the Y-axis. Alternative measures of potential benefits, like contribution to local economy or volume of lumber milled at regional facilities would be positioned lower on the Y-axis scale and be more or less relevant to different stake holders or managers. Timber Revenue and Merchantable Wood were both provisioning ecosystem services.

Fire Re-sprouting Understory, Climate Change Resistant Understory, Carbon Stock, and Pollinator Supporting Understory were supporting and regulating services all positioned to the upper right in the matrix. These ES proxies were all important for the ecosystem's resistance and resilience in the face of future change. The first two were indicators of the plant community's ability to persist in the face of expected climate change. Carbon Stock was an indicator of the systems contribution to mitigating carbon emissions and global warming. Pollinator Supporting Understory was indicative of the system's ability to support native pollinating insects which in turn support the perpetuation of many plant communities and were increasingly important for the pollination of agricultural crops as honey bee colonies decline (Kremen et al., 2004). All four of these ES contributed to the ecosystems' ability to perpetuate the conditions critical to human habitation and were therefore fundamental-relational (Muraca, 2011). Carbon stock was significant for global atmospheric greenhouse gas concentrations and therefore was positioned highest of all the ES on the Y-axis. Although some individuals and groups could benefit disproportionately from the other three ES, their contributions to system resistance and resilience would contribute to the livability of the region and therefore benefit the entire community.

Table 4.2. Description of the nine ecosystem service proxies analyzed.

Service	Type	Data	ES Description	Values Category
Scenic Beauty (1-11 scale)	Cultural	Survey Instrument	Indicator of aesthetic value, a commonly recognized cultural service.	Primarily Relational, eudemonistic. Significant mostly to the individual for itself.
Edible/Medicinal/Decorative Plants (m^2/m^2)	Cultural/ Provisioning	Understorey functional traits	May be considered provisioning services but also a cultural service because in this system non-commercial uses are of great significance and the primary benefit to people is the recreational or historic/cultural significance of gathering and using small quantities.	While instrumental in so far as collected goods are consumable, we consider non-subsistence foraging as primarily Relational, eudemonistic. Foraging is tied to sense of individual and cultural identity, heritage, and living a good life (Hall, 2013; Nugent and Beames, 2017). Significant mostly to the individual or groups for itself.
Herbivore Forage (m^2/m^2)	Supporting/ Provisioning/ Cultural	Palatability (moderate or high) and fleshy fruit	Indicator of habitat suitability for herbivores, habitat being the supporting ecosystem service. Animals like deer and elk provide cultural and provisioning services through hunting and recreation.	Primarily relational/eudemonistic. Important to people for whom non-subsistence hunting and/or wildlife viewing is integral to their relationship with nature (Peterson et al., 2010). As an indicator of wildlife in a specific place it is not easily substitutable.
Merchantable Wood (m^3/ha)	Provisioning	DBH, HT, upper stem diameter	Merchantable portions of the log are used as raw material of human used consumptive goods.	Primarily instrumental. A commodity that is easily substitutable and globally exchanged. Not very significant to the individual for itself.
Timber Revenue (USD/ha)	Provisioning	DBH, HT, Upper stem diameter, market data	Indicates direct product revenue which drives many benefits to people both direct (employing foresters and loggers) to indirect (injects capital into local economy).	Primarily instrumental. A commodity that is easily substitutable and globally exchanged. Not very significant to the individual for itself.
Carbon Stock (Mg/ha)	Regulating	DBH, HT	Important for regulation of global climate	Fundamental-Relational. Impacts global atmospheric conditions that are essential to the persistence of human life.
Climate Change Resistant Understorey (m^2/m^2)	Supporting	Drought and Heat Tolerance (moderate or high)	Indicator of ability of the plant community to persist in hotter or drier conditions expected under climate change scenarios. The persistence of the plant community is a supporting service providing habitat for animals, aesthetic quality, and regulating services like soil health and stability.	Primarily fundamental-relational. Impacts the ability of the system to adapt to climate change and perpetuate conditions that support regional life. Not easily substitutable.
Fire Re-sprouting Understorey (m^2/m^2)	Supporting	Ability to sprout after fire	Indicator of the plant community ability to persist following the disturbance of fire, which is expected to increase in frequency and severity as the climate changes. Supporting service ensuring continued habitat for animals, recovery of aesthetic quality and perpetuation of regulating services like soil health and stability.	Primarily fundamental-relational. Impacts the ability of the system to adapt to climate change and perpetuate conditions that support regional life. Not easily substitutable.
Pollinator Supporting Understorey (m^2/m^2)	Regulating	Insect pollinated	Supports insect populations which provide the regulating service of plant and crop pollination in the region.	Primarily fundamental-relational. Integral to integrity of natural systems the life they support. Not easily substitutable.

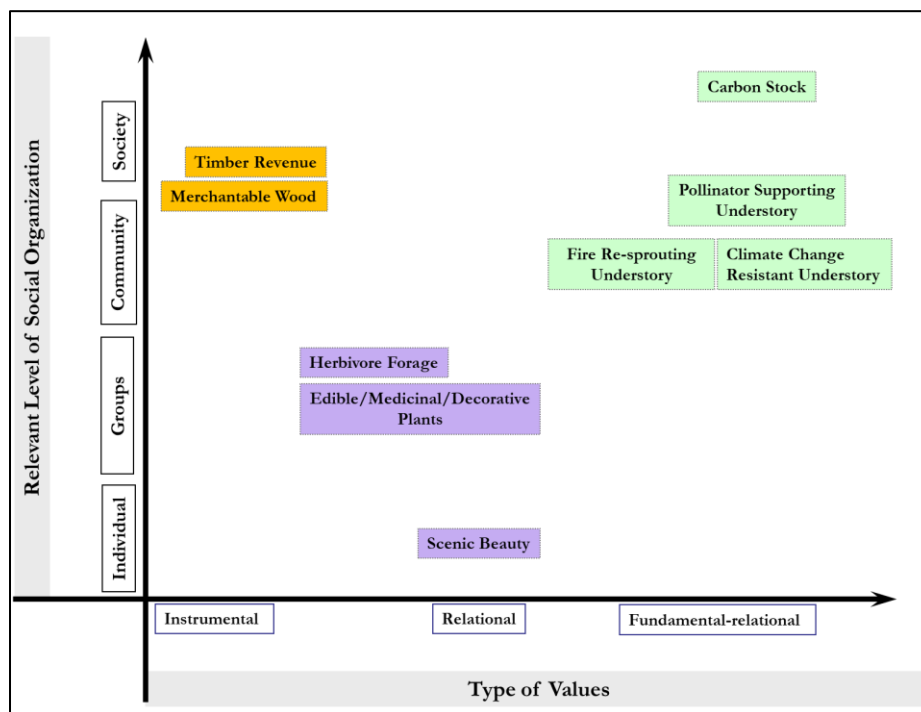


Figure 4.1. Values Matrix. The x-axis of the value matrix represents a continuum of human nature relationships as described in Muraca (2011) in so far as those relationships correspond to the content of ecosystem service valuation (Himes and Muraca, 2018). Near the origin are merely instrumental values of ecosystem services, i.e. those that are easily substitutable in principle (although not always in practice). Further along the x-axis are values whose substitutability is barely possible or highly problematic because they are specific to a place, constitute a sense of identity, are essential components of a “good life” (Constitutive/Eudaimonic Relational) or are fundamental to the conditions that make human habitation and life as we know it possible (Fundamental Relational). The y-axis represents the relevant scale corresponding to ES benefits that ranges from individuals to society adapted from Small et al. (2017). The placement of ES proxies within the matrix of value type indicate the author’s interpretation of the value articulation best suited to each ES and the primary level of social organization at which the ES benefits represented by the measured proxies are likely to be accrued. Colors correspond to different frameworks.

Defining Frameworks

These three groups of ES conceptually aligned with different management frameworks. These frameworks were selected to emphasize extremes and are not necessarily reflective of existing management objectives. For example, most industrial forest managers in the region are voluntarily certified to a sustainable forestry standard that requires consideration of many values including aesthetics and continued forest cover of the land.

Framework 1, *Local Conservation*, prioritized Scenic Beauty, Edible/Medicinal/Decorative Plants, and Herbivore Forage ES (purple boxes in figure 4.1). The objectives of the managers in this framework may be aligned with a local conservation strategy focused on the preservation of the local system so that its natural beauty can be enjoyed by recreationalists. Constitutive/Eudemonic relational values were the primary consideration.

Framework 2, *Production*, prioritized Timber Revenue and Merchantable Wood production ES (yellow boxes in figure 4.1). The objectives of managers in this framework may be aligned with industrial timber managers. The priority was to optimize return on investment or timber production to support manufacturing. Instrumental values were the primary consideration.

Framework 3, *Preserving the Future*, prioritized Climate Change Resistant Understory, Fire Re-sprouting Understory, Pollinator Supporting Understory, and Carbon Stock ES (green boxes in figure 4.1). The objectives in this framework may align with large international environmental NGOs investing in climate change mitigation and adaptation. Managers may be interested in conserving the study region as a sink for atmospheric carbon and a climate change refuge. Fundamental-relational values were the primary consideration.

Framework 4, Value Pluralism, considered all ES and weighed them equally. This was a multi-objective framework that may roughly align with some government agencies or many small private landownerships. This framework indiscriminately emphasized a plurality of values. This was a tractable compromise at simulating management where value pluralism would be embraced. In practice, management based on value pluralism would integrate deliberative process among stakeholders (Kenter et al., 2011), where the values of different ES could be articulated in instrumental, intrinsic, and relational terms and collectively prioritized. This framework may align with government agencies which adhere to multi-objective management.

Analytical Model

The analytical approach was similar to the one used in Himes & Puettmann (*in review*) and is briefly described here. My study design approximated a simplex centroid design (Cornell, 2011), so I used a special cubic mixture model, i.e., a polynomial model that fits a response surface to three component mixtures with a centroid (Scheffe, 1963).

Equation 4.1. Special Cubic Model (from Himes & Puettmann *in review*).

$$Y_t = \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_{12} x_1 x_2 + \beta_{13} x_1 x_3 + \beta_{23} x_2 x_3 + \beta_{123} x_1 x_2 x_3 + \varepsilon_t$$

where

$Y_{t,r}$	Is the estimated ES from the t th plot, $t=1-43$
β_1	parameter for the x_1 pure mixture
β_2	parameter for the x_2 pure mixture
β_3	parameter for the x_3 pure mixture
β_{12}	parameter for the mixture of x_1 and x_2
β_{13}	parameter for the mixture of x_1 and x_3
β_{23}	parameter for the mixture of x_2 and x_3

β_{123}	parameter for the mixture of x_1 , x_2 and x_3
x_1	proportion of western hemlock in mixture
x_2	proportion of Douglas-fir in mixture
x_3	proportion of red alder in mixture
ε_t	random error of the t^{th} plot, $\varepsilon_t \sim N(0, \sigma_r^2)$

By definition, the sum of x_1 , x_2 , and x_3 must always equal to 1. Residuals are assumed to be independent, normally distributed, and have constant variance.

I quantified the mixture proportions of each species (x) based on aboveground biomass of trees for each plot. Aboveground biomass was chosen because of its simplicity and its suggested indication of the ability of each species to access resources (Pretzsch and Forrester, 2017). The species proportions and total AGB of all 43 plots are depicted in figure 4.2.

The special cubic model was fit in R statistical software using the package *mixexp* (Lawson and Willden, 2016). Visual inspection of residuals plots indicated that model assumptions were adequately met except for the assumption of normality in Climate Change Resistant Understory, which showed signs of multi-modality, and Edible/Medicinal/Decorative Plants, which showed signs of symmetrical deviation from the normal distribution. In addition, variance was very small around WH monoculture plots for variables derived from the understory because most WH plots had very little understory cover. However, linear models are robust against the assumption of normality and the small variance around WH plots should only result in conservative standard error estimates.

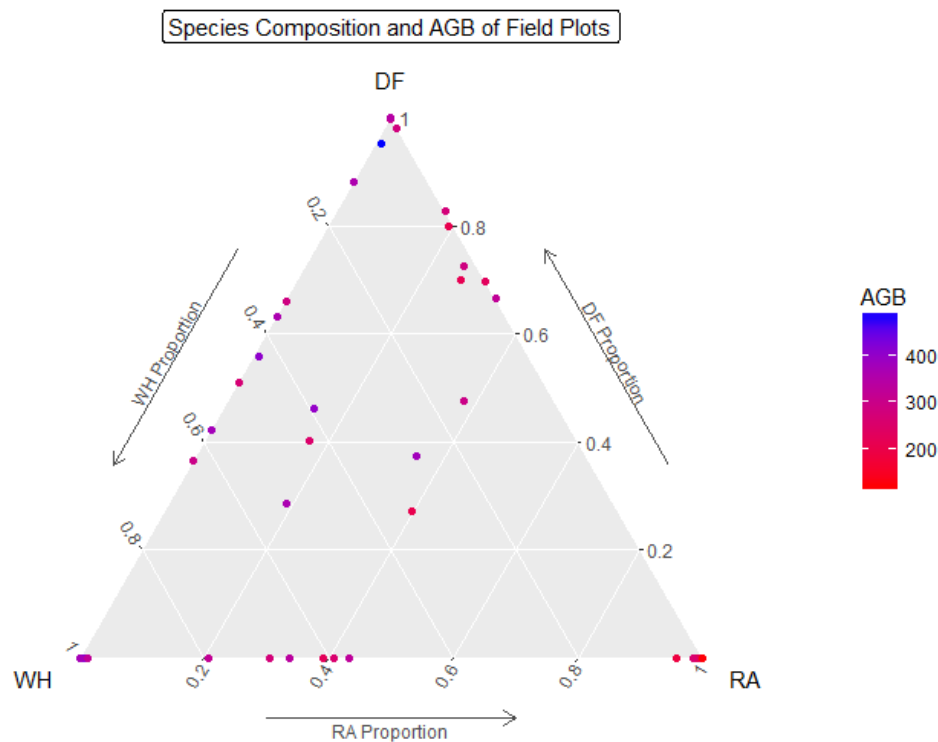


Figure 4.2. Species mixture based on above ground biomass (AGB) of 43 field plots (from Himes and Puettmann *in review*). Total plot AGB represented by shading is in Mg/ha. Each corner for the tertiary plots represents a monoculture (DF=Douglas-fir, WH=western hemlock, RA=RA), the edges of the plots represent two species mixtures and the interior of the triangle represents all three species mixtures. The proportion of each species can be determined at any point by the corresponding value on each of the three axes.

Procedure for optimizing several ecosystem services simultaneously

The goal of the procedure was to determine the species composition that provided the highest level of all the prioritized ES in each framework. Conceptually, the objective was to find the efficient solution for the simultaneous production of the two or more

ES prioritized in each framework. This was the same as finding the species composition that produces the most of each priority ES in a framework with minimal reduction to the amount of any of the other priority ES. I accomplished this objective using a procedure for optimizing several responses simultaneously in mixture experiments (Cornell, 2011). The area of each priority ES response surface that represented 99% of its maximum were graphed and overlaid on one another, then each ES was decreased in lockstep by intervals of 1% of their respective maximum output until the graphs overlap, signaling a region of the response surface (a range of species composition) that produced the greatest equal percent of each ES simultaneously. Next, model predictions for the range of species compositions indicated in the overlapping area were compared for each of the priority ES. The species composition with the largest combined priority ES output was determined to be best for that framework.

Ecosystem Service Trade-off Analysis

To better understand the relationship between the investigated ES, two-way comparisons of the predicted responses of each ES to all 1% incremental combinations of WH, DF, and RA were plotted against each other (a total of 5,151 combinational proportions of the three species). A smoothed line was drawn along the top of the resulting scatter plot by dividing the range of values into 100 equal sized bins and connecting the point with the greatest value in each bin to the point with the greatest value in adjacent bins. The resulting line approximated the maximum value of one ES for any given value of the other, representing efficient outputs of the two ES. If the resulting line had a negative slope or primarily negative slope with intermittent flat regions, the two ES were considered to have a negative relationship (i.e. as one ES increases, the other ES stays the same or decreases). If the slope was consistently positive or positive with intermittent flat regions the relationship between the two ES was considered positive (i.e. as one ES increases the other ES either increases or stays the same). If there were humps or U-shaped patterns in the line, the

relationship of the two ES was considered inconsistent (i.e. there were interactions such that as one ES increases the other ES increases for some of the range of values and decreased at some other range of values of the first ES).

Framework Comparisons

Frameworks were compared based on the predicted output of all nine ecosystem services, reported in table 4.2. In addition, because I was interested in understanding possible relationships between the biodiversity and the value types represented in the four frameworks, I calculated the Shannon Diversity Index for the tree species composition that optimized each framework. Shannon Diversity Index is commonly used as an index of species diversity (Spellerberg and Fedor, 2003). It is a measure of both the number and evenness of species. Shannon Diversity Index is calculated as shown in equation 4.2.

Equation 4.2. Shannon Diversity Index. n_i is the relative abundance of species i based on cover in all understory sampling frames within a plot and all n_i sum to $N=1$ (Shannon, 1948).

$$-\sum_i \left(\frac{n_i}{N} * \ln \left(\frac{n_i}{N} \right) \right)$$

Results

Ecosystem Services Relationship to Tree Species Composition

The response surface for each of the nine ES proxies and corresponding R^2 are shown in figure 4.3. The R^2 , which describes the proportion of variation explained by the model, ranged from 0.30 to 0.68. The response surfaces for ES variables derived from understory plant species (Edible/Medicinal/Decorative Plants, Herbivore Forage, Climate Change Resistant Understory, Fire Re-sprouting Understory, and Pollinator Supporting Understory) tended to be greatest near the RA vertex, decreased toward the WH vertex, and had variable responses toward the DF vertex. ES proxies derived

from tree properties (Volume of Merchantable Wood, Timber Revenue, and Carbon Stock) had a similar but opposite pattern with the greatest values near the WH vertex, decreased values toward the RA vertex and more variable values near the DF vertex. Scenic beauty, on the other hand peaked around the centroid of the response surface but declined sharply toward the WH vertex.

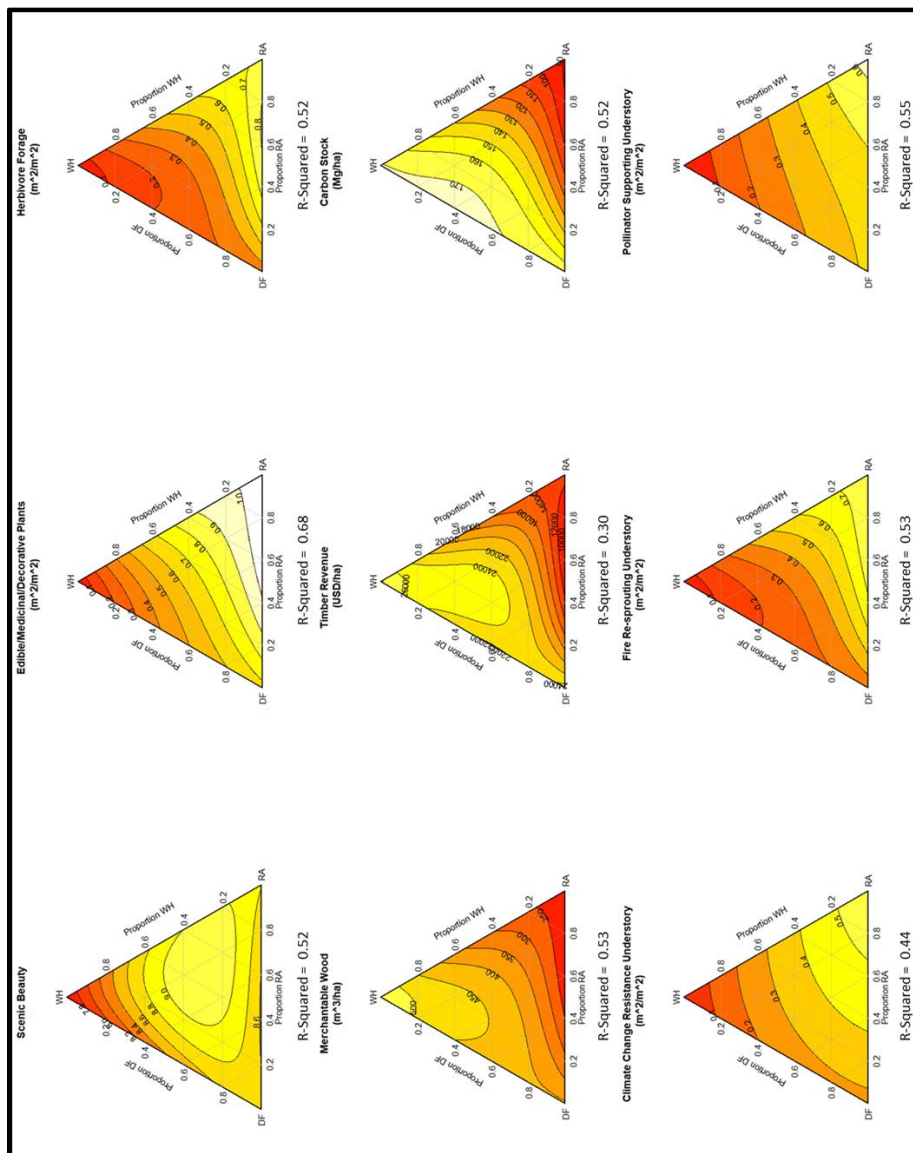


Figure 4.3. Ecosystem service proxy response surfaces and corresponding R-squares. Red indicates lesser values and yellow/white greater.

Trade-offs Between ES

The shape of the response surfaces showed trade-offs between ES derived from the understory community and those derived from trees, particularly near the RA and WH vertices representing the monocultures of those species. However, there was substantial curvature to many of the response surfaces leaving open the possibility for positive relationships between selected understory ES and overstory ES at selected ranges of tree species composition.

The two-way trade-offs between different ES are summarized in figure 4.4. ES derived from the trees tended to have positive or inconsistent relationships with each other but negative or inconsistent relationships with ES derived from understory plants. In inconsistent relationships, ES are positively related to each other in portions of the variable range and negatively correlated in other portions. ES derived from understory plants also had positive or inconsistent relationships with each other. Scenic beauty, on the other hand had inconsistent relationships with all other ES. Some climate related ecosystem services had trade-offs, such as carbon stock and climate resistant understory. ES within and between frameworks had a wide range of relationships. For example, the ES prioritized in the *Production* framework were positively related to each other but had negative or inconsistent relationships with all other ES except for carbon stock. The ES prioritized in *Local Conservation* had positive or inconsistent relationships with one another and negative or inconsistent relationships with the ES prioritized in *Production*. The priority ES in *Preserving the Future* had a mix of positive, negative, and inconsistent relationships and as such, some ES aligned with the first two frameworks and others did not. The difference of ES quantities within and between *Production* and *Local Conservation* highlighted that ES with primarily instrumental values in this study were positively related to each other but tended to be negatively related to ES with constitutive/eudemonic relational values.

	Local Conservation			Production			Preserving the Future		
	Edible/Medicinal/ Decorative Plants (m ² /m ²)	Herbivore Forage (m ² /m ²)	Scenic Beauty	Volume of Merchantable Wood (m ³ /ha)	Timber Revenue (USD/ha)	Carbon Stock (Mg/ha)	Climate Change Resistant Understory (m ² /m ²)	Fire Re- sprouting Understory (m ² /m ²)	Pollinator Supporting Understory (m ² /m ²)
Edible/Medicinal/ Decorative Plants (m ² /m ²)	Gray	Blue	Gray	Gray	Gray	Gray	Gray	Gray	Gray
Herbivore Forage (m ² /m ²)	Blue	Gray	Gray	Red	Red	Gray	Gray	Gray	Gray
Scenic Beauty	Gray	Gray	Gray	Gray	Gray	Gray	Gray	Gray	Gray
Volume of Merchantable Wood (m ³ /ha)	Gray	Red	Gray	Gray	Blue	Gray	Gray	Gray	Gray
Timber Revenue (USD/ha)	Gray	Red	Gray	Blue	Gray	Gray	Gray	Gray	Gray
Carbon Stock (Mg/ha)	Gray	Gray	Gray	Blue	Blue	Gray	Gray	Gray	Gray
Climate Change Resistant Understory (m ² /m ²)	Gray	Gray	Gray	Gray	Gray	Red	Gray	Gray	Gray
Fire Re- sprouting Understory (m ² /m ²)	Gray	Blue	Blue	Red	Red	Gray	Gray	Blue	Gray
Pollinator Supporting Understory (m ² /m ²)	Gray	Gray	Gray	Gray	Gray	Gray	Red	Gray	Gray
Carbon Stock (Mg/ha)	Gray	Gray	Gray	Gray	Gray	Gray	Red	Gray	Gray
Climate Change Resistant Understory (m ² /m ²)	Gray	Gray	Gray	Gray	Gray	Gray	Gray	Blue	Gray
Fire Re- sprouting Understory (m ² /m ²)	Gray	Blue	Blue	Red	Red	Gray	Gray	Blue	Gray
Pollinator Supporting Understory (m ² /m ²)	Gray	Gray	Gray	Gray	Gray	Gray	Red	Gray	Gray

Figure 4.4. Two-way relationships between individual ES proxies. Red indicates a negative relationship, blue indicates a positive relationship, and gray indicates relationships that were not consistently positive or negative but showed interactions such that for some range of values the relationship was positive and for a different range of values the relationship was negative.

Table 4.3. Maximum predicted output of ecosystem services proxies and output under the four frameworks with 95% CI in parenthesis.

ES	Optimal	Local Conservation	Production	Preserving the Future	Value Pluralism
<i>Local Conservation</i>					
Scenic Beauty (1-11 scale)	9.2 (8.8-9.6)	8.7 (8.3-9.1)	7.6 (7.2-8.0)	9.0 (8.7-9.4)	9.0 (8.7-9.4)
Edible/Medicinal/Decrative Plants (m ² /m ²)	1.07 (0.82-1.31)	1.06 (0.85-1.26)	0.20 (0.0-0.21)	0.91 (0.74-1.09)	0.86 (0.67-1.06)
Herbivore Forage (m ² /m ²)	0.82 (0.56-1.08)	0.79 (0.58-0.99)	0.03 (0.00-0.22)	0.58 (0.40-0.76)	0.53 (0.33-0.73)
<i>Production</i>					
Merchantable Wood (m ³ /ha)	551 (467-635)	213 (123-302)	551 (467-635)	316 (238-394)	342 (254-430)
Timber Revenue (USD/ha)	\$28,226 (\$21,353-\$35,100)	\$10,654 (\$3,353-\$17,956)	\$28,226 (\$21,353-\$35,100)	\$17,604 (\$11,221-\$23,988)	\$19,145 (\$11,948-\$26,342)
<i>Preserving the Future</i>					
Carbon Stock (Mg/ha)	171.6 (151.5-191.8)	92.2 (65.9-118.4)	170.9 (146.1-195.6)	123.6 (100.7-146.6)	133.3 (107.4-159.1)
Climate Change Resistant Understory (m ² /m ²)	0.57 (0.41-0.73)	0.53 (0.35-0.71)	0.00 (0.00-0.17)	0.46 (0.30-0.61)	0.43 (0.26-0.60)
Fire Re-sprouting Understory (m ² /m ²)	0.78 (0.55-1.01)	0.77 (0.57-0.97)	0.02 (0.00-0.21)	0.59 (0.41-0.76)	0.53 (0.33-0.73)
Pollinator Supporting Understory (m ² /m ²)	0.64 (0.49-0.78)	0.56 (0.40-0.72)	0.01 (0.00-0.16)	0.47 (0.33-0.61)	0.44 (0.28-0.60)

Comparing Ecosystem Service Results for Frameworks

Predicted quantities and confidence intervals for all nine ES proxies under the four frameworks as well as the maximum predicted quantity of each ES are reported in table 4.3. The largest trade-offs existed between *Local Conservation* and *Production*. For example, timber Revenue and Merchantable Wood were less than half of their maximum value in *Local Conservation* compared to *Production* where both were maximized.

Under the *Production* framework, provision of Edible/Medicinal/Decorative Plants, Herbivore Forage, Climate Change Resistant Understory, Fire Re-sprouting Understory, and Pollinator Supporting Understory ES proxies were all very close to zero and Scenic Beauty was less than in any other framework. All ES optimized in the *Local Conservation* framework except for Scenic Beauty were greatest in that framework. Scenic Beauty was slightly greater in the *Preserving the Future* framework than the *Local Conservation* framework because of trade-offs between it and Herbivore Forage when both ES proxies were maintained at high levels. Scenic Beauty was still at 95% of its maximum in the *Local Conservation* framework. The ES optimized in *Production* were greatest in that framework. In the *Preserving the Future* framework, all prioritized ES were maintained at 72% of their maximum or greater. The negative relationship of Carbon Stock with Climate Change Resistant Understory and Pollinator Supporting Understory drove their simultaneous output in *Preserving the Future* to a lower level than *Local Conservation* or *Production*, and as a result the four priority ES in *Preserving the Future* had greater values in different frameworks. Predictably, the *Value Pluralism* framework resulted in moderate quantities of all ES.

The tree species composition that simultaneously optimized the priority ES for each framework are shown in table 4.4 and further illuminate some of the differences in ES trends between the frameworks. *Local Conservation* was heavily weighted toward

RA while the *Production* framework was optimized with WH monoculture. The countering trends of ES derived from understory plants and ES derived from trees between the RA and WH vertices played out between *Local Conservation* and *Production* resulting in the substantial trade-offs between them. On the other hand, *Preserving the Future* and *Value Pluralism* had more even mixtures of all three species and fewer extreme trade-offs compared to the other two frameworks. The *Production* framework had the lowest Shannon Diversity Index with zero, since it was optimized with a monoculture. The next lowest was *Local Conservation*, which included all three species, but in very uneven mixture predominated by RA. *Preserving the Future* and *Value Pluralism* both had substantially greater Shannon Diversity Index values for their corresponding optimal tree species mixtures. *Value Pluralism*'s mixture had the greatest Shannon Diversity Index driven by the more even mixture of the three species.

Table 4.4. Proportion of WH, DF and RA that yielded optimal priority ES values for the four frameworks along with the corresponding Shannon diversity index.

Scenario	WH	DF	RA	Shannon Diversity Index
Local Conservation	0.01	0.19	0.8	0.54
Production	1	0	0	0
Preserving the Future	0.17	0.24	0.59	0.96
Value Pluralism	0.17	0.36	0.47	1.02

Discussion

All ES proxies derived from understory species cover generally aligned positively with understory species diversity measured by Shannon diversity index (Himes&Puettmann, *in review*; Shannon, 1948). This suggests a positive relationship between species diversity and ES, at least with regard to understory plants. For these services, my result supported the hypothesis that there is a general positive

relationship between biodiversity and ES proposed by others (Haines-Young and Potschin, 2010; Tilman et al., 2014). Similarly, ES derived from the overstory were well aligned with estimated above ground biomass of trees in the same plot network reported previously by Himes&Puettmann (*in review*), supporting the supposition that tree productivity is a good proxy for many ecosystem functions and services (Balvanera et al., 2006). In contrast, Scenic Beauty—presumably a function of both understory and trees—was somewhat intermediary between above ground biomass and understory species diversity. I believe this was because respondents simultaneously view the understory and overstory components of the plot when rating scenic beauty and other studies have shown that the basal area of trees and variability in understory both positively correlated to scenic beauty (Ribe, 2009, 1989).

Most of the individual ES proxies were maximized or very nearly maximized in monocultures. Scenic beauty was a notable exception in which a high diversity mixture of all three species (31% WH, 22% DF, and 47% RA) rated most beautiful. All the other ES proxies were relatively simple services in comparison, i.e. derived from a small set of functional traits or physical parameters while scenic beauty was multidimensional and sensitive to complex interactions in the ecosystem and between the physical world, social context, cognitive processes and values (Ford et al., 2014; Gundersen et al., 2017; Ribe, 1989). My results suggest the hypothesis that ES derived from more complicated processes, i.e. those derived from interactions of multiple ecosystem functions, may be more reliant on higher levels of biodiversity. Examples from the literature support this hypothesis: the ecosystem service of pest control in organic coffee farms in Chiapas, southern Mexico depends on at least thirteen different species and multiple levels of interaction between them (Vandermeer et al., 2010), and simulations show that ES dependent upon multiple species will illicit higher levels of biodiversity conservation in economically optimal solutions (Dee et al., 2017). According to Hooper et al. there is certainty in the conclusion that, “more species are needed to insure a stable supply of ecosystem

goods and services as spatial and temporal variability increases” (2005:4), thus it is reasonable to expect that ES which are affected by multiple factors or multiple levels of temporal and spatial scales maybe more likely to have a positive relationship with biodiversity.

Trade-offs between ecosystem services demonstrated the need to consider understory vegetation in conjunction with tree components when investigating the impacts of plant diversity on ecosystem services in forests. Forest understory vegetation has been linked to important aspects of ecosystem function in forest types around the world (Gamfeldt et al., 2013; Neill and Puettmann, 2013; Nilsson and Wardle, 2005). Understory species are typically light limited and closely tied to tree canopy structure (Barbier et al., 2008), which can result in trade-offs between understory plants and trees. Despite the high potential for such trade-offs a disproportional number of studies investigating relationships between biodiversity and ecosystem function or services in forests focus exclusively on tree biomass (Brockhoff et al., 2017).

I observed trade-offs between ES represented by relational values with benefits specific to individuals and groups (*Local Conservation* framework) and ES which were primarily instrumental with near globally transferable benefits (*Production* framework). This is particularly concerning because a recent literature review of ecosystem services in mixed species forests found nearly 12 times as many publications on provisioning services derived from wood biomass as there were total papers on cultural ecosystem services (Brockhoff et al., 2017). This differential in the literature heavily favors instrumental values. My results suggested ES with primarily constitutive/eudemonic values likely to be specific to individuals and groups in the system region (*Local Conservation*) tended to be cultural services and were severely reduced when globally transferable instrumental values were prioritized. Marín-López et al. (2014) recommend pluralistic valuation to avoid missing trade-offs between incommensurate value dimensions based on empirical results from their study in the Doñana region of Spain. My results and the literature

highlight the impetus for plural valuation frameworks that include relational values when making natural resource management decisions, particularly with regard to cultural ES (Fish et al., 2016; Himes and Muraca, 2018). Empirical evidence supports that cultural services and relational values can be associated with more biodiverse systems and tend to be more important for marginalized groups (Cáceres et al., 2015). Also, plural approaches to valuation more fully capture the importance of ES to people around the world (Arias-Arévalo et al., 2017; Klain et al., 2017). All of which support arguments that instrumental value monism perpetuates social/environmental injustice (Berbés-Blázquez et al., 2016; Jax et al., 2013; Kosoy and Corbera, 2010).

The *Value Pluralism* framework, which prioritized all nine ES equally, was optimized with the most diverse tree species composition. This result was consistent with other forestry studies which found the importance of biodiversity increased when multiple ecosystem functions or services were considered (Gamfeldt et al., 2013, 2008; Plas et al., 2016). However, the selection effects of the specific tree species included in this case study, and not biodiversity per se, could also be affecting results (Hooper and Vitousek, 1997). The inclusion of red alder may have impacted many of the ES indicators. Unlike the other two species, red alder is a deciduous species which fixes nitrogen. If red alder were replaced with another conifer in the study, there would likely be smaller difference between understory species diversity and composition which likely respond to the seasonal and persistent increased light availability under red alder canopies as well as likely higher available nitrogen levels (Deal et al., 2017). However, inclusion of red alder in the study provided a greater diversity of functional traits compared to three conifer species, and the diversity of species traits may actually be a better (although harder to quantify) indicator of biodiversity than species richness and evenness (Hillebrand and Matthiessen, 2009).

The observed relationships between species diversity and the different ecosystem service bundles aligned with different values. Moving from left to right along the x-axis of the value matrix, the optimal tree species composition increases in diversity

from *Production to Local Conservation to Preserving the Future*. Within the matrix, the *Value Pluralism* framework included the broadest range of values and social organization, most aligned with a value pluralist approach to managing ES and had the optimal mixture of trees that was the most species diverse, as indicated by Shannon Diversity Index. This trend suggest the following hypotheses: ES or ES bundles which support a plurality of values are related to higher levels of biodiversity than ES that primarily support a single type of value. This hypothesis aligns with the IPBES value framework (Pascual et al., 2017) and deserves further investigation.

Conclusion

I conclude by summarizing the findings and interpretation of the study with following four points:

- 1.) I found evidence of trade-offs between selected ecosystem services while others were compatible. Trade-offs aligned biologically (understory vs. trees), and along value domains (merely instrumental vs. relational/eudemonic).
- 2.) Most ES were optimized, or nearly optimized, by monocultures except for Scenic Beauty. Scenic Beauty was derived from multiple dimensions of ecosystem function while the other ES were more simple. I hypothesized that the relationship between plant diversity and ES may be mediated by the degree of complexity inherent or quantified in the ES.
- 3.) Management frameworks prioritizing ES with primarily fundamental-relational value were optimized with higher levels of tree species diversity than those with primarily constitutive/eudemonic relational value or those with merely instrumental value. The highest level of tree species diversity supported the framework where a plurality of values was considered.
- 4.) Based on these results I hypothesize that biodiversity may be important not just for increasing ecosystem functions and services, but also increasing the types of value supported by ecosystem services.

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Chapter 5. General Conclusions

Study synthesis

The overarching objective of this study was to understand how the potential provisioning of ecosystem services responded to tree species composition and diversity in plantation forests in the Pacific Northwest. I also aimed to understand potential trade-offs and synergies between different ecosystem services across a tree species diversity gradient and in doing so determine how different values and management objectives affect overall ecosystem service provisioning and trade-offs.

In chapter two I focused on the basic philosophical issues underlying implementation of the ecosystem services framework and promoted the use of relational values as an alternative to the traditional instrumental/intrinsic value dichotomy historically debated in environmental ethics (Chan et al., 2016; Muraca, 2011). I provided a concise framework for relational values that clearly distinguished them from instrumental and intrinsic values. I argued that as the content of valuation, relational values are key to more inclusive and pluralistic articulations of why nature and ecosystem services are important to people. I further showed that ecosystem service valuations, and therefore assessments of trade-offs between ecosystem services, which only consider instrumental values have the potential to underestimate the overall importance of ecosystem to people and bias assessments in ways that can perpetuate injustice (Muraca, 2016).

In chapter three I used field data from intensively managed plantation forests in the Pacific Northwest to determine the relationship of above ground biomass of trees, live crown length, and understory plant species diversity to changes in tree species composition and diversity. The results suggested that management actions, like planting density and thinning interact with species identity and diversity to shape aspects of the ecosystem. In so far as the measured variables represent the structure of the ecosystem and were the culminations of ecological processes at the time of

measurement, they can be considered proxies for ecosystem functions defined as the subset of ecosystem structures and processes that support benefits to people (de Groot et al., 2002). The results showed higher levels of tree species diversity were related to higher levels of the three variables, thus supported the theory that greater tree species diversity supports high levels of multiple ecosystem functions, even though monocultures produced the highest levels of individual responses (Gamfeldt et al., 2008; Isbell et al., 2011; Plas et al., 2016).

Finally, in chapter three I transformed my field data into proxies for nine ecosystem services by drawing on previously literature, published models, public records, and survey results. I segregated the nine ecosystem services into four frameworks based on the grouping of the services within a value matrix that integrated a continuum of relational values and the level of social scale that benefits from the ecosystem services would be accrued. I identified trade-offs between specific ecosystem services and show that management frameworks representing different objectives and values were optimized by very different species composition and levels of tree species diversity. Importantly, I identified a trend of increasing optimal trees species diversity with increasing number of services and range of values included in a management framework.

Integrating findings

The three study chapters (2,3 and 4) were conceptually bound by three theories prevalent in the literature that logically connect to one another. The first is the theory that biodiversity is positively related to ecosystem function (Tilman et al., 2014). The next is the ecosystem services cascade theory that makes the distinction between ecosystem function and ecosystem services, positing that functions are a necessary pre-condition for ecosystem services (Haines-Young and Potschin, 2010). These two theories combine to form a connection between biodiversity and ecosystem services which has been a primary justification for international efforts to conserve

biodiversity (www.ipbes.net). The third theory stems from a critique of ecosystem service cascades theory that showed human action and not ecosystem function alone is necessary for the provisioning of ecosystem services (Spangenberg et al., 2014). It is only a small logical extension to suggest that the actions humans take to mobilize ecosystem services reflects what is important to them, i.e. what they value. Thus, these theories considered holistically point to human values and biodiversity as fundamental components of ecosystem services.

In this dissertation, I attempted to link these fundamental aspects of ecosystem services by first establishing a more complete framework for the ways humans value nature in chapter two, then testing the relationship between ecosystem functions and a single aspect of biodiversity that humans can easily control (tree species diversity in plantations) in chapter three. Then, in chapter four, I integrated human values and the biodiversity ecosystem functioning relationship in my evaluation of ecosystem service trade-offs and synergies. I was only able to explore a narrow range and singular aspect of biodiversity with tree species in a plantation system, but my results supported the theory that higher levels of biodiversity are necessary for supporting multiple ecosystem services (Gamfeldt et al., 2013; Isbell et al., 2011) and highlighted the ways in which the type of values considered impact trade-offs (Martín-López et al., 2014). In the context of intensively managed forest plantations both biodiversity, as indicated by tree species diversity, and human values were related to provisioning of and trade-offs between ecosystem services. Higher levels of biodiversity were related to a broader diversity of values and incorporating more values and biodiversity into management decisions minimized trade-offs between ecosystem services and maximizes the simultaneous provision of multiple services. Thus, the empirical evidence from this study supports the theoretical conclusion above that biodiversity and human values are fundamentally related to the provisioning of ecosystem services.

Future Work

The data collected for this study could be further leveraged to test hypothesis about mechanisms behind the relationships I observed in understory species diversity, live crown length, and above ground biomass of trees. For example, tree measurements and increment cores that were collected as part of the field protocol could be combined with historic meteorological data to model species interactions impact on tree growth through time using process-based models. Existing models, like the mixed species 3PG model for forests could simulate past and future growth to explore how climate and soil variables impact the dynamics of tree species interactions to explicitly test stress-gradient hypothesis and differentiate selection and complementarity effects in managed forests systems (Forrester and Tang, 2016). The data I collected combined with simulations of dynamic changes with stand age could improve understanding of how tree species diversity and composition related to functional diversity and could be leveraged to increase system resistance and resilience to future conditions (Messier et al., 2019). Tree growth simulations could also facilitate comparison of some ecosystem services relationship to tree species composition through time, i.e. carbon stock, timber revenue, and wood fiber, to compare different management regimes with variable stand densities, extended rotations, natural regeneration or continuous cover forestry (Diaz et al., 2018).

This study could also be extended to a next phase in which stakeholders and/or experts are engaged in actual valuation of the ecosystem services I quantified proxies for. Integrative methods could be employed with a focus on capturing a plurality of values and comparing the nine ecosystem services considered in chapter 4 to support decision makers (Rincón-Ruiz et al., 2019). Multiple methods could be employed and compared to test their efficacy for eliciting values (Saarikoski et al., 2016). Engaging stakeholders directly could also empirically validate my placement of ecosystem services within the values matrix proposed in chapter 4.

Finally, the lessons learned from this study can be applied elsewhere to capture a larger set of land management paradigms, ecosystem functions, ecosystem services, and stakeholder representing a broader range of values to further test the generalizability of the foundational nature of biodiversity and values to ecosystem services. In other words, expanding this research simultaneously up and down in scales of time, space, and social relevance by creating new observational studies and experiments that include biophysical processes transpiring in seconds to centuries at spatial scales from the cell to the landscape, and in social/cultural context beyond western dominated world views. This larger scope of research would depend on the cooperation of experts from diverse fields. For example, environmental scientists focused on mechanisms behind ecosystem function response to tree species and broader biodiversity, social scientist engaged in directly quantifying benefits, and interdisciplinary scientists that could integrate results in meaningful ways.

Future studies concentrated on expanding the mechanistic understanding of ecosystem responses to biodiversity, how human values shape ecosystem service mobilization, and the role of temporal and spatial dynamics in ecosystem service provisioning would further test the ecosystem service cascade model and increase understanding of the relationship between biodiversity, human values, and ecosystem services.

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