SOCIAL-ECOLOGICAL RESILIENCE OF AGROFORESTS IN FIJI

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAI'I AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

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This dissertation is dedicated to my parents, Judy and Shaun McGuigan, and the people of Waitabu, Korovou, Kiobo, Natokalau, Waisa, Namarai, Saioko, Verevere, Kalokolevu, and Togalevu.

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ABSTRACT

Global change, including climate and socioeconomic change, has major impacts on linked human and environmental health. In food systems, this precipitated the rise of industrialized agriculture and related increases in nutrition-related non-communicable diseases. Agroforestry has the potential to serve as a food production system that addresses issues of environmental degradation, food security, and nutrition. In Fiji, agroforests are a part of a larger socialecological system that has also enabled Pacific Island people to be resilient to disasters and disturbances for centuries. However, knowledge about how these systems are adapting to global change and their capacity is for resilience in this changing context, remains incomplete. I address this knowledge gap by exploring the dynamics of agroforests and their capacity for resilience after a catastrophic Category 5 cyclone. Specifically, I used a combination of farmer interviews, agroforest vegetation surveys, and nutritional analyses in 50 agroforests across five districts in Fiji, pre-cyclone Winston, and 1 and 3 years post-cyclone to address: How did Cyclone Winston affect agroforest starch crop and cultivar richness? How did Cyclone Winton affect agroforest trees, and what traits and management practices increase resistance to damage? Does the diversity of ecological functional traits in agroforests predict their nutritional diversity? Starch crop richness was highly dynamic and largely resilient to the cyclone, but cultivar richness declined. Post cyclone tree survival was high across all agroforests (87.8%). Bigger trees experienced more damage than smaller trees, and survival increased as a function of increasing wood density. In addition, the purposeful management of trees in agroforests likely buffered them against damage and mortality. A novel application of functional diversity metrics showed that nutritional functional diversity increased as a function of ecological functional diversity, indicating that agroforests are able to provide important levels of ecological and nutritional functions in the same space. This interdisciplinary research outlines the importance of agroforests in Fiji and their contributions to food system resilience and nutritional security. Understanding how agroforests in social-ecological systems are adapting to current changes is critical to inform the global community on resilience to future disturbances.

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CHAPTER 1. INTRODUCTION

Global change, including environmental and socioeconomic change, impacts economies, cultures, and ecosystems worldwide. Environmentally, climate change has induced sea-level rise, ocean acidification, changes in precipitation, temperature, and seasonality, and changes in storm intensity, frequency, and geographic occurrence (IPCC 2021). Socioeconomic conditions and social-ecological systems in many countries are also changing due to rapid globalization (Janssen et al. 2007).

Food systems are inextricably connected to such environmental and socioeconomic changes, with implications for human and environmental health and resilience. Food systems involve multiple interrelated activities, including food production, processing, distribution, and consumption (Ericksen 2008; Hodbod and Eakin 2015). Achieving food security is a primary goal of any equitable food system at every scale. The 1996 World Food Summit states that food security "exists when all people, at all times, have physical and economic access to sufficient, safe and nutritious food to meet their dietary needs and food preferences for an active and healthy life" (FAO 2006). The FAO identifies four dimensions of food security: food availability, access, utilization, and stability (FAO 2006). Food system resilience is a function of food security, and is usually conceptualized as a social-ecological system (Allen and Prosperi 2016; Herrera de Leon and Kopainsky 2019; Tendall et al. 2015).

At the same time, modernized agricultural systems are a primary driver of climate change and ecosystem degradation, spurring massive biodiversity loss (Cicuzza et al. 2011; Tscharntke et al. 2012; Benton et al. 2021); simultaneously the food produced is losing nutritional value at the individual (Fan et al. 2008), food group (Davis et al. 2004; Davis 2009), and food system scales (Alexander et al. 2017). Frequent and intense applications of chemical fertilizers and pesticides are required to maintain these systems, causing deleterious downstream effects on human and environmental health (Benton et al. 2021). A concomitant nutrition transition induced by global socioeconomic change has also led to increased production and consumption of energy dense, nutritionally poor foods prompting the rise of NCDs (Popkin et al. 2012). Climate change conditions will further reduce crop nutritional content (Myers et al. 2014b; IPCC 2019), and increase global food demand by 30% to 62% between 2010 and 2050 (van Dijk et al. 2021). This is also expected to also bring an increase in more intense cyclone occurrence across a greater geographic area (IPCC 2021). Therefore, we face not only the challenge to provide food for a growing population, but to do so in ways that allow for sustainable and nutrition-focused production resilient to major disasters and disturbances (International Fund for Agricultural Development 2014; Berry et al. 2015).

Historically, across cultures and continents, locally-adapted agroecological systems provided a sustainable and stable source of food for large populations (ICRAF 1987; Kurashima and Kirch 2011; Zomer et al. 2014; Lincoln 2020; Dhyani et al. 2021). Agroforestry represents a diverse subset of these agroecological management practices, where trees and shrubs are cultivated with crops and/or livestock in varying scales, structures, and compositions dependent on use, location, and culture (Fernandes and Nair 1986; Clarke and Thaman 1993; Webb and Kabir 2009). Globally, between 25-33% of the population is estimated to rely on forests, including agroforestry (FAO and UNEP 2020; UN 2021), and 43.5% of agricultural land is estimated as agroforestry (tree cover greater than 10%) (Zomer et al. 2014). Biodiverse and multi-functional, agroforests deliver a range of critical ecosystem services within a relatively small space (Lasco et al. 2014; Bhagwat et al. 2008) and can support social-ecological resilience to economic and environmental shocks and disturbances (McSweeney and Coomes 2011; Simelton et al. 2015). Agroforestry also presents a potentially scalable option to support linked ecosystem and food security goals (Clough et al. 2011; Kiptot et al. 2014; Kurashima et al. 2019; Hastings et al. 2020) helping mitigate climate change induced risks such as cyclones (Lasco et al. 2014; Waldron et al. 2017; Shin et al. 2020).

Indigenous communities in Fiji, like in other Indigenous Pacific Island Nations, have a long history of resilience to cyclones and other sources of disturbance, conferred, in part, from their biodiverse agroecosystems, traditional marine resource management strategies, and strong social networks (Campbell 2015; McMillen et al. 2014; Veitayaki 2002). Agroforestry, described as a complex, dynamic, agroecosystem where trees and shrubs grow in tandem with crops and/or livestock (Fernandes and Nair 1986), is a main component of this resilience. However, the diversity of Fijian agroecosystems has been declining due to socioeconomic, cultural, and environmental changes (Thaman 2014). As food systems worldwide are impacted by global change, it becomes important to understand how places with a history of food system resilience to climate variability may be successfully coping, or not, with increased disturbances.

GOALS OF THE DISSERTATION

The overall goal of this dissertation is to gain a better understanding of agroforestry in Fiji as a social-ecological system and the mechanisms through which it is, and can support, resilience to disasters and disturbances. There are therefore three primary goals of this dissertation to address this goal: 1) assess how crop and cultivar richness changed post-cyclone and the implications for agroforest-based food system resilience; 2) analyze the impact of major cyclone disturbance to trees in agroforests, and the traits and conditions associated with survival and damage resistance; and 3) examine the relationship between plant ecological and nutritional functions in agroforests, as assessed via their compositional traits, linking environmental and human health.

OUTLINE OF THE DISSERTATION

Chapters 2 and 3 assess the effects of cyclone disturbance agroforestry in Fiji with Chapter 2 focusing on the impacts on understory starch crops and Chapter 3 assessing the effects on trees. Specifically, in Chapter 2, I operationalize a theorized framework for food system resilience using changes in the richness of important starch crop species to describe the four interacting components of the framework. I then explore the impact these changes may have for future resilience to disturbance both ecologically and nutritionally. In Chapter 3, I describe the effects of cyclones on tree and stem survival and damage in agroforests and test if these are predicted by tree traits and management practices.

In Chapter 4, I then assess the ecological and nutritional functional diversity of agroforests in Fiji and their capacity for multifunctionality. Specifically, I assess if ecological functional traits important to disturbance ("response traits") predict nutritional functional diversity.

In Chapter 5, I provide a brief outline of barriers and knowledge gaps and describe avenues for future interdisciplinary and applied research.

UNIVERSITY OF HAWAI'I INSTITUTIONAL REVIEW BOARD

Record of the Human Studies Program approval of this study as exempt.





Office of Research Compliance **Human Studies Program**

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NOTICE OF APPROVAL FOR HUMAN RESEARCH

This letter is your record of the Human Studies Program approval of this study as exempt.

On January 11, 2017, the University of Hawai'i (UH) Human Studies Program approved this study as exempt from federal regulations pertaining to the protection of human research participants. The authority for the exemption applicable to your study is documented in the Code of Federal Regulations at 45 CFR 46.101(b) 2.

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CHAPTER 2. POST-CYCLONE RESILIENCE OF AN AGROFOREST-BASED FOOD SYSTEM IN THE PACIFIC ISLANDS

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ABSTRACT

As climate change increases the probability and/or severity of major disturbances worldwide, understanding how agroecological food systems can be resilient to the effects of major disturbances becomes critical. Farm-level crop and cultivar richness are critical to food security and nutritional dietary diversity, but quantitative research of how they are impacted by major disturbances, including the dynamics of their recovery, is largely lacking. We assessed the resilience of an agroforest-based food system to a recent Category 5 cyclone. Specifically, we carried out vegetation surveys in Fijian agroforests pre-cyclone, and one and three years postcyclone, to assess changes in staple starch crop and cultivar richness over time. Resilience, measured as robustness, redundance, reactivity, and resourcefulness, varied with the scale of analysis. At both the crop and cultivar scale, the agroforestry systems were highly reactive to cyclone disturbance. Crop richness increased immediately post-cyclone and three years later remained higher than pre-cyclone levels, largely due to the increased presence of famine food crops, indicating system robustness, redundancy, and resourcefulness as well. Farmers also planted many new starch crop cultivars post-cyclone, especially of sweet potatoes, but the total number of cultivars declined over time, indicating limited redundance and resourcefulness. Frequent crop substitutions for cassava over taro or yams; and high cultivar dynamism that resulted in the loss of traditional varieties, can have consequences both for nutritional diversity and the maintenance of cultural traditions. This research suggests resilience is present in Fijian agroforest systems, yet greater focus on crop cultivar diversity is needed.

INTRODUCTION

Global change, including environmental and socioeconomic change, impacts economies, cultures, and ecosystems worldwide. Environmentally, climate change has induced sea-level rise, ocean acidification, changes in precipitation, temperature, and seasonality, and changes in storm intensity, frequency, and geographic occurrence (IPCC 2021). Socioeconomic conditions and social-ecological systems in many countries are also changing due to rapid globalization (Janssen et al. 2007).

Food systems are inextricably connected to such environmental and socioeconomic changes, with implications for human and environmental health and resilience. Food systems involve multiple interrelated activities, including food production, processing, distribution, and consumption (Ericksen 2008; Hodbod and Eakin 2015). Achieving food security is a primary goal of any equitable food system at every scale. The 1996 World Food Summit states that food security "exists when all people, at all times, have physical and economic access to sufficient, safe and nutritious food to meet their dietary needs and food preferences for an active and healthy life" (FAO 2006). The FAO identifies four dimensions of food security: food availability, access, utilization, and stability (FAO 2006). Food system resilience is a function of food security, and is usually conceptualized as a social-ecological system (Allen and Prosperi 2016; Herrera de Leon and Kopainsky 2019; Tendall et al. 2015).

The resilience of a food system is influenced by multiple interacting factors (Ericksen 2008; Hodbod and Eakin 2015). One factor that can enhance resilience is the level of diversity in an agroecosystem. Agroecosystems that contain high biodiversity, including agrobiodiversity, have a higher potential to adapt and recover than those of lower diversity (Mijatović et al. 2013) proffering them greater resilience. Agrobiodiversity encompasses the diversity of all biotic organisms at multiple scales in an agroecosystem (Mijatović et al. 2013), and supports increased resilience via increased diversity and redundancy of functional groups and functional traits (Hodbod and Eakin 2015; Laliberté et al. 2010; Wood et al. 2015). Specifically, a high diversity of functional groups and traits allows for non-food species, crops, and crop cultivars to employ varying levels and types of tolerances to disturbances. This buffers against shocks and disturbances to the system which might cause food insecurity.

How major disturbances impact the agrobiodiversity, and associated resilience of food systems, has been studied in various ways in different parts of the world (Altieri et al. 2015;

Kundermann 2000; McSweeney and Coomes 2011; Paulson 1993). Some studies have shown that agroecosystems with greater diversity at the species and landscape level exhibit resilience to major disturbances like flooding and cyclones (Altieri et al. 2015). In systems with low agrobiodiversity, many studies have shown further immediate post-disturbance declines in agrobiodiversity, leaving these agroecosystems, and the people who rely on them, more vulnerable to future disturbance (e.g. Krishnamurthy and Reddiar 2011; Thaman 2014). In some cases, however, disturbance has encouraged positive adaptation and fostered resilience. Flooding caused by Hurricane Mitch in Honduras (1998) triggered endogenous social reform that increased resilience to subsequent natural disasters by re-instituting more biodiverse agricultural practices, and relocating primary farming plots to areas of lesser risk and by diversifying incomes (McSweeney and Coomes 2011). Similarly, in Amazonia, Ávila et al. (2021) found that after major flood disturbance, communities reported that they selectively replanted with crops and crop cultivars that survived the event more successfully, and replanted in areas less prone to subsequent flooding. Agroecosystems that have withstood such catastrophic disturbances are important to identify and assess the practices that allowed for resilience for broader implementation (Altieri et al. 2015). This is especially relevant for the longer term, as models suggest that while crop losses from extreme disturbances will be generally moderate in the early 21st century (Adams et al. 1998), the effects will be progressively worse in the later half (Altieri et al. 2015).

Crop and cultivar richness are critical to food security and nutritional dietary diversity (Hunter et al. 2019; Kennedy et al. 2017). Despite their importance, however, quantitative research is lacking on the impacts of major disturbance events on crop and cultivar richness, including the dynamics of their recovery and the implications for food system resilience. Tendall et al. (2015) provide a framework to assess the latter. Specifically, they propose four interacting components of food system resilience that can be assessed over time: robustness, redundancy, reactivity, and resourcefulness. Robustness is a measure of resistance to negative change after a disturbance and is defined as the ability of a system to continue to immediately provide the same or increased level of food post-disturbance as pre-disturbance; redundancy is represented as the number of food items that are able to replace each other if the supply of one is compromised; reactivity is the rapidity with which a system returns to pre-disturbance production levels after a disturbance to reclaim food security; and resourcefulness refers to the ability of a system to adapt

and source exogenous food supplies and/or, locally available famine foods, after a period of relative stasis.

Indigenous communities in Fiji, like in other Indigenous Pacific Island Nations, have a long history of resilience to cyclones and other sources of disturbance, conferred, in part, from their biodiverse agroecosystems, traditional marine resource management strategies, and strong social networks (Campbell 2015; McMillen et al. 2014; Veitayaki 2002). Agroforestry, described as a complex, dynamic, agroecosystem where trees and shrubs grow in tandem with crops and/or livestock (Fernandes and Nair 1986) is a main tenant of this resilience. However, the diversity of Fijian agroecosystems has been declining due to socioeconomic, cultural, and environmental changes (Thaman 2014). As food systems worldwide are impacted by global change, it becomes important to understand how places with a history of food system resilience to climate variability may be successfully coping, or not, with increased disturbances.

In this study we operationalize Tendall et al. (2015)'s food system resilience framework to assess a key component of food system resilience in Fijian villages after Cyclone Winston, which made landfall in Fiji in February 2016 and was the strongest cyclone in recorded history of the South Pacific at the time. Tropical storms, including cyclones, are of particular importance in the Pacific Islands due to their widespread and common reoccurrence (Campbell 2015; Lin et al. 2011; Marler 2014). Various studies and projection models predict diverse changes in tropical cyclone frequency, geographic occurrence, and intensity under climate change conditions (Emanuel 2013; Kossin et al. 2013; Mendelsohn et al. 2012; Zhang and Wang 2017). Additional studies have shown a notable increase in the predicted frequency of the most intense cyclones (Emanuel 2013; Mendelsohn et al. 2012), true also in the South Pacific (Zhang and Wang 2017). The intensity of Pacific cyclones has recently increased (Kossin et al. 2013) and is likely to increase in the future (Walsh et al. 2012), with substantial effects from the El Niño-Southern Oscillation phenomenon in Fiji (Chand and Walsh 2011; Magee et al. 2017).

We build on agroforest biodiversity data collected pre-cyclone (2014) (Ticktin et al. 2018), with new biodiversity data monitored one year post-cyclone (2017), and three years post-cyclone (2019), to assess changes in the richness of starch crop species and cultivars in Fijian agroforestry systems. Previous work (Ticktin et al. 2018) demonstrated that Fiji agroforests are important conservation areas for native trees, which are important to agroecological resilience (Cabel and Oelofse 2012; Ticktin et al 2018), but did not assess crop or crop cultivar richness.

We use Tendall et al. (2015)'s framework to interpret food system resilience as a function of changes in starch crop and cultivar richness. We use starch crop richness as a proxy for the Indigenous Fijian agroforest food system resilience due to the foundational role starch crops, and particularly roots and tubers, play in key nutritional, cultural, economic, and ecological functions in Fiji, and across the Pacific Islands (Barrau 1958; Pollock 1985, 1986; SPC 1976; Wairiu et al. 2012; but see Hidalgo et al. 2020). Underscoring this, starch crops are often perceived as categorically different from other food plants (Barrau 1958; Pollock 1986; Ravuvu 1991). Specifically, in Fiji, root and tree starch crops are referred to as kakana dina, which roughly conceptually translates to "real food" or "true food" (Pollock 1985, 1986; Ravuvu 1991; Turner 1984). Fijian world view places the most importance on the starch component of the meal, and if kakana dina are lacking, this is seen as a weakness in the ability of the farmers to provide food for the household (Ravuvu 1991).

Today in Fiji, the four kakana dina root crops of greatest significance are: taro, or dalo, (*Colocasia esculenta* (L.) Schott), cassava, or tavioka, (*Manihot esculenta* Crantz), sweet potato, or kumala, (*Ipomoea batatas* (L.) Lam.), and yam, or uvi, (*Dioscorea alata* L.), (hereafter collectively referred to as the "four primary root crops") (Barrau 1958; Iese et al. 2018; SPC 1976; Wairiu et al. 2012). Because tubers are mostly protected from moderate intensity natural disasters (except flooding) they have also been important in recovery in Fiji (Benson 1997). Given their nutritional, cultural, and recovery importance, we use various metrics of starch crops (scales of species and cultivar richness) as indicators of food system resilience. We also recognize that food systems are complex, dynamic, and multifaceted, and that a full analysis of food system resilience requires consideration of all foods, including purchased and imported foods, across the entire food supply chain.

We address the following questions: 1) How do starch crop and crop cultivar richness in agroforests change across time after a major category 5 cyclone disturbance? 2) Based on this, how resilient is the agroforest-based food system in rural Indigenous Fijian communities? Given the recorded gradual decline of agrobiodiversity in Fiji (Thaman 1982a, b, 2014) we hypothesized that richness of the four primary root crops as well as their cultivars would decline immediately post-cyclone and not recover to pre-cyclone levels, indicating lowered robustness and reactivity. Conversely, we hypothesized that in the agroforests, the species richness of all starch crops combined would remain stable, since many Fijians still hold knowledge and

practices related to emergency starch food plants (Ticktin et al. 2018), indicating redundancy and resourcefulness.

METHODS

Study site and context

Fiji is an archipelago of over 300 islands, most of which are inhabited. According to the 2017 census, the total population is just under 900,000; 44.1% (390,635) of which reside in rural areas while the remaining 55.9% (494,252) reside in urban areas (Fiji Bureau of Statistics 2018).

Fijian agroforests are mosaics of forested, fallow (uncultivated), and planting areas under continuous rotation (Ticktin et al. 2018). The length of time an area remains within a given management type is dependent on multiple factors, including soil health and land productivity, time since and intensity of past disturbances, and changes in land tenure and agricultural goals, among other socioeconomic or environmental circumstances. Similar to other traditional agroforest practices across the Pacific (Clarke 1994), planting areas are often composed of diverse root crop assemblages including taro, cassava, yam, and sweet potato in addition to semi-managed and lesser consumed famine foods such as Polynesian arrowroot, or yabia (*Tacca leontopetaloides* (L.) Kuntze), and two wild yams, spiny yam and aerial yam, or tivoli and kaile (*Dioscorea numnularia* Lam. and *D. bulbifera* L.) (Thaman 1982a). Endemic, native, and introduced trees, shrubs, and herbs producing various fruits and vegetables are also cultivated or otherwise protected in these areas including Fiji sago palm trees (*Metroxylon vitiense* (H.Wendl.) Hook.f.), Fiji Longan (*Allophylus cobbe* (L.) Raeusch), mangos (*Mangifera indica* L.), slippery cabbage (*Abelmoschus manihot* (L.) Medik), and many more (Thaman 2008; Ticktin et al., 2018). Many plants not explicitly used for food are also found in these agroforestry systems.

Of the root crops, the two foremost culturally important species are yam and taro, in that order (Ravuvu 1983, 1991), which were brought by some of the first Austronesian voyagers to the Pacific Islands (Walter and Lebot 2007) and would have been highly important in early settlers' diets. Most scholars agree that sweet potato was introduced to the Pacific Islands from South America first by early Polynesians and then again by European explorers in the 1500s (Roullier et al. 2013). Comparatively, cassava is a more recent introduction brought during European colonization (Barrau 1958). Today cassava and taro are the most consumed root/tuber

crops in the country (Wairiu et al. 2012), followed by sweet potato and yam, respectively (Ministry of Agriculture 2014).

Taro may be planted at any time of year and is harvestable 6 to 18 months later, depending on the cultivar and agroecological zone it is planted in (Ministry of Agriculture 2014, 2015a; Sivan 1982). Depending on the cultivar, yam is planted between June and September and may be harvested between February and July (Ministry of Agriculture 2014; Sivan 1982). Sweet potato can be grown year-round (Ministry of Agriculture 2015b) but is typically planted in April or May and is unique in that it matures quickly, within 4 to 5 months, making it an important post-disaster crop (Ministry of Agriculture 2014). Cassava can be planted year-round and matures 8 to 12 months later (Ministry of Agriculture 2014), though some cultivar names, such as vula tolu, suggest some cultivars mature in as little as 3 months. However, planting times are shifting to accommodate climate change induced alterations in weather patterns (Hidalgo et al. 2020).

Each species consists of many different cultivars. To our knowledge, no exhaustive list of cultivars for any of these four crops exists for Fiji, although partial lists have been compiled over time, (Guarino and Jackson 1986; Lebot 1992; SPC 1976). Overall, the number of cultivars is thought to have been declining over the past several decades as farmers plant a smaller number of traditional varieties in favor of commercial varieties (Masibalavu et al. 2002 (unpublished); Thaman 2014). However, the system is dynamic and cultivars can be lost or replaced as a result of economic (e.g. market demand and affordability) (Masibalavu et al. 2002 (unpublished); Tisdell 2014), sociocultural (e.g. change in dietary preference or ceremonial practices) (Lebot and Siméoni 2015), and environmental (e.g. pests and diseases) (Lebot 1992) changes.

Agroforest Surveys

In 2014 Ticktin et al. (2018) carried out a study of social-ecological resilience in Indigenous Fijian communities, which included botanical surveys of 100 agroforest sites and socioeconomic interviews with members of the associated households, in 20 coastal villages across 5 districts in Fiji. The villages support mixed subsistence economies, where agroforest and fishing harvests are used for both subsistence and sale. We carried out a participatory mapping exercise with each farmer to establish the number, size, use, and location of agroforest parcels the household manages. Then, of the parcels that were used for subsistence, actively managed, and within an hour's walk of the village, we randomly selected one parcel per farmer to survey. Farms outside of these specifications tend to be monocultural and used only for commercial purposes. Parcels were between 0.25 to 5.00 ha in size and all below 100 m elevation, save for one parcel located at 196 m asl. With each farmer, we recorded all tree and understory crop species observed in crop, forest, and fallow areas. Some agroforest areas are shared within the community, and so all adjacent areas where farmers had access to were included. We identified any unknown species at the South Pacific Regional Herbarium, Suva, Fiji. When a farmer did not know the name for a crop cultivar, it was recorded as unidentified. If a crop was growing in the farmer's agroforest but the farmer did not purposefully plant it or report to use it, it was identified as a 'wild' variety. Wild types are not included in these analyses. We assumed that cultivar names referred to the same phenotype within villages and districts. However, because synonymous and homonymous names may apply at larger scales (SPC 1976), we could not assess cultivar richness at the country level. Last, during each agroforest survey, we carried out a semi-structured interview with the farmer on their management practices including, but not limited to, questions about changes to emergency food cultivation, decisions to replant in the same area or not, and any plants now desired (Ticktin et al. 2018).

In 2017, one-year post Cyclone Winston (hereafter referred to as "the cyclone"), we selected a subset of 10 of the original 20 villages in the four districts of Kubulau, Nakorotubu, Suva, and Wainikeli (on the islands of Viti Levu, Vanua Levu, and Taveuni) (Appendix Table 2.1) to resurvey the agroforests. The subset of villages was selected based on their proximity to cyclone impact (Fig. 2.1) and to represent a range of pre-cyclone indicators of social-ecological resilience, including agroforest biodiversity, traditional ecological knowledge, and socioeconomic characteristics as reported by Dacks et al. (2018). The same agroforests were then surveyed again in 2019 (three years post-cyclone) to record all tree species and understory crops, following the 2014 protocol. In the few cases where farmers were ill, deceased, and/or had passed on their parcels to their next of kin, we worked with said relative instead (three in 2017; four in 2019).

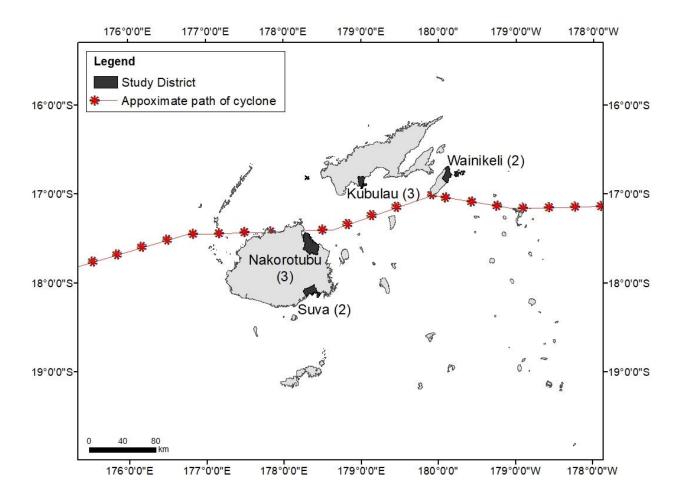


Figure 2.1 Map of the Fiji Islands indicating the path of Cyclone Winston and the districts of the villages in this study.

We also conducted semi-structured interviews with farmers using the same methods as Ticktin et al. (2018), about their observations and management practices after the cyclone. Interviews included questions about how farmers replanted their agroforest areas, where they sourced their planting materials, and observations about tree and crop recovery post cyclone. We were unable to collect data in one village, Togalevu, in 2017 and where that data is necessary for accurate analysis as described below, we exclude it from the results. In total, we surveyed 43 farms from 9 villages in 2017, and 48 farms from 10 villages in 2019.

We applied the Tendall et al. (2015) framework to our data as follows:

<u>Robustness:</u> Starch crops, and the four primary root crops and their cultivars, exhibited robustness if species/cultivar richness one-year post-cyclone (2017) was the same or greater than

pre-cyclone (2014) richness. We calculated a robustness index as the percent increase in species/cultivar richness from pre-cyclone to one-year post-cyclone. If the percent change was 0 or greater, we concluded robustness was present.

Redundancy: We used the total number of starch species, the four primary root crops, and their cultivars present across all villages at all three years (2014, 2017, and 2019) as a measure of redundancy, which was classified as either "high", "moderate", or "low". We determined a threshold of redundancy based on the approximate number of species or cultivars that could sustain production over different seasons and climatic conditions (e.g. drought or wet years, dry or wet microclimates, etc.). For starches overall, a village had "high" redundancy if 6 or more species were present in a village across all three years; if 6 or more species were only present in one or two years we labeled this "moderate"; if there were less than 6 species across all three years, we labelled this "low". For the four primary root crops, the threshold was 3 or more species present in a village across all three years for "high" redundancy; if 3 or more species were only present in one or two years, we labelled this "moderate"; if there were less than 3 species present in all three years, we labelled this "low". For the crop cultivars, we identified the two most abundant root crop species in each village and assessed the redundancy of crop cultivars for those two crops. Because each root crop has a different overall count of the number of cultivars recorded, we used different thresholds for each species when determining redundancy. We assumed "high" redundancy if there were at least 5 cultivars for taro, 4 cultivars for cassava, or 4 cultivars for yam present in a village across all three years. If these values were only met in one or two years, we determined the redundancy to be "moderate"; if these values were never met, we labeled this as "low". Sweet potato was not evaluated as a primary root crop in any village. We recognize these values are approximate and context-specific, and necessarily will vary across different agroecosystems.

<u>Reactivity:</u> As a proxy for the return to potential production levels, we used the presence of a new species or cultivar in a village at either one year (2017) or three years post-cyclone (2019) when compared to pre-cyclone records (2014) as a measure of reactivity regardless of whether species or cultivars were lost at any point post-cyclone. For the four root crop cultivars, we first assessed cultivar reactivity of each root crop across both years. If new cultivars were recorded in

either 2017 or 2019 for each of the four root crops, then that crop was considered to have cultivar reactivity in that village. Then we assessed the composite cultivar reactivity across all four crops by determining that if at least three of the crops have cultivar reactivity in that village, then reactivity was present at the cultivar level.

Resourcefulness: We determined resourcefulness was present if the species/cultivar richness levels for starch crops overall, the four root crops, and the root crop cultivars, rebounded or exceeded the pre-cyclone (2014) richness levels by three-years post-cyclone (2019), regardless of their composition (e.g. the species/cultivar richness might rebound but with a totally different set of species or cultivars). This is expressed as percent change from pre-cyclone to three-years post-cyclone where the change must be 0 or greater to be considered resourceful. For starches overall and the four primary root crops individually, we assessed this at the species level. For the four root crop cultivars, we first determined the two most prevalent root crops in each village and then assessed only those two crops' changes in cultivar richness to account for regional differences in microclimate, and therefore the natural variation in species presence. Given the predominance of food-sharing across households within villages (Dacks et al. 2018), all calculations were made at the village level, rather than at the individual farmer level. For each village, we analyzed resilience at three scales: all starch species, the four primary root crops, and the cultivars of the four primary root crops. We received permission for this research from Fiji national and district governments, village leadership (village headmen (Turaga ni Koro)), and the University of Hawai'i Institutional Review Board (2016-30418; 2018-30418) (Appendix Figure 2.1). Our team consisted of one member from the University of Hawai'i at Mānoa and two Indigenous Fijian (iTaukei) research assistants each field season. These research assistants were well versed in iTaukei village protocols and ceremony, fluent in Fijian and English languages, knowledgeable about agroforest biodiversity, and at least one had assisted in the 2014 iteration of the research. The research assistants led and organized all village and field visits to the agroforests, and conducted, translated, and interpreted the interviews with the farmers. Informed oral consent was obtained from all farmers.

RESULTS

Over the course of the study we recorded a total of 16 starch species, the names of 36 cultivars of taro, 32 of yam, 30 of cassava, and 9 of sweet potato across all 10 villages (see Appendix Table 2.2 and 2.3). The average number of starch species observed per village was lowest in 2014 (7.00 ± 0.54 se) and increased through to 2019 (9.80 ± 0.79 se) (see Appendix Table 2.4). Of the four primary root crops, cassava had the greatest average cultivar richness per village in 2014 and 2017 (5.70 ± 0.42 and 5.22 ± 0.85 se), and similar richness to that of dalo (4.60 ± 0.92 se) in 2019 (cassava richness was 4.50 ± 0.62 se). Mean richness of yam cultivars was only 2-3 per village, though the pre-cyclone range across villages was very high (0-18). Sweet potato showed the lowest range and mean number of cultivars per village (see Appendix Table 2.4).

Robustness (number of starch crop species and cultivars pre versus one-year post cyclone) Starch species richness one-year post-cyclone (2017) was greater than or equal to pre-cyclone (2014) richness in 89% of the villages studied (Fig. 2.2a), indicating robustness to cyclone disturbance. Similarly, in 78% of the villages studied, the number of primary roots crops remained stable or increased (Fig. 2.2c), indicating robustness to cyclone disturbance. However, robustness varied with scale of analysis and was most variable at the cultivar level (Fig. 2.3a, c, e, g). Fifty-six percent of villages increased cultivar richness by 18-86% (Table 2.1c). Cultivar richness decreased between 7-29% one-year post-cyclone in the remaining villages (Table 2.1c).

Redundancy (presence of multiple starch crops and cultivars over time)

We found that starch species overall were redundant in the agroforests we studied. In only two villages, less than 6 starch species were observed in at least one of the three years studied and were thus only moderately redundant (Fig. 2.2a). Redundancy in the four primary root crops, however, was much weaker, as less than 3 species were present on farms in numerous years across most villages (Fig. 2.2c); thus, most villages only exhibited moderate redundancy (Table 2.1b). The crop assemblage most commonly observed was taro, cassava, and yam. The crop cultivars varied even more greatly; some villages had high redundancy in crop cultivars whereas some had only moderate redundancy, meaning that for the two most prevalent crops recorded in a village, the number of cultivars recorded fell below the number of cultivars needed to be

present to be considered redundant for at least one of the crops selected (Table 2.1c). Cassava had the highest levels of cultivar redundancy across villages where the average total number of cultivars present per village across all three years ranged from 4.50 to 5.70 (see Appendix Table 2.4). Redundancy was never low at any scale.

Reactivity (presence of newly recorded starch crops and cultivars)

Overall, reactivity was present in all villages across all levels of analysis (Table 2.1a-c; Fig. 2.2b, d). In almost all of the farms, new starch crops were recorded at one and three years post-cyclone (Fig. 2.2b). Reactivity of the four primary root crops was also present in all villages; however, in two villages where all four root crops had been present in 2014, the number of root crops recorded declined (Fig. 2.2d). The reactivity in the four primary starch crop cultivars was high but varied the most across time and space. For taro and cassava, between 2014 and 2019 there was an average of 3.7 ± 0.1 se and 3.3 ± 0.1 se new cultivars added per village, respectively (Fig. 2.3d, b). Reactivity in cultivars of yam and sweet potato was lower with an average of 2.7 ± 0.1 se and 2.3 ± 0.1 se new cultivars appearing, respectively (Fig. 2. 3h, f).

Resourcefulness (number of starch crop species and cultivars pre versus 3 years post-cyclone) Generally, resourcefulness was present in the agroforest systems we studied. Overall, we observed total starch crop resourcefulness across all the farms we surveyed in all villages, with starch crop richness in 2019 equal to or higher than pre-cyclone levels in all villages except one, where there was a slight decrease in the number of starch species present (Fig. 2.2a). Similarly, for the four primary root crops resourcefulness was present in all villages, with the number of primary root crops present in 2019 equal to or higher than pre-cyclone levels. The one exception was a village where two fewer root crops, specifically taro and yam, were observed three years post-cyclone (2019) compared to pre-cyclone levels (Fig. 2.2c). However, there was large variation in resourcefulness at the cultivar level across the villages (Table 2.1c). Farms of only four villages, by 2019 the number of cultivars had not rebounded to pre-cyclone levels. The lowest level of resourcefulness was observed for cassava which experienced declines in cultivar richness ranging from 20% to as much as 71% (Fig. 2.3a).

(a)

Starch Level Resilience Summary

Village	Robust	Reactive	Redundant	Resourceful
Waitabu	0.0	12	High	11.1
Korovou	40.0	10	Moderate	100.0
Kiobo	116.7	15	High	116.7
Natokalau	22.2	14	High	33.3
Waisa	20.0	11	Moderate	100.0
Namarai	22.2	13	High	11.1
Saioko	0.0	12	High	57.1
Verevere	50.0	15	High	37.5
Togalevu	NA	6		0.0
Kalokolevu	-14.3	9	High	-14.3

(b)

Four Primary Root Crops Resilience Summary

Village	Robust	Reactive	Redundant	Resourceful
Waitabu	0	4	High	0.0
Korovou	0	3	Moderate	50.0
Kiobo	100	4	Moderate	100.0
Natokalau	0	3	Moderate	50.0
Waisa	0	4	Moderate	100.0
Namarai	-25	4	High	0.0
Saioko	0	4	High	33.3
Verevere	-25	4	Moderate	-50.0
Togalevu	NA	2		0.0
Kalokolevu	50	3	Moderate	0.0

(c)

Cultivar Level Resilience Summary

Village	Robust	Reactive	Redundant	Resourceful	
Waitabu	-28.5		Moderate	-18.8	
Korovou	-8.0		Moderate	-67.0	
Kiobo	37.5		Moderate	-4.2	
Natokalau	41.4		High	10.0	
Waisa	-6.7		Moderate	50.0	
Namarai	86.1		High	49.2	
Saioko	29.2		Moderate	11.1	
Verevere	18.1		High	-40.3	
Togalevu				-45.8	
Kalokolevu	-18.8		Moderate	-18.8	

Table 2.1: Summary of robustness, reactivity, redundancy, and resourcefulness of starch crops and cultivars at each village. A green cell indicates that the agroforest in that village showed resilience post-cyclone, as measured respectively by robustness, reactivity, redundancy, and resourcefulness (as defined in the methods). A yellow cell indicates moderate resilience, and red indicates the aspect was not observed to contribute to resilience. Data was unavailable for Togalevu in 2017 and summary results were omitted where that data was necessary

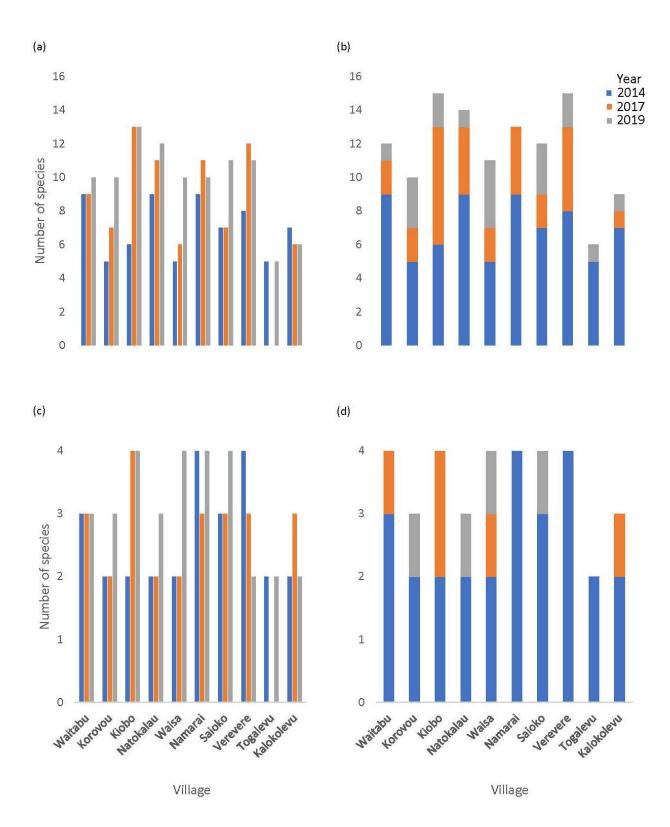


Figure 2.2: Count of (a) total and (b) newly recorded starch crop species; and (c) total and (d) newly recorded primary root crop species by village per year. Data does not exist for Togalevu in 2017

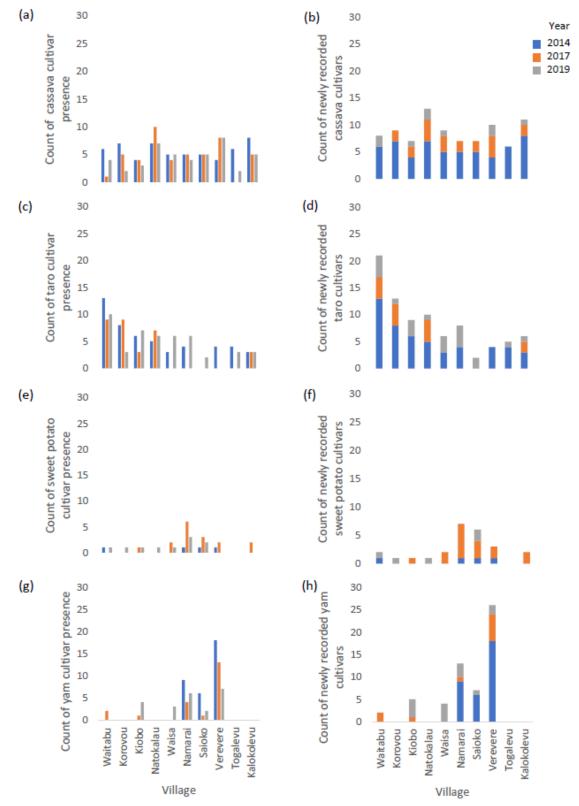


Figure 2.3: Number of cassava (a), taro (c), sweet potato (e), and yam (g) cultivars recorded in each village per year. Number of newly recorded cassava (b), taro (d), sweet potato (f), and yam (h) cultivars in each village per year. Data does not exist for Togalevu in 2017

DISCUSSION

We assessed the resilience of a Fijian agroforest-based food system to a major disturbance by assessing variation in starch species and cultivar richness pre and post Cyclone Winston. Although most scholars contend that species and cultivar richness of Indigenous crops has declined across the Pacific (Thaman 2014; Tisdell 2014), we found that at the scale of starch crops, at least, the agroforests in the Fijian villages in our study were largely resilient to Cyclone Winston, generally increasing in richness over time. This increase from the pre-cyclone levels contributed to redundance and robustness, and the new starch crop species observed in 2017 and 2019 highlights the reactivity and resourcefulness of the system. These trends were similar for the four primary root crops. At the cultivar level however, while many new cultivars were added, making reactivity high, the total number of cultivars present declined and remained lower three years post-cyclone, indicating limited redundance and resourcefulness at this scale.

Contributions of famine food crops

Famine foods, or those foods that are consumed infrequently during normal times but that come into play in times of need (McMillen et al. 2014), played a critical role in the resourcefulness of the Fijian agroforest food system. The increase in the richness of starch species we recorded in 2017 and 2019 was largely due to the appearance mostly of aroid and yam species, as well as yabia. While there were also increases in tree or tree-like starch crops, such as breadfruit, or uto (*Artocarpus altilis* (Parkinson ex F.A.Zorn) Fosberg), and plantain, or vudi, (*Musa* L.), these increases were much more variable by village and year.

One of the greatest increases we recorded was in the number of tannia, or dalo ni tana (*Xanthosoma sagittifolium* K.Koch). A recent introduction of the 19th century from the Americas, either by missionaries or whalers, tannia is a robust, prolific crop increasing in use across the Pacific Islands (Lebot 2013; Lebot and Siméoni 2015). While some scholars believe the introduction of new crops such as tannia undermine the resilience of agroforest ecosystems in the Pacific (Sardos et al. 2016), others argue it effectuates a positive impact on agroecosystems due to their ease of cultivation (Lebot 2013). Here it appears to have played a role in helping farmers withstand and recuperate from the impacts of Cyclone Winston. Our results suggest that the impact of new plant introductions on the resilience of agroforests in Fiji is context and species specific, as discussed below in our examination of cassava.

The number of aerial yam (*D. bulbifera*) plants also increased over time. Aerial yam is unique in that while it is a yam, the edible tubers of this naturalized species also form aerially on the vines of the plant; therefore, although it is not protected from the wind produced during a cyclone, the plant may actually benefit from strong winds via dispersal of the aerial tubers (Horvitz et al. 1998) and seeds (Lebot and Sam 2019), and simultaneous forest canopy disturbance (Horvitz and Koop 2001). This may account for increased observations of aerial yam post cyclone in Fiji, as has been in recorded in hardwood forests in Florida where an increasing frequency of occurrence, as well as coverage, of aerial yam over time was recorded posthurricane Andrew (Horvitz and Koop 2001). Although we did not observe people actively consuming aerial yam as we did with tannia, it was frequently cited by farmers as a well-known emergency food.

Famine foods are often only used in cases of emergency because they require greater input to prepare them for consumption (Campbell 1984; Martin 1974), and in some cases are not as palatable as other food options. This is the case for aerial yam where the bulbils are toxic if not properly prepared (Martin 1974). While tannia also requires special preparation methods to eliminate its acridity, these preparation methods are less intense and include baking or boiling (Sakai et al. 1972) similar to the processes required for taro and other edible aroids. While some scholars had expected tannia to gain importance as a subsistence or commercial crop in the Pacific, (Lebot 1992; Sakai et al. 1972), today it is more commonly considered a wild or emergency food (McClatchey 2012), which our interviews confirmed (data not presented). Easy access and availability of imported and processed starch foods such as rice, wheat flour, and wheat noodles may have influenced this change in use and importance.

High dynamism of crops and crop cultivars

The introduction of new starch crop species on the farms we surveyed was accompanied also by the introduction of many new crop cultivars, illustrating the very high dynamism of the Fijian agroforests. Dynamic agroecosystem management is critical for resilience in that it allows for substitutions and modifications to be made that enables adaptation and recovery (Mijatović et al. 2013). Globally, crop and crop cultivar diversification or substitution is a common adaptation strategy in farming communities in response to environmental changes and disturbances (Labeyrie et al. 2021). In our study, the most commonly listed emergency food crops farmers cited for this purpose included sweet potato, tannia, and spiny yam, listed in order of overall citation frequency.

Many cultivars exist for sweet potato and while we recorded a large relative increase in the number of newly recorded cultivars in 2017 (16) as compared to 2014 (4) across 9 villages (Fig. 2.3f), we only recorded 9 unique cultivar names over the course of the study (see Appendix Table 2.3). Therefore, many of these new occurrences may have been of the same cultivars. The Fiji Ministry of Agriculture promotes sweet potato as an important disaster recovery crop, since it matures quickly, can be grown relatively easily in many environmental conditions, and is less affected by natural disasters (Iese et al. 2018; Veitayaki 2002). Over 49,100 sweet potato cuttings were distributed across Fiji post-Cyclone Winston (Iese V, 2021, Member of 2017 Food Security and Livelihood Cluster, FAO, Suva, Fiji, personal communication). Thus, this increase in new cultivar observations we recorded likely stems from government aid. At the same time, strong social networks within and across villages in Fiji (Dacks et al. 2020; Ravuvu 1983) also likely played a role in facilitating the exchange of planting materials of sweet potato and other emergency food crops that we observed. In China, Jianjun et al. (2015) also reported that 80% of farmers adapted to drought occurrence by planting new varieties of their crops. Interestingly, this response was much lower in Ethiopia and South Africa in response to perceived changes in temperature where only 19% and 3% of farmers in each respective country cited this adaption method (Bryan et al. 2009). In our study, we found that 79% of farmers who grew sweet potato were planting new cultivars one year post-cyclone as compared to pre-cyclone records.

Another clear demonstration of the high reactivity of Fijian agroforest food systems, but at the crop level, was the quick substitution of taro with sweet potato. On the farms in our study, increases in sweet potato temporarily replaced taro post-cyclone. Although taro has high cultural and culinary importance as a historically high status crop in parts of the Pacific (Leach 2005), especially Fiji (Wairiu et al. 2012), its longer life-cycle and more specific growing conditions means it cannot be harvested for anywhere between 6 to 18 months after planting (Ministry of Agriculture 2014, 2015a; Sivan 1982).

The reliance on sweet potato when taro supply is compromised has also been observed in the Solomon Islands in response to environmental disturbances (Iese et al. 2015) and Papua New Guinea in response pests and diseases (Bourke 2005). In the latter cases, these changes remained more permanent, transforming entire agricultural and cultural systems (Ballard 2005). In

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contrast, in Fiji, three years post-cyclone sweet potato cultivar richness had already decreased in our study. When we asked farmers why they were not growing as many sweet potato cultivars in 2019 as compared to 2017, many cited that sweet potato is less desirable as it is less filling than the other three primary root crops. This may also explain why we observed an inverse relationship in cultivar richness between taro and sweet potato; as taro began to reach or surpass pre-cyclone richness levels, sweet potato richness declined. This lower preference may be different in Fiji, as compared to other Pacific Island countries where sweet potato has played a pivotal role, and as a result, sweet potato may have lower potential for climate change adaptation and mitigation strategies. Nonetheless, despite this relative decrease, sweet potato richness remained higher in 6 of the 10 villages despite differences in microclimatic conditions three years post-cyclone then the pre-cyclone richness levels, increasing redundancy. More research is needed to develop an appropriate distribution model for the Pacific Islands for sweet potato cultivars (lese et al. 2018) and culinary distaste in Fiji should be incorporated into such an evaluation.

Cultivar decline

Despite the high dynamism of crop cultivars, the incorporation of new cultivars was accompanied by a loss of other cultivars, especially of traditional cultivars, which were often cited by village elders as hardier and more resistant to environmental disturbances. Based on our interviews, many farmers expressed a desire to plant the "old" or "traditional" cultivars, especially of yam and taro. Efforts to source and distribute these plants of cultural, culinary, and post-disaster recovery importance may not only improve resilience to natural disasters, but also aid in the passing on of cultural knowledge about these plants and their significance.

In addition, for most villages and crops, resourcefulness at the cultivar level was compromised, as cultivar richness in 2019 had still not recuperated to pre-cyclone levels. This trend has been observed in other agroecosystems; some farmers surveyed two to four years after a major flood disturbance in Amazonia actively chose not to replant varieties of cassava after a natural disaster, either to prevent further damage or loss to their current stock should another disturbance occur, because they preferred to replant with cultivars that survived better, or because planting materials were unavailable (Ávila et al. 2021). Moreover, there has been a decline in the number of cassava cultivars grown on small farms elsewhere, as seen in the

Republic of Congo (Kombo et al. 2012), and crop and crop cultivar diversity is decreasing across most agricultural species worldwide (FAO 2019).

Although cultivar decline may be a result of many factors, labor requirements and yield are often cited as among most important in planting decisions (Guarino and Jackson 1986; Hashimoto 1990; Kombo et al. 2012; Teshome et al. 2016), likely because of the importance of these variables in cash economies. The crop that showed the highest decline in cultivars across the time of our study was yam. Moreover, while 90 to 100 yam cultivars have been recorded across Fiji in the recent past (Chandra 1979; Guarino and Jackson 1986; Sivan 1982), our study only recorded 33 cultivars of yam (some of which may be synonyms or homonyms). Yam is the most prestigious root crop in Fiji (Ravuvu 1991), holds historical culinary and other cultural importance across the Pacific (Bourke 2005; Chandra 1979; Leach 2005; Sivan 1982), and has previously been promoted for disaster recovery in Fiji (Benson 1997). Although we observed new plantings on farms in three villages in the years after Cyclone Winston where none had been recorded before, the three villages where we had recorded high richness pre-cyclone experienced large losses in cultivar richness, even though climatically they are well-suited for yam cultivation. While yam has superior storage capabilities compared to the other three primary root crops (Chandra 1979), it is also more labor intensive to cultivate than taro and cassava (Rothfield and Kumar 1981) and as shelf-stable processed foods increasingly replace local food production, the need for easily stored root crops decreases. For these reasons, and a lack of planting materials, yam may be the most vulnerable to cultivar richness loss of the four primary root crops. Indeed, the overall production of yam as a species has declined from an estimated 7,000 tons per year in 1982 (Sivan 1982), to 4,447 tons in 2018 (Ministry of Agriculture 2018), despite advances in yield success. Studies of Dioscorea species consumption in general in Fiji also show declines (Lako 2001).

The decline in cultivar richness we observed may be temporary, however. A study in Ethiopia found that sorghum *(Sorghum bicolor* (L.) Moench) landrace diversity in places most exposed to stress from drought or extreme heat or cold actually increased over 11 years (Teshome et al. 2016). It is possible that the cultivar richness in Fijian agroforests needs more time to recover as traditional knowledge keepers often maintain higher levels of intra- and intergenetic species diversity (Ticktin et al. 2018) which takes time to re-distribute. Accounting for scale and time is important in assessing resilience and more long-term cultivar richness and recovery. Further research on the decline of yam cultivation and cultivar richness is needed.

Nutrition and crop introductions

Assessing the resilience of any food system also includes consideration of nutritional quality. Cassava was recorded more frequently than any other starch crop across all the farms we visited, and while the number of cultivars 3-years post-cyclone had still not recovered to precyclone levels in more than half of the villages, the redundancy of cultivars was still high. The important role of cassava in Fiji has implications for human nutrition. An extremely versatile crop that can grow in many climate conditions and matures relatively quickly depending on the cultivar, cassava is now one of the most commonly grown and consumed starch crops in the South Pacific, replacing taro, yam, and sweet potato in cultivation (Aalbersberg and Limalevu 1991; but see Bourke 2005). However, cassava is also one of the least nutritious crops, with lower protein content than taro, yam, and sweet potato (Bradbury and Holloway 1988), and antinutrients that may inhibit nutrient absorption if overconsumed (Montagnac et al. 2009). Additionally, cassava contains relatively high concentrations of cyanogens and if not properly prepared, or in cases where it serves as the primary food source, the risk of cyanide toxicity and irreversible illness or death is high (Aalbersberg and Limalevu 1991; Burns et al. 2010). Of the farmers who participated in our interviews and who were actively replanting one-year postcyclone, 78.3% indicated they were replanting with cassava, whereas the percent of farmers who indicated they were replanting with taro, sweet potato, and/or yam was only 47.8%, 26.1%, and 8.7%, respectively. It is therefore critical to recognize that cassava does not provide true redundancy to the system in a nutritional sense. Agroforest food systems that maintain diverse starch crops as well as cultivars, of especially yam and sweet potato, can help sustain redundancy at the crop level while ensuring adequate access to nutritional diversity.

Variation in resilience across villages

The variation in measures of resilience across villages may be due to a number climatic, social, and economic factors. For example, Taveuni experiences an average yearly rainfall of 2696mm and maintains a relatively wetter microclimate than Nakorotubu and Kubulau. These conditions facilitate taro production and may explain the comparatively higher taro richness in the villages of Waitabu and Korovou. The Ministry of Agriculture also focuses their taro farming

programs for export in Taveuni, which may also contribute to increased cultivar richness. Suva experiences high average yearly rainfall as well, however, the villages in Suva are much closer to town and the lack of taro richness is likely due to a lower focus on farming as more individuals are employed in town, and therefore have a higher reliance on foods from the market. Intravillage network cohesion was high in villages in Wainikeli, Taveuni (Dacks et al. 2020), where we found resourcefulness was also often high, and thus we pose that stronger social networks may have helped facilitate cultivar richness recovery. In addition, villages in Nakorotubu, Kubulau, and Wainikeli were among the most damaged by the cyclone (Fig. 2.1), however those in Suva were comparatively unscathed. This may also explain why species/cultivar richness remained relatively static there. Finally, additional factors we did not measure could explain differences as well. For example, species and their production levels are influenced by soil conditions, but this data was not available. Similarly, the suite of species and cultivars farmers plant is often influenced by traditional knowledge, which is commonly higher in elders (Souto and Ticktin 2012), but we did not record the age of the farmers interviewed.

Future outlook

Despite changes in biodiversity and a historical decline in overall cultivar diversity for most crops across the Pacific (Lebot 1992; Lebot and Siméoni 2015; Masibalavu et al. 2002 (unpublished); Thaman 2014; Tisdell 2014), our research indicates that Fiji agroforest systems still provide important levels of food system resilience to extreme weather events, especially of energy-dense staple crops. However, even given their importance in disaster recovery, agroforests in the South Pacific remain under constant threat from agrodeforestation (Thaman 2014) and socioeconomic change catalyzing changes in land tenure and use (Nari 2000), and must be prioritized as a critical component of climate change adaptation measures and food security plans. Our research focused on measures of species and cultivar resilience, but information on productivity would provide further insight. Additional research on the resilience and nutritional content of cultivars, and the impact of access to these crops and cultivars on diet and human health would also improve our understanding of these complex food systems and the potential they have to not only provide food, but also nutritional security. Finally, in preparation for increases in climate change induced disturbances, this framework can be applied to other systems, to assess food system resilience and identify the ways it may be improved.

APPENDIX

Island	District	Villages	Number of agroforests re- surveyed (after 2014)	Number of farmer interviews conducted	Most common staple starch crops	Mean annual rainfall (mm)	Average distance to most frequented town (km)
Taveuni	Wainikeli	Waitabu Korovou	2017:10 2019:10	2017:10 2019:10	taro cassava	2696	34
Vanua Levu	Kubulau	Kiobo Natokalau Waisa	2017:15 2019:14	2017: 13 2019:11	taro cassava	2366	87
Viti Levu	Nakorotubu	Namarai Saioko Verevere	2017:14 2019:14	2017:13 2019:12	yam cassava	2263	88
Viti Levu	Suva	Kalokolevu Togalevu	2017:4 2019:10	2014:4 2019:9	cassava	3002	19

Table 2.1 The ten villages spanned across four districts on the three largest islands in Fiji. Since not all farmers were available for interviews, the number of interviews conducted is less than the number of agroforests. All respondents were men, age 18 years or older. The two most important root crops are the two root crops observed most often in those agroforests across the time of our study. Mean annual rainfall information was provided by the (Fiji Meteorological Service 2010, 2011, 2013a, b, 2015) and is based on the information collected at the nearest climatological station(s) across a range of years and where data was available. Information detailing the average time and distance to the most frequently village was obtained from Dacks et al. (2018).

Dacks R, Ticktin T, Jupiter SD, Friedlander A (2018) Drivers of fishing at the household scale in Fiji. Ecol Soc 23:37. https://doi.org/10.5751/ES-09989-230137

Fiji Meteorological Service (2015) Climatological Summary for Laucala Bay, Suva. Data available from https://www.met.gov.fj/"

Fiji Meteorological Service (2013a) Climatological Summary for Penang Mill. Data available from https://www.met.gov.fj/"

Fiji Meteorological Service (2013b) Climatological Summary for Matei Airfield, Fiji. Data available from https://www.met.gov.fj/"

Fiji Meteorological Service (2011) Climatological Summary for Savusavu Airfield. Data available from https://www.met.gov.fj/"

Fiji Meteorological Service (2010) Climatological Summary of Nabouwalu Fiji Islands. Data available from https://www.met.gov.fj/"

Starch Species (16)	Form	Fijian Name	English Adopted Name
Alocasia macrorrhizos	herbaceous	via	giant taro
Artocarpus altilis	tree	uto	breadfruit
Colocasia esculenta	herbaceous	dalo	taro
Cyrtosperma merkusii	herbaceous	via	swamp taro
Dioscorea alata	climber	uvi	yam
Dioscorea bulbifera	climber	kaile	air potato yam
Dioscorea cayennensis subsp. rotundata	climber	filipani; filipine	NA
Dioscorea esculenta	climber	kawai	lesser yam
Dioscorea nummularia	climber	tivoli	spiny yam
Dioscorea pentaphylla	climber	bulou	five-leaved yam
Ipomoea batatas	herbaceous	kumala	sweet potato
Manihot esculenta	herbaceous	tavioka	cassava
Musa AAB	herbaceous (tree-like)	vudi	plantain
Musa ABB	herbaceous (tree-like)	pata	NA
Tacca leontopetaloides	herbaceous	yabia	arrowroot
Xanthosoma sagittifolium	herbaceous	dalo ni tana	tannia

Table 2.2 List of all starch species and their common names in Fijian and English recorded in all villages across all three years. Note common names listed are not exhaustive for either the Fijian or English language.

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maleka dinafutunaloasarimaleka dina (black stripe variant)jamanilokalokavulamoalakadomatkalevumoalakadomatkalevumoanakasokasomelaiamunisukalekalekamerelesitanayavulokalokanabuaqau ev urauqaidavanew hebridesqiloarauvaniu kinigilosadropiqisamoasucuvanuasailosisikavidamutaniela balavusaravasikavidamutaniela balavusarava vulasikavidamutaniela lekalekasarava vulasolomonitaniela lekalekasarava vulatausalavalagisokobaletausalavalagisokobaletausalavalagivula onotausalavula vula tolu dromodromotoa vulavula tolu dromodromotoa vulavueti wainunuvula tolu dromodromotongavueti wainunuvula tolu dromodromotongavueti wainunuvula tolu dromodromotonga/dromovuraiwaiseitotkułavurai balavuvula tolu dromodromotonga/dromovurai balavuvula tolu dromodromotongavueti wainunuvula tolu dromodromotonga/dromovurai balavuvula tolu dromodromotonga/dromovurai balavu <td>jabeni</td> <td>damoni</td> <td>dravuni</td> <td>makusi</td>	jabeni	damoni	dravuni	makusi
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moanakasokasomelaiaImagemunisukalekalekamerelesitaImagenayavulokalokanabuaImageqameteniu madunaseaniImageqau ve urauqaidavanew hebridesImageqiloarauvaniu kiniImageqiloasadropiqiImagesalusalu ni samoasarirausamoasucuvanuasailosisikeci damutanielasaravasikeci damutaniela balavusarava dromodromosiswataniela lekalekasarava vulasolomonitaniela vimamaseserautausalavalagisokobaletausalavalagisokobaletausalavalagivula tolutoa vulavetiwa balavuvula tolutongavueti wainunuvula tolutongavueti wainunuvula tolutongavueti wainunuvula tolu dromodromotongavueti wainunuvula tolutongavueti wainunuvula tolutositosi-solomonivurai balavuvula tolutositosi-solomonivurai balavuvula tolutositosi-solomonivurai balavuvula tolutositosi-solomonivurai balavuvula tolutongavueti wainunuvula tolu dromodromotongavueti wainunuvula tolutositosi-solomonivurai balavuvula toluvavaiuorai balavuvula toluvavai <t< td=""><td>variant)</td><td>jamani</td><td>lokaloka</td><td>vula</td></t<>	variant)	jamani	lokaloka	vula
munisukalekalekamerelesitanayavulokalokanabuaqameteniu madunaseaniqau ve urauqaidavanew hebridesqiloarauvaniu kiniqiloasadropiqisalusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikavidamutaniela balavusarava dromodromosikavidamutaniela lekalekasarava vulasolomonitaniela vimamaseserautausala ni samoavavailano/tongatongatavaalavalagisokobaletavaalavalagitongatoa vulavala clubavuvula conotoa vulavokaivula tolutonga-dromovuraiwaiseitoklavurai balavuvula tolu dromodromotonga-dromovurai balavuvula tolutositosi-solomonivurai balavuvula conotonga-dromovuraiwaiseitokulavurai balavuvula tolu dromodromotositosi-solomonivurai balavutositosi-solomoni	moala	kado	matakalevu	
nayavulokalokanabuaqameteniu madunaseaniqau ve urauqaidavanew hebridesqiloarauvaniu kiniqilosadropiqisalusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokataveuniveiwa balavuvula onotongavueti wainunuvula tolu dromodromotongavueti wainunuvula tolu dromodromotongavueti wainunuvula colutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavuvula tolu dromodromovavaivurai balavuvula tolu dromodromovavaivurai balavuvula tolu dromodromovavaivurai balavuvula tolu dromodromo	moana	kasokaso	melaia	
qameteniu madunaseaniqau ve urauqaidavanew hebridesqiloarauvaniu kiniqilosadropiqisalusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokataveunivalagisokobaletaveuniveiwa balavuvula onotoa vulavula tolutoa vulavula tolutongavueti wainunutongavueti wainunutongavueti wainunutonga-dromovuraitositosi-solomonivurai balavuvavaiuro ni vonuvavaiuro ni vonuvavai loaloavurai balavuvavai loaloa<	munisuka	lekaleka	merelesita	
qau ve urauqaidavanew hebridesqiloarauvaniu kiniqiloasadropiqisalusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokatausala ni samoavawailano/tongatongatongavueti wainunuvula tolutongavueti wainunuvula tolutongavueti wainunuvula tolutonga-dromovuraiwaiseitongavurai balavusieitongavurai balavuvula tolu dromodromotonga-dromovuraiwaiseitoxitosi-solomonivurai balavuvula toluvavaivurai balavuvula toluvavaivurai balavuvula toluvavai loaloavurai balavuvula tolu	nayavu	lokaloka	nabua	
qiloarauvaniu kiniqilosadropiqisalusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokatausalavalagisokobaletaveuniveiwa balavuvula onotongavueti wainunuvula tolutongavueti wainunuvula tolutongavueti wainunuvula tolu dromodromotongavuraiwaiseitokulavurai balavuvula tolu dromodromotostosi-solomonivurai balavuvula tolu dromodromotostosi-solomonivurai balavuvula tolu dromodromovavaivurai balavuvula tolu dromodromovavaivurai balavuvurai balavu	qamete	niu madu	naseani	
qilosadropiqisalusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokatausala ni samoavakajisokobaletaveuniveiwa balavuvula onotongavueti wainunuvula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavuvula tolu dromodromotositosi-solomonivurai balavuvula tolu dromodromovavaivurai balavuvula toluvavaivariasiseivavai loaloavurai lekalekasisei	qau ve urau	qaidava	new hebrides	
salusalu ni samoasarirausamoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokatausala ni samoavawailano/tongatongatongavueti wainunuvula onotongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavuwaiseitokulavurai balavusolovavaionuinternetvavailoaloainternetvavailoaloainternetvavailoaloainternetvavai loaloainternetinternetvavai loaloainternetinternevavai loaloain	qiloa	rauva	niu kini	
samoasucuvanuasailosisikavidamutanielasaravasikeci damutaniela balavusarava dromodromosisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokatausalavalagisokobaletaveuniveiwa balavuvula onotoga dromovueti wainunuvula tolutongavueti wainunuvula tolutonga dromovuraiwaiseitokulavurai balavuvula tolu dromodromotositosi-solomonivurai lekalekauro ni vonuvavaioni vonuinterfectionalvavai loaloainterfectionalinterfectionalvavai loaloaoneinterfectionalvavai loaloainterfectionalinterfectionalvavai loaloainterfectionalinterfectional <td>qilo</td> <td>sadro</td> <td>piqi</td> <td></td>	qilo	sadro	piqi	
sikavidamu taniela sarava sarava sarava taniela balavu sarava dromodromo sisiwa taniela balavu sarava vula sarava vula solomoni taniela vimama seserau tania soulo uvai sigatoka valagi sokobale vawailano/tonga tonga vawailano/tonga tonga sokobale vawailano/tonga tonga vueti wainunu vula ono vula vula vula vula tolu dromodromo vurai vai sigai vueti wainunu vula tolu dromodromo tonga vueti wainunu vula tolu dromodromo vurai balavu vula tolu dromodromo vurai balavu vula tolu dromodromo vurai vurai balavu saisei vueti kaleka vurai balavu vuai solomoni vurai lekaleka sei sokobale tositosi-solomoni vurai lekaleka sei sokobale vueti vainunu vuai tonga vueti kaleka vurai balavu vuai vuai balavu suai ba	salusalu ni samoa	sari	rau	
sikeci damu taniela balavu sarava dromodromo sisiwa taniela lekaleka sarava vula solomoni taniela vimama seserau tamai soulo uvai sigatoka tausala valagi sokobale tausala ni samoa vawailano/tonga tonga taveuni veiwa balavu vula ono toa vula vokai vula tolu tonga vueti wainunu vula tolu dromodromo tonga-dromo vurai waisei tokula vurai balavu suisei tokula vurai balavu suisei tositosi-solomoni vurai lekaleka	samoa	sucuvanua	sailosi	
sisiwataniela lekalekasarava vulasolomonitaniela vimamaseserautamai soulouvaisigatokatausalavalagisokobaletausala ni samoavawailano/tongatongataveuniveiwa balavuvula onotoa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitositosi-solomonivurai lekalekauro ni vonuvavaivavai loaloa	sikavidamu	taniela	sarava	
solomonitaniela vimamaseserautamai soulouvaisigatokatausalavalagisokobaletausala ni samoavawailano/tongatongataveuniveiwa balavuvula onotoa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitositosi-solomonivurai lekalekauro ni vonuvavaivavai loaloa	sikeci damu	taniela balavu	sarava dromodromo	
tamai soulouvaisigatokatausalavalagisokobaletausala ni samoavawailano/tongatongataveuniveiwa balavuvula onotoa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavutositosi-solomonivurai lekalekauro ni vonuImage: Constant of totagevavai loaloaImage: Constant of totage	sisiwa	taniela lekaleka	sarava vula	
tausalavalagisokobaletausala ni samoavawailano/tongatongataveuniveiwa balavuvula onotoa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavuurai balavutositosi-solomonivurai lekalekauro ni vonuvavai	solomoni	taniela vimama	seserau	
tausala ni samoavawailano/tongatongataveuniveiwa balavuvula onotoa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavaivavai loaloa	tamai soulo	uvai	sigatoka	
taveuniveiwa balavuvula onotoa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavai	tausala	valagi	sokobale	
toa vulavokaivula tolutongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavaivavai	tausala ni samoa	vawailano/tonga	tonga	
tongavueti wainunuvula tolu dromodromotonga-dromovuraiwaiseitokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavaivavai loaloa	taveuni	veiwa balavu	vula ono	
tonga-dromovuraiwaiseitokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavaiuota lekalekauota lekaleka <td>toa vula</td> <td>vokai</td> <td>vula tolu</td> <td></td>	toa vula	vokai	vula tolu	
tokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavaivavai loaloa	tonga	vueti wainunu	vula tolu dromodromo	
tokulavurai balavutositosi-solomonivurai lekalekauro ni vonuvavaivavai loaloa	tonga-dromo	vurai	waisei	
uro ni vonu vavai vavai loaloa I I I I I I I I I I I I I I I I I I I		vurai balavu		
vavai vavai loaloa	tositosi-solomoni	vurai lekaleka		
vavai vavai loaloa	uro ni vonu			
vavai loaloa				
vavai tositosi	vavai loaloa			
	vavai tositosi			

 Table 2.3 List of all cultivar names recorded in all villages across all three years.

Crop	Year	Mean ± SE number observed per village	Range	
Stansh as	2014	7.00 ± 0.54	5-9	
Starches (16)	2017	9.11 ± 0.90	6-13	
(10)	2019	9.80 ± 0.79	5-13	
	2014	5.70 ± 0.42	4-8	
M. esculenta	2017	5.22 ± 0.85	1-10	
	2019	4.50 ± 0.62	2-8	
	2014	5.00 ± 1.11	0-13	
C. esculenta	2017	3.44 ± 1.30	0-9	
	2019	4.60 ± 0.92	0-10	
	2014	0.40 ± 0.16	0-1	
I. batatas	2017	1.78 ± 0.64	0-6	
	2019	1.00 ± 0.30	0-3	
	2014	3.30 ± 1.92	0-18	
D. alata	2017	2.33 ± 1.40	0-13	
	2019	2.20 ± 0.85	0-7	

Table 2.4 Mean number of starch crop species and cultivars of the four primary root cropsobserved per village. Totals exclude data from Togalevu.

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CHAPTER 3. PREDICTORS OF TREE DAMAGE AND SURVIVAL IN AGROFORESTS AFTER MAJOR CYCLONE DISTURBANCE IN THE PACIFIC

ABSTRACT

Many studies relate the impact of agroforestry to the ability of human communities to recover following extreme weather disturbances. Tree richness and density on farms is also a good indicator of crop richness and dietary diversity important to food security post-disturbance. Understanding the dynamics of tree damage and survival in these ecosystems is critically important, however, understudied. Here we assess the relationship of individual and speciesspecific traits, and management type, to damage and survival of trees in agroforests and discuss the resistance and resilient qualities of trees and management actions in these systems. We find that agroforests in Fiji experienced low stem mortality post-cyclone and that survival was not linked to damage severity. We also determine that agroforest management type, and the associated survival of tree stems in planted, fallow, and forested areas was not significantly different. This is an important finding as it suggests agroforest systems may be highly resilient to extreme disturbances, despite some of the landscape level changes that may make them highly vulnerable to damage (i.e. edge effects, altered species composition and structure). Conversely, we posit such structural and compositional differences may have actually conferred them greater resilience. Additionally, we show that some of the species with the highest wood density, which we found to be positively related to survival, were also of native trees, further underlining their importance to native species conservation.

INTRODUCTION

Global cyclone events

Climate change has induced changes in storm intensity, frequency, and geographic occurrence; spurred sea-level rise and ocean acidification; and altered patterns of precipitation, temperature, and seasonality (IPCC 2021). While the number of cyclone storm events globally are projected to remain constant or even decrease, the proportion of cyclones of greatest intensity (Categories 4-5 Saffir Simpson scale) is expected to increase, with peak windspeeds of those cyclones also rising (IPCC 2021). Additionally, region-specific changes project a northward shifting latitude of peak wind intensity for western North Pacific cyclones (Feng et al. 2021), as well as increased windspeeds for Southern Hemisphere extratropical cyclones (IPCC 2021), effectively increasing the geographical range of more intense cyclones. Despite data limitations detailing past cyclone events, it is likely that the proportion of major (Category 3-5) cyclone events has been increasing over the past forty years (IPCC 2021). Tree-based studies of growth rings indicate cyclone events were less frequent in the past than today and also provide evidence suggesting recent poleward expansion in cyclone occurrence is new (Altman et al. 2018). However, while the social and economic repercussions of these storms have been well documented across the globe, the ecological impacts remain comparatively incomplete, necessitating concerted research efforts (Pruitt et al. 2019).

Cyclones in the Pacific

Furthermore, of studies conducted, the majority have focused on Atlantic and Caribbean systems leaving a severe lack of research concerning Pacific cyclones and their ecological and social impacts (Marler 2014, 2015; Monoy et al. 2016; Lin et al. 2020). The applicability of Atlantic and Caribbean-based socioeconomic and ecological studies to understanding Pacific Island systems' damage and recovery dynamics is inapt for multiple reasons, notably their geographic insularity, socioeconomic and cultural differences, and cyclone incidents rates (Marler 2014, 2015). Additionally, cyclone events in the Pacific region have exhibited unprecedented behavior (trajectory, velocity, geographic occurrence) in recent years, and emphasized the need to better understand their dynamics (Magee et al. 2016) and ecological impacts (Asbridge et al. 2018). Research particularly highlights the unusual magnitude and behavior of sequential South Pacific catogory-5 cyclones Pam in Vanuatu (2015) (Magee et al.

2016) and Winston in Fiji (2016) (Sharma et al. 2021); Winston surpassing Pam as the strongest cyclone on record in the South Pacific (WMO 2016; Terry and Lau 2018). The extreme magnitude of these cyclones has raised questions as to if a Category-6 cyclone intensity classification should be added (WMO 2016). In 2018, these events were followed by the highest frequency of occurrence records for cyclones in the western North Pacific since the 1980s (Basconcillo et al. 2021).

Pacific cyclones and forest ecological studies

Ecologically, cyclones play key roles in shaping the structure and composition of forests (Harrington et al. 1997; Lugo 2008; Keppel et al. 2010; McGroddy et al. 2013; Lin et al. 2020). Of the forest-related cyclone (also called typhoons and hurricanes depending on geography (Kerr 2000)), studies conducted comparatively few have assessed forest damage and recovery in the Southwest Pacific Islands (Lin et al. 2020). Of these studies, all have been conducted following cyclones of category-4 magnitude or lower (c.f Elmqvist et al. 1994; Franklin et al. 2004; Goulding et al. 2016 but see Webb et al. 2014), or for cyclones that have only indirectly impacted sites (Burslem et al. 2000; Webb et al. 2011). Indeed, the first cyclone impact assessment in Pacific Island forests east of the Solomon Islands with established longitudinal data took place after cyclone Waka in Vava'u, Tonga by Franklin and colleagues in 2001 (Franklin et al. 2004). Importantly, there appears to be some variation among damages trees sustained, their predictive circumstances and traits, and the recovery dynamics both between and within forests in the Pacific, and other Ocean basins.

Generally, the major damages sustained by trees during a cyclone include defoliation, branch and crown/stem snapping, and tree uprooting (Burslem et al. 2000; Imbert and Portecop 2008; McGroddy et al. 2013; Webb et al. 2014). However, the factors that determine tree resistance to damage are inconsistent across storms and locations (McGroddy et al. 2013; Webb et al. 2014). Some of these factors include wood density, growth rate, and tree architecture, which includes diameter at breast height (dbh), tree height, and canopy characteristics such as canopy cover and bole height (Webb et al. 2014). Of major cyclones (Category 4 & 5), wood density has been shown to be negatively correlated with all damage types in the Pacific Islands (Webb et al. 2014), however, in the North Atlantic (Uriarte et al. 2019) and Australia (Metcalfe et al. 2008), damage was unrelated to wood density. Windspeed (Imbert and Portecop 2008) and topography (Tanner and Rodriguez-Sanchez 2014) is also known to be an important determinant of damage in the Caribbean, whereas in the Pacific, the impact of topography to damage is less consistent (Burslem and Whitmore 1999; Burslem et al. 2000; Webb et al. 2011).

The recovery of forest structure after cyclones proceeds through resprouting, recruitment, and the emergence of understory seedlings and saplings (Burslem and Whitmore 1999; Burslem et al. 2000) although this process may be slower for Pacific Island systems than in the Caribbean (Elmqvist et al. 1994). Relatedly, while canopy cover and light availability have been found to impact understory seedling and sapling emergence in Puerto Rico's island systems (Zimmerman et al. 2014), studies in the Solomon Islands did not find this effect to be substantial (Katovai et al. 2012). El Niño Southern Oscillation can also intensify cyclone activity in the Pacific and, during El Niño periods, this may create drought-like conditions in islands in the southwest Pacific, including Fiji (Murphy et al. 2014). This can exacerbate the effects of cyclones on communities, and push cyclogenesis eastwards in the South Pacific (Terry and Etienne 2010).

Cyclones and agroforest studies

Cyclones also have a dramatic impact on the human communities that rely on forestbased ecosystems (McSweeney and Coomes 2011; Lazos-Chavero et al. 2018). Agroforestry is a forest-based agroecological system whereby crops and understory plants are cultivated with overstory trees and shrubs of food and non-food value (Kumar and Nair 2004). In the Pacific, agroforestry has been a part of a larger social-ecological system that provided diverse food, medicinal, building, and other resources to communities for centuries enabling resilience to disturbance (McMillen et al. 2014; Thaman 2014b). Although it is changing with socioeconomic and environmental change, agroforestry remains important to food system resilience in Fiji (McGuigan et al. 2022). While damage to agroecological systems was extensive and severe in Fiji immediately post-cyclone (Government of Fiji 2016), trees in these agroforest systems are often actively managed and pruned or pollarded (Thaman 2008). This decreased stature may reduce the magnitude and distribution of cyclone wind damage to trees (Gilman et al. 2008; McGroddy et al. 2013).

Very few studies have assessed the impact of cyclones on agroforests and the damage and recovery dynamics of associated trees. A few studies show varying effects of trees on agricultural lands to damage resistance and recovery (Holt-Giménez 2002; Uriarte et al. 2004;

Philpott et al. 2008; Lazos-Chavero et al. 2018). Two studies have incidentally assessed the effects of cyclones on abandoned agroforest areas in the Pacific Islands. Webb and colleagues (2014) studied this using a 20-year-old abandoned agroforest site in their forest damage assessment after a category-5 cyclone passed within 28km of their plots in Samoa. Webb et al. 2014 is also one of the few Pacific Island studies to assess forest damage following a category-5 cyclone. They found that survival was dependent on the type of damage sustained, which was variable by species. They also found that higher wood density may allow for greater resistance to wind damage but did not always confer greater survival. An additional study by Franklin (2007) also assessed the impact of various disturbances - including cyclones to 30-40 year-old abandoned agroforest areas in Tonga - on species composition. To our knowledge, no studies have examined what types of damage trees sustain in active agroforests in the Pacific Islands or their survival rates.

Studies outside the Pacific Islands have shown that forests with a history of prior productivity-focused land-use may resist and recover from cyclone damage more effectively (Philpott et al. 2008; Lazos-Chavero et al. 2018). This may proceed through a legacy of purposefully planted nitrogen-fixing trees facilitating higher recovery productivity (Beard et al. 2005), human use effectuated tree architecture modifications, like reduced height, allowing for resistance to wind damage (McGroddy et al. 2013), or long-term effects like soil stabilization from deep-rooted trees protecting against cyclone induced landslides (Perotto-Baldiviezo et al. 2004).

As cyclone frequency, intensity, and geographic occurrence patterns change in the Pacific, trending towards more frequent intense cyclones (IPCC 2021), the need to understand how trees in agroforest systems experience and recover from cyclone damage becomes great and warrants further assessment.

We studied the immediate impacts of cyclone Winston on stem survival and damage in agroforests in Fiji. We tested three hypotheses related to predictors of stem survival and stem damage. We hypothesized that survival would increase with increasing tree size (dbh) and wood density, and in actively managed agroforest plot types (planted and fallow). Second, we hypothesized that survival would decrease with increasing severity of stem damage. Last, we hypothesized that the severity of damage sustained would increase with tree size (dbh) and wood density, and in non-actively managed agroforest plot types (forest).

METHODS

Study Site and context

Fiji is archipelago of over 300 islands, most inhabited, in the Near Oceania region of the South Pacific. The most recent census shows Fiji's population to be 884,887; 55.9% residing in urban areas, while the remaining 44.1% reside in rural areas (Fiji Bureau of Statistics 2018). Agroforests were historically part of a larger land-sea based social-ecological system that met communities' food, medicinal, social, infrastructural, and other subsistence needs, either directly or through trade with other communities (McMillen et al. 2014; Thaman 2014a). Global change has influenced agroforestry management practices and their general composition (Thaman 2008; Shah et al. 2018), but they remain an important source of food and other resources (McGuigan et al. 2022).

Similar to other agroforests in the Asia-Pacific region (Shin et al. 2020), and more specifically, the Pacific Islands (Clarke and Thaman 1993a), agroforests in Fiji are shifting mosaics of forested, fallow, and planted areas (Clarke and Thaman 1993b; Ticktin et al. 2018; McGuigan et al. 2022). Trees are present at all times across these areas; however, their composition and stand density varies (Thaman 2008). Rotation between fallows and planted areas is most common, though fallows may also succeed into secondary forests and forested areas may be transformed into planted areas in response to environmental and socioeconomic changes and disturbances (Clarke and Thaman 1993a). When forested areas are selectively cleared for planting, farmers deliberately retain certain trees that are important culturally and/or ecologically (Thaman 2008; Shah et al. 2018), and often prune or pollard them to increase light availability, return organic material to the soil, or provide structural support for climbing crops (Clarke and Thaman 1993b). At the same time, trees that enhance agroforest production are also purposefully planted (Thaman 2008; Shah et al. 2018).

Cyclone Winston

On February 20th, 2016, Cyclone Winston became the first cyclone in recorded history to make landfall in Fiji as a category-5 storm (WMO 2016). It sustained an average 10 minute windspeed of 160 knots (296.32 km/h) and gusts of up to 210 knots (388.92 km/h) (WMO 2016), and exhibited erratic track behavior (Terry and Lau 2018; Sharma et al. 2021). Winston originated East of Vanuatu and initially traveled southeast, eventually shifting northeastward

crossing Ono-i-lau, the southernmost Fiji islands, as a Category-2 cyclone on February 15th (WMO 2016). After crossing into Tonga, Winston turned back westward gaining intensity and entered the Northern Lau group on February 20th as a Category-5 cyclone (WMO 2016). It continued its westward projection as it crossed the three largest islands of Fiji - Viti Levu, Vanua Levu, and Taveuni - exiting Fiji on the 21st (WMO 2016). It is estimated to have destroyed 30,369 homes, affected 540,400 people, and 44 fatalities were reported (Government of Fiji 2016; Nakamura and Kanemasu 2020).

Agroforest damage and survival surveys

Between January and March of 2017, we worked with farmers in six coastal villages in three districts on the three largest islands in Fiji - Viti Levu, Vanua Levu, and Taveuni - to establish twenty-two semi-permanent 5x20m plots in forest, fallow, and planted agroforest areas. Villages were all located within 40km of the estimated center of Cyclone Winston's path (Esri 2016) and all agroforest sites were within one hour's walk from the village, between 0.25 to 5.00 ha in size, and below 100 m elevation. Agroforests within these specifications are primarily subsistence farms and not used for commercial purposes (Ticktin et al. 2018). Based on access and availability, three plots were established in planting areas, thirteen in fallow areas, and six in forest areas of the agroforests. In each plot, the stems of every woody tree greater than 2cm diameter at 1.4 m height from the base (dbh) were mapped, recorded to species, measured for dbh, and observed for damages sustained and survival (stem information was still recorded even if they did not survive the cyclone). We recorded 16 stems of 6 species in planted plots, 68 stems of 13 species in fallow plots, and 50 stems of 15 species with 1 unidentifiable species in forest plots. Planted and fallow plots were grouped as actively managed plots and forest plots were categorized as unmanaged.

We assessed stem damage based on in-field observations (2017) and farmers' observations immediately post cyclone (2016). Damage types, in ascending level of severity, included none, defoliation, branch snapping, crown snapping, and uprooting. Only two trees were uprooted and were then removed during data analysis. Farmers' observations mostly detailed the level of defoliation and branch snapping each stem sustained, and confirmed mortality from cyclone disturbance where stems were already dead. We returned to these sites two years later (2019) and again recorded stem survival. In some cases, stems had been

purposely cut by the farmer because the cyclone damages it had sustained were so great that the tree was slowly senescing and the remaining individual was no longer beneficial and productive for the farmers' agroforest. We considered this a cyclone-related mortality and recorded it as such. In other cases, farmers had cleared otherwise healthy trees as part of their agroforestry management practices and we considered this a non-cyclone-related fatality and did not record it as a mortality for the purposes of this study. During these visits we also recorded stem DBH and later collected wood density data from the TRY database (Kattge et al. 2020) Where wood density information was incomplete, we used the mean of the genera. We also calculated stand density (number of stems per plot).

Stem survival and damage models

We developed generalized linear mixed models (GLMMs) to assess 1) the effect of individual and species level traits and management type on stem survival (Table 3.1); and 2) the effect of damage type sustained on stem survival (Table 3.2). For the survival models we used the package 'glmmTMB' (version 1.1.2.3) (Brooks et al. 2017) to create binomial GLMMs. For the damage sustained model, we used an multivariate generalized linear mixed model (MCMCglmm) using package 'MCMCglmm' (version 2.33) (Hadfield 2010) and created ordinal models (Table 3.3). Model variables were examined for homogeneity of variance and multicollinearity. Multi-stemmed trees can snap or experience damage independently of each other (Webb et al. 2014) and trees located within a plot may not be independent. To account for possible non-independence of multi-stemmed trees we also included individual tree nested within individual plots as a random effect within our models. We started with full models and removed terms sequentially and then compared Akaike's Information Criterion (AICc) to determine the best supported model.

RESULTS

Across all sites and plots, 58.2% of tree stems suffered some type of damage, either defoliation, branch or crown snapping, or uprooting. Overall, 50% of stems experiences defoliation, 29.9% had branch snapping, 27.6% had crown snapping, and 1.5% (2 trees) were uprooted (Fig 3.1.). While nearly 45% of stems sustained damage of branch snapping of more severe, stem mortality was relatively low (12.2%).

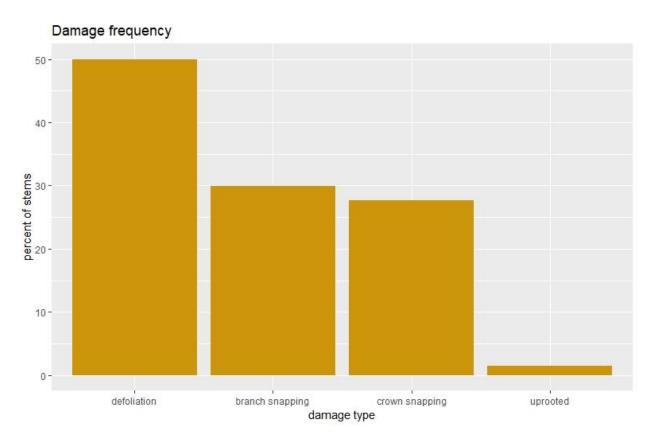


Figure 3.1: Overall rate of damage to individual stems by damage type.

Stem survival increased with increased wood density (Fig. 3.2). No other predictors were in the best fit model (Table 3.1). When we assessed the relationship between survival and damage type sustained, we found no significant differences in survival across damage types, although survival did decrease with the severity of damage sustained (Fig. 3.3, Table 3.2). Severity of stem damage increased with increasing dbh. No other predictors of damage severity were in the best fit model (Fig 3.4, Table 3.3).

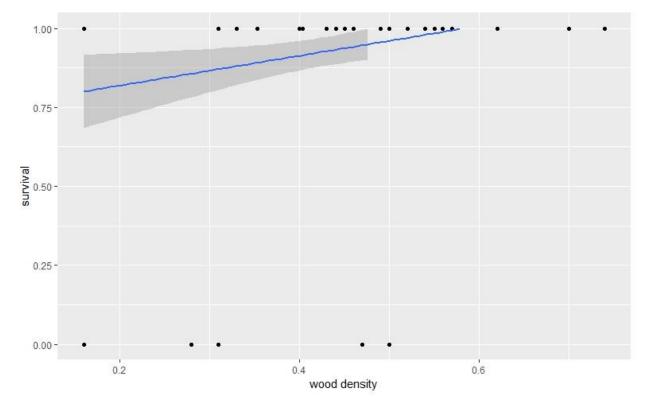


Figure 3.2: Relationship between wood density and survival.

Survi	val Base N	Iodel	1	SBM-1		5	SBM-2		5	SBM-3	
Estimate	std. Error	р	Estimate	std. Error	р	Estimate	std. Error	р	Estimate	std. Error	р
9.54	5.84	0.102	9.64	5.78	0.095	10.40	5.03	0.039	10.44	5.03	0.038
5.95	12.97	0.646	5.59	12.55	0.656	6.13	12.54	0.625	4.52	10.99	0.681
-0.03	0.07	0.629	-0.02	0.06	0.704	-0.02	0.06	0.699			
6.57	86.72	0.940	18.58	82.70	0.822						
13.40	1767.10	0.994									
91 unique_tree		91 unique_tree		91 _{uniqu}	91 unique_tree			91 unique_tree			
21 unique_plot		21 unique_plot		21 _{uniqu}	21 unique_plot		21 unique_plot				
124		124	124		124			124			
48.916		46.883		44.729			42.674				
-	<i>Estimate</i> 9.54 5.95 -0.03 6.57 13.40 91 _{uniqu} 21 _{uniqu} 124	Estimate std. Error 9.54 5.84 5.95 12.97 -0.03 0.07 6.57 86.72 13.40 1767.10 91 unique_tree 21 unique_plot 124	9.54 5.84 0.102 5.95 12.97 0.646 -0.03 0.07 0.629 6.57 86.72 0.940 13.40 1767.10 0.994 91 unique_tree 21 unique_plot 124	Estimate std. Error p Estimate 9.54 5.84 0.102 9.64 5.95 12.97 0.646 5.59 -0.03 0.07 0.629 -0.02 6.57 86.72 0.940 18.58 13.40 1767.10 0.994 91 unique 91 unique_pto 91 unique 124 124	Estimate std. Error p Estimate std. Error 9.54 5.84 0.102 9.64 5.78 5.95 12.97 0.646 5.59 12.55 -0.03 0.07 0.629 -0.02 0.06 6.57 86.72 0.940 18.58 82.70 13.40 1767.10 0.994 - - 91 unique_tree 91 unique_tree 21 unique_plot 21 unique_plot 124 124 124	Estimate std. Error p Estimate $\frac{std.}{Error}$ p 9.54 5.84 0.102 9.64 5.78 0.095 5.95 12.97 0.646 5.59 12.55 0.656 -0.03 0.07 0.629 -0.02 0.06 0.704 6.57 86.72 0.940 18.58 82.70 0.822 13.40 1767.10 0.994	Estimate std. Error p Estimate std. Error p Estimate 9.54 5.84 0.102 9.64 5.78 0.095 10.40 5.95 12.97 0.646 5.59 12.55 0.656 6.13 -0.03 0.07 0.629 -0.02 0.06 0.704 -0.02 6.57 86.72 0.940 18.58 82.70 0.822 - 13.40 1767.10 0.994 - 91 unique_tree 91 unique_tree 91 unique_tree 91 unique_tree 124 124 124 124 124	Estimate std. Error p Estimate std. Error p Estimate std. Error 9.54 5.84 0.102 9.64 5.78 0.095 10.40 5.03 5.95 12.97 0.646 5.59 12.55 0.656 6.13 12.54 -0.03 0.07 0.629 -0.02 0.06 0.704 -0.02 0.06 6.57 86.72 0.940 18.58 82.70 0.822 - - 91 unique_tree 91 unique_tree 91 unique_tree 91 unique_tree 91 unique_tree 21 unique_plot 124 124	Estimate std. Error p Estimate $\frac{std.}{Error}$ p Estimate $\frac{std.}{Error}$ p 9.54 5.84 0.102 9.64 5.78 0.095 10.40 5.03 0.039 5.95 12.97 0.646 5.59 12.55 0.656 6.13 12.54 0.625 -0.03 0.07 0.629 -0.02 0.06 0.704 -0.02 0.06 0.699 6.57 86.72 0.940 18.58 82.70 0.822 - 0.625 - - 0.625 - - - 0.629 - 0.620 - 0.822 -	Estimate std. Error p Estimate $\frac{std.}{Error}$ p Estimate $\frac{std.}{Error}$ p Estimate 9.54 5.84 0.102 9.64 5.78 0.095 10.40 5.03 0.039 10.44 5.95 12.97 0.646 5.59 12.55 0.656 6.13 12.54 0.625 4.52 -0.03 0.07 0.629 -0.02 0.06 0.704 -0.02 0.06 0.699 6.57 86.72 0.940 18.58 82.70 0.822 - - 91 unique_tree 124 124 124 124	Estimate std. Error p Estimate std. Error estimate std. Error estimate std. Error estimate std. Error estimate std. Error estimat

Table 3.1: Table of model predictors and reduction process for the relationship between survival and individual and species traits, and plot management type. The best fit model was SBM-3.

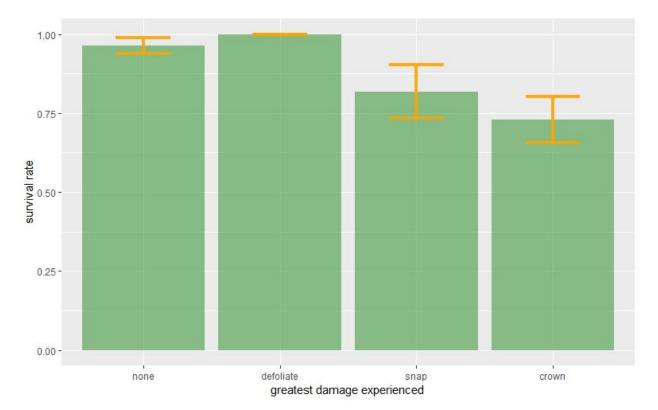


Figure 3.3: Survival by damage type sustained per stem. Uprooting is not included.

Predictors	Estimate	std. Error	р
(intercept)	13.29	4.24	0.002
defoliation	14.79	757.67	0.984
branch snapping	-1.23	4.17	0.767
crown snapping	4.67	7.57	0.537
N unique_tree	98		
N _{unique_plot}	21		
Observations	132		
AIC	62.831		

Table 3.2: Table of the relationship of survival to damage type sustained. There were no significant relationships.

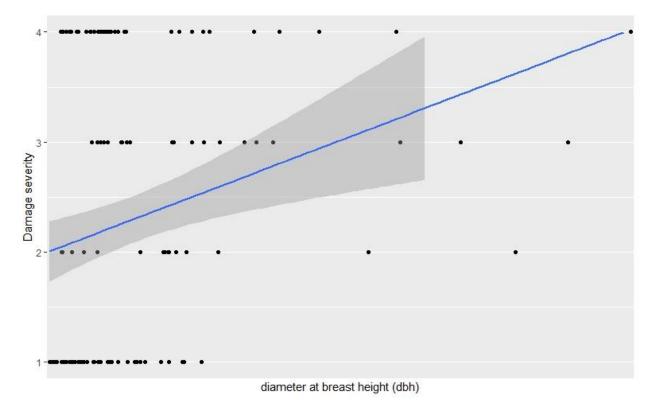


Figure 3.4: Relationship between diameter at breast height (dbh) and increasing severity of damage sustained. Severity level 1 is no damage, 2 is defoliation, 3 is branch snapping, and 4 is crown snapping. Uprooting is not included.

	Damage Type Base Model		DTBM-1		DTB	M-2	DTBM-3	
Predictors	post.mean p MCMC		post.mean	р МСМС	post.mean	р МСМС	post.mean	р МСМС
(Intercept)	1.006958	0.606	1.86268	0.438	0.11584	0.812	4.0676	0.748
dbh	0.017609	0.1	0.02792	0.238	0.00288	0.174	0.3576	0.11
plot type [forest]	1.445826	0.362	3.06672	0.334	1.287889	0.114		
stand density	-14.35511	0.552	-41.60538	0.39				
wood density	-1.002254	0.786						
AICc		145.42		107.06		186.07		19.81

Table 3.3: Table of model predictors and reduction process for the relationship between severity of damage type sustained and individual and species traits, and plot management type. The best fit model was DTBM-3.

In the unmanaged plots, all of the stems that did not survive were found in a single plot and of the same species, *Storckiella vitiensis* Seem. Additionally, all these trees experienced defoliation, or branch or crown snapping, and some experienced all three. In the managed plots, the stems

that did not survive varied in species identity and damage type sustained, including none, and all but one were of singular-stemmed trees. Although the two uprooted trees were removed from these analyses because of the small sample size, both were *Cocos nucifera* L. from two separate locations, and existing in different management plot types.

DISCUSSION

Cyclones play key roles in shaping the structure and composition of forests (Harrington et al. 1997; Lugo 2008; Keppel et al. 2010; McGroddy et al. 2013), and the dynamics of the human communities that rely on them (McSweeney and Coomes 2011; Lazos-Chavero et al. 2018). Cyclone Winston was the strongest cyclone in recorded history in the South Pacific (WMO 2016) and caused catastrophic damage ecologically, economically, and societally (Government of Fiji 2016). Cyclones of extreme intensity are expected to increase in frequency with climate change (IPCC 2021) and threatens multiple facets of human communities, including food security. Very little is known about how cyclones impact agroforestry across regions (Philpott et al. 2008) despite 25-33% of the world population relying on these systems (FAO and UNEP 2020; UN 2021). Agroforestry in Fiji has been shown to support important food system resilience to cyclone disturbance when assessed at the understory crop level (McGuigan et al. 2022), however how cyclones directly damage trees, and what individual, species, and landscape level traits may account for damage resistance and survival, is significantly understudied. Our results suggest that agroforests are highly resistant to cyclone damage: despite the fact that nearly half of stems experienced severe damage we found very low rates of mortality. This is similar to results found by Webb et al. (2014) after a category-5 cyclone in Samoa, as well as in Mexico where low mortality post-cyclone has also been observed (McGroddy et al. 2013). This is especially important in the context of food system resilience in Fiji where agroforests are heavily relied upon for daily subsistence needs. This research provides important base-line data about impacts of cyclones to trees in agroforest-based food systems with implications for socialecological resilience.

Wood density is positively associated with survival

We found that species with higher wood density had higher stem survival in our agroforest sites. Although wood density has been found to have varying effects on stem survival

across locations and storms (Lin et al. 2011), very few studies have assessed the relationship of wood density to stem survival in the Pacific Islands. Of the studies conducted, contrasting results were observed. In American Samoa a positive relationship was observed, though only significant in one study, between wood density and survival after cyclone disturbance (Webb et al. 2011, 2014b). In cyclone damaged forests in the Solomon Islands, this relationship was less clear (Burslem et al. 2000). Although untested statistically, Burslem et al. (2000) observed that the tree species with the second highest wood density suffered the greatest mortality. In an additional study in the Solomon Islands, Burslem and Whitmore (1999) found that the least cyclone disturbed forest was dominated by high wood density trees.

Our results have important implications for the composition of agroforests post-cyclone as these disturbance events also influence the overall wood density, and thus species in the community (Lin et al. 2020). In Australia, post-cyclone communities were found to be composed primarily of more dense species as they resist damage more effectively (Read et al. 2011), though less dense and faster growing species (pioneer species) may be present in greater stem densities in disturbed forests initially due to their ability to resprout more quickly (Curran et al. 2008). The species with greatest wood density in our study included Leucaena leucocephala (Lam.) de Wit, Bischofia javanica Blume, and Citrus limon (L.) Osbeck in managed plots, and Intsia bijuga (Colebr.) Kuntze, Premna serratifolia (L.), and Pittosporum arborescens Rich ex A. Gray in unmanaged plots. Notably, all these species except L. leucocephala and C. limon are native to Fiji and all survived the cyclone. Although agroforest species composition is heavily influenced by human activity as compared to native forests, the impacts of cyclones on trees is still likely to affect long-term species composition. As such, these native species may then be selected for and resultant communities may continue to host important native biodiversity, further highlighting the importance of agroforests to conservation in Fiji (Ticktin et al. 2018). Human activity and farmers' management decisions also heavily determine agroforest species composition, but as famers desire plant species more resilient to disturbance (McGuigan et al. 2022), this may also positively influence species composition towards higher wood density native flora such as these. Furthermore, given predicted decreases in overall cyclone frequency, this may also allow for slower growing dense trees to re-establish their populations more effectively, despite cyclone intensity increasing (IPCC 2021).

Relationship of damage severity to survival

We found no relationship between the type of damage sustained and stem survival, meaning the likelihood of survival did not significantly differ between stems that experienced no damage, defoliation, branch snapping, or crown snapping. This contrasts with other studies in the Pacific Islands (Webb et al. 2014), as well as other regions such as the Caribbean (Tanner and Rodriguez-Sanchez 2014), that have found significant negative relationships between damage severity and survival. The most severe damage type, uprooting, often has high mortality rates because roots lose access to soil resources necessary for recovery (Webb et al. 2014). In our study, the only two trees that were uprooted also died. However, since there were only two trees in this category we were unable to test if survival differed from other types of damage. The least severe damage type, defoliation, is often overlooked in its significance to recovery and resistance (Lin et al. 2020). Defoliation immediately reduces photosynthesis and thus productivity (Yao et al. 2015) which may negatively impact long-term recovery. In the short-term in areas prone to higher frequency cyclone events, this loss in foliage which reduces windspeed when present, may increase vulnerability of trees and stems to wind damage (Lin et al. 2020) and possible mortality. In our study more than half of the stems observed experienced defoliation. This is consistent with studies outside the region (56% defoliation in Puerto Rico) (Walker 1991). Within the region, Webb et al. (2011) found 29% total stem defoliation after a category 4-5 cyclone in American Samoa, however this storm passed much farther away from the field sites (400km). Even in the absence of extreme winds, high levels of defoliation can occur when seawater is picked up by cyclone winds and deposited on near-shore coastal trees with negative repercussions on multiple taxa (Kerr 2000).

Our relatively small sample size (132 stems) may have influenced our findings In addition, we did not account for phylogenetic dependence in our models. However, our results may also relate to the impacts of human management actions buffering against mortality. For example, Webb et al. (2014) found that trees in a 20 year-old abandoned agroforest were less likely to be uprooted, and when uprooted, had greater survival rates. This may be because humans often intentionally plant trees in agroforests areas (Thaman 2008; Shah et al. 2018), the methods of which help trees set deeper roots with better anchorage against wind disturbance (Fazio 2014). These trees may also be planted in groups to allow for more convenient harvesting, which also confers resistance to damage (Gilman 2007). Finally, trees in agroforests are often

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pruned or pollarded in Fiji (Clarke and Thaman 1993b; Thaman 2008), dramatically reducing their height and canopy diameter. This reduction in stature and dimension may confer greater resistance and survival to cyclone wind disturbance (Gilman et al. 2008; McGroddy et al. 2013).

Predictors of damage severity

The type of damage sustained has been found in some cases to be predicted by species or individual trait such as wood density (Curran et al. 2008) or dbh (McGroddy et al. 2013). We found that dbh was an important predictor of severity of damage sustained. Although the relationship of dbh to damage type also varies across locations and storms (Webb et al. 2014), in Tonga, dbh was also positively related to severe damage (Franklin et al. 2004). A similar result was also found in the North Atlantic basin in the continental subtropical coastal region of the U.S. post disturbance (Gresham et al. 1991). Agroforests are often composed of various different species and various size-classes. Older trees with a larger dbh, or fast-growing trees with correspondingly larger dbh, are then also susceptible to cyclone damage in agroforests, similar to other forests.

Our finding that wood density did not affect damage type differs from Webb et al. (2014)'s study in American Samoa where wood density was an important predictor of severe damage. However, in Puerto Rico wood density was also found not to be a good predictor of damage severity (Walker 1991). These contrasting results highlights the need not only for more longitudinal studies of cyclone-forest dynamics in general (Pruitt et al. 2019), but especially of agriculturally important areas (Philpott et al. 2008) such as agroforests.

Resilience of agroforests as a function of management

Management type (i.e. managed – planted and fallow areas; and unmanaged – forest areas) was not found to be a statistically significant predictor of stem survival or type of damage sustained in our models. However, in other studies tree-related agricultural management regimes have been shown to impact multiple facets of agroecological outcomes (Holt-Giménez 2002; Philpott et al. 2008; Lazos-Chavero et al. 2018). Although we separated agroforest management types into planted and fallow versus forest for this study because of important structural, management, and compositional differences, agroforests incorporate and are characterized by all three of these rotational landscape types (planted, fallow, and forest) (Ticktin et al. 2018) and

associated relative management schemes (managed and unmanaged). Furthermore, the spatial heterogeneity and associated differences in biodiversity of these agroforests act to improve resilience (McSweeney and Coomes 2011; Cabel and Oelofse 2012; Mijatović et al. 2013). Our finding that no statistically significant differences in survival or damage type were observed between these two management subtypes supports the assertion that agroforestry, and its interacting social-ecological properties, may be more resilient against cyclone disturbance than other forest types. This likely proceeds through protective ecological and anthropogenic interactions which increase the resistance and resilience of both managed and unmanaged agroforest areas to cyclone disturbance.

For example, although agroforestry causes a certain type of habitat fragmentation via their mosaic nature, the resultant edge effects and the associated greater susceptibility of trees to wind damage (Laurance and Curran 2008) may be mediated by human activities (Darnhofer et al. 2010) that help forested agroforest areas resist damage. This may include pruning and pollarding (Thaman 2008) of edge trees creating a more gradual transition of planted or fallow area to forested, or purposeful planting of windbreak trees to reduce wind damage (Taylor et al. 2016). In Fiji, we observed one tree in particular used often as a windbreak, *Gliricidia sepium* (Jacq.) Walp., also appropriately named bai ni cagi, which translates roughly to wind fence. Other plants used as windbreakers in the Pacific Islands include Musa sp L. (Nakamura and Kanemasu 2020), Mangifera indica L., Bischofia javanica Blume, and Casuarina equisetifolia L. (Taylor et al. 2016). The effect of windbreak trees on agroecological resilience was also observed post cyclone in the Caribbean where pollarded citrus trees helped buffer coffee plants from wind damage (Perfecto et al. 2019). Large trees, although effective at reducing windspeed, are likely to topple and inflict further damage to coffee plants (Perfecto et al. 2019). In the same way trees in planted and fallow areas may help prevent damage in forested parts of agroforests, those forested areas may also help protect trees in planted and fallow areas. This might proceed through the reduction of windspeed as a product of forested areas structure and composition (Zhang et al. 2022).

Future research

In the face of global social and environmental change, including increases in cyclone intensity (IPCC 2021), understanding how ecosystems (Pruitt et al. 2019), and agroecosystems

(Philpott et al. 2008), experience and recover from cyclone disturbance is critical. Cyclones have a widespread and common reoccurrence in the Pacific (Lin et al. 2011; Marler 2014; Campbell 2015), where the social and economic systems better reflect those of societies globally (Marler 2014, 2015), as compared to those in the Atlantic where most cyclone research is focused (Pruitt et al. 2019). Diverse traditional knowledge about disaster preparedness and recovery (Veitayaki 2002; Veitayaki and Sivo 2010; Iati 2014; Janif et al. 2016; Nakamura and Kanemasu 2020) suggests that cyclones and other shocks were important disturbances in the past. Going forward research should also focus on understanding how to adapt the resilient principles observed in these societies to other systems as future disturbance events will increase. Research should also assess the social and economic impacts of cyclones and their resulting effects on agroforests and species compositions, as this has been shown to be an important factor in resistance and resilience in other places (Perfecto et al. 2019).

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CHAPTER 4. ECOLOGICAL FUNCTIONAL DIVERSITY PREDICTS NUTRITIONAL FUNCTIONAL DIVERSITY IN COMPLEX AGROFORESTS

ABSTRACT

Two of the largest global challenges - biodiversity loss due to agricultural expansion and the rise in diet-related noncommunicable disease mortality, both exacerbated by climate change are inextricably linked through food systems. Agroecological approaches to food production strive to fulfill linked environmental and human health goals, but our understanding of these linkages and their underlying mechanisms remains poorly understood. In agroecosytems, the functional diversity of species traits is important for resilience to shocks and disturbances. Analogously, the functional diversity of food species nutritional traits is important to human dietary health and disease resilience. Using an innovative application of functional diversity indices we demonstrate how measures of ecological functional diversity predict nutritional functional diversity in complex agroforestry systems. Managing for and maintaining a diversity of plant traits in agroecosystems has direct benefits for human nutrition.

INTRODUCTION

Two of the most pressing issues facing the planet today are the loss of biodiversity (Tscharntke et al. 2012) and increases in mortality from nutrition related non-communicable diseases (NCDs) (Tilman and Clark 2014). Seemingly unrelated, these issues are inextricably linked through our food systems (Tilman and Clark 2014; Wittman et al. 2017; Willett et al. 2019).

Modernized agricultural systems are a primary driver of climate change and ecosystem degradation, spurring massive biodiversity loss (Cicuzza et al. 2011; Tscharntke et al. 2012; Benton et al. 2021); simultaneously, the food produced is losing nutritional value at the individual (Fan et al. 2008), food group (Davis et al. 2004; Davis 2009), and food system scales (Alexander et al. 2017). Frequent and intense applications of chemical fertilizers and pesticides are required to maintain these systems, causing deleterious downstream effects on human and environmental health (Benton et al. 2021). A concomitant nutrition transition induced by global socioeconomic change has also led to increased production and consumption of energy dense, nutritionally poor foods prompting the rise of NCDs (Popkin et al. 2012). Climate change conditions will further reduce crop nutritional content (Myers et al. 2014; IPCC 2019), and increase global food demand by 30% to 62% between 2010 and 2050 (van Dijk et al. 2021). Therefore, society faces not only the challenge to provide food for a growing population, but to do so in ways that allow for sustainable and nutrition-focused production (International Fund for Agricultural Development 2014; Berry et al. 2015).

Historically, across cultures and continents, locally-adapted agroecological systems provided a sustainable and stable source of food for large populations (ICRAF 1987; Kurashima and Kirch 2011; Zomer et al. 2014; Lincoln 2020; Dhyani et al. 2021). Agroforestry comprises a diverse subset of these agroecological management practices, where trees and shrubs are cultivated with crops and/or livestock in varying scales, structures, and compositions dependent on use, location, and culture (Fernandes and Nair 1986; Clarke and Thaman 1993; Webb and Kabir 2009). Globally, between 25-33% of the population is estimated to rely on forests, including agroforestry (FAO and UNEP 2020; UN 2021), and 43.5% of agricultural land is estimated as agroforestry (tree cover greater than 10%) (Zomer et al. 2014). Biodiverse and multi-functional, agroforests deliver a range of critical ecosystem services within a relatively small space (Lasco et al. 2014; Bhagwat et al. 2008) and can support social-ecological resilience

to economic and environmental shocks and disturbances (McSweeney and Coomes 2011; Simelton et al. 2015). Agroforestry also presents a potentially scalable option to support linked ecosystem and food security goals (Clough et al. 2011; Kiptot et al. 2014; Kurashima et al. 2019; Hastings et al. 2020) helping mitigate climate change induced risks (Lasco et al. 2014; Waldron et al. 2017; Shin et al. 2020) in a cost-effective manner (Mbow et al. 2014).

However, the connections between biodiversity and nutrition in agroecological systems generally, and agroforestry specifically, remain poorly understood (Powell et al. 2015). Most research has focused on caloric production inadequately addressing complex nutritional needs (Pingali 2012). Moreover, the mechanisms underlying the relationship of biodiversity to improved nutritional potential have been largely assumed without supporting evidence or theoretical framework (Berti and Jones 2013). Understanding this relationship at a functional trait level is critical to achieve linked environmental and human health goals and outcomes (Wood 2018).

Plant ecological traits (i.e., growth form, dispersal syndrome, seed mass, etc.) are traits that influence one or more ecosystem functions (Petchey and Gaston 2002; Laliberte and Legendre 2010) and are hypothesized to be linked to nutritional traits, both directly and indirectly (Fig. 4.1) (Declerck et al. 2011; Wood et al. 2015; Ahmed and Stepp 2016; Stratton et al. 2020). For example, plant primary metabolites, such as carbohydrates, fats, and proteins, facilitate traits involved in plant growth (i.e. plant height) and reproduction (i.e. seed mass) (Ahmed and Stepp 2016), and attract pollinators (i.e. pollination syndrome) (Sakai et al. 1999) and seed dispersers (i.e. dispersal syndrome) (de Melo et al. 2020), among other ecological functions. Nutritionally, these metabolites are considered macronutrients and are essential for human growth and development. Environmental and agroecological management practices can interplay with plant ecological traits to impact primary metabolite production (Lamarque et al. 2014) such as when nitrogen fixing leguminous plants are intercropped with non-leguminous plants, a common agroforestry practice. Leguminous plants supply nitrogen to the soil for uptake in other species and thereby increase the overall yield of both crops (Li et al. 2016) and ecological and nutritional functional diversity.

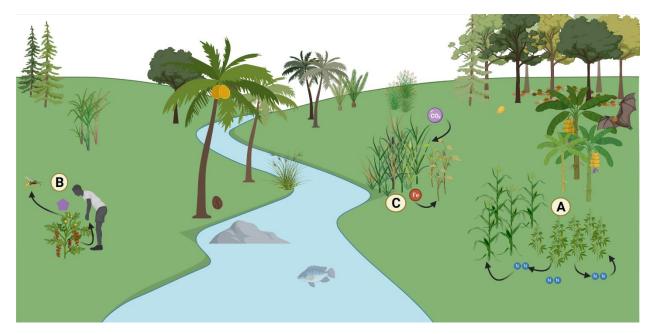


Figure 4.5: Select examples of linkages between ecological and nutritional traits and their functions in an agroecosystem. A: leguminous cover crops fix nitrogen in the soil which is then taken up by the corn for increased overall yield of both crops, and protein content in the corn. B: Nectar (sugar) in flowers attract pollinators. Once pollinated, the fruit provides carbohydrates (sugars) to people in diets. C: Climate change is predicted to increase levels of CO₂. Some C3 and C4 grasses react differently to increased CO₂. C4 grasses continue to produce iron (Fe) normally and leaf detritus returns iron to the soil for uptake in nearby edible plants, such as dark leafy greens, which is a source of iron in diets.

Functional trait approaches, "ecological functional diversity," have primarily been used in ecology to assess ecosystem productivity and/or resilience to disturbance (Garnier and Navas 2012). Food provisioning is an ecosystem service and recently the application of trait-based approaches have extended to nutritional spaces as "nutritional functional diversity" (c.f. Declerck et al. 2011; Luckett et al. 2015; Remans et al. 2014; Wood 2018), in relation to the FAO food security dimension of "utilization" (Stratton et al. 2020). However, no research has assessed if both ecological and nutritional functional diversity may be obtained in the same agroecological space, despite the fact that this would represent a critical step forward in planning sustainable, nutrition-focused agroecosystems (Remans and Smukler 2013).

We apply an innovative, transdisciplinary trait-based approach to identify if and how agroforests may simultaneously provide diverse nutritional and ecological functions by assessing the relationships between measures of plant functional traits important for ecosystem resilience and human nutritional health. To do this, we conducted plant biodiversity surveys of 48 agroforests in 10 villages across the 3 largest islands in Fiji and collected data for nine ecological traits and fifteen nutritional traits for those species. We show that ecological functional trait diversity (Laliberte and Legendre 2010; Laliberte et al. 2014) is a significant predictor of nutritional functional diversity for the two measures of functional trait diversity most relevant to nutrition: richness and evenness. We also show that functional dispersion and divergence, though relevant in ecology, are less informative for nutrition. Finally, we present a set of universal terms that can be used to help communicate and apply functional diversity concepts across fields (Fig 4.2). Additional information about the specific traits used in the analyses is described in the Methods.

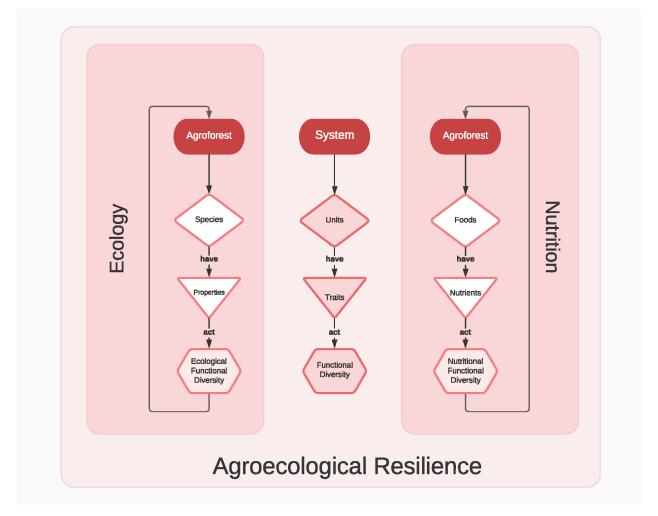


Figure 4.2: Conceptual diagram of the parallels between ecological and nutritional functional diversity with a proposed universal terminology linking the two fields. Ecologically, examples of species traits (properties) include vegetative traits like plant growth form or leaf phenology, regenerative traits such as dispersal mode or seed mass, and below ground traits such as nutrient uptake strategy or rooting depth, among many other response and effect trait

types. Nutritionally, traits (food components) include macronutrients carbohydrate, protein, and fat, and micronutrients such as vitamins A and C, or minerals such as potassium and magnesium, and may be expanded to include bioactive compounds such as phenolics and alkaloids important in medicinal practices.

METHODS

Study site and context

Fiji is an archipelago of over 300 islands in the South Pacific. Most of these islands are inhabited. The total population is just under 900,000; 55.9% (494,252) reside in urban areas, while the remaining 44.1% (390,635) reside in rural areas (Fiji Bureau of Statistics 2018). Historically, Fijians practiced agroforestry as a part of a larger land and sea-based socioecological system that provided communities with a stable source of food, medicine, building materials, and other resources for daily living (McMillen et al. 2014; Thaman 2014). Socioeconomic and environmental change has influenced the degree to which agroforestry is relied upon for these functions, however it remains a critical source of food and other resources (McGuigan et al. 2022).

Like traditional multistory/multipurpose agroforests in the Asia-Pacific region (Shin et al. 2020), and the global tropics (Schroth et al. 2004), Fijian agroforests are spatially heterogeneous and represent mosaics of forest, fallow, and planted areas (Ticktin et al. 2018, McGuigan et al. In Press). They host native and introduced food and non-food trees and shrubs and serve as important conservation areas (Thaman 2008; Ticktin et al. 2018). Staple root crops and emergency and uncommon food plants are interspersed across these agroforests (Thaman 1982, McGuigan et al. 2022).

Agroforest surveys

We worked with farmers in 10 villages across 3 islands in Fiji to record food and non-food plant biodiversity in 48 agroforests in 2019. Villages were selected where we had established rapport with communities based on previous research, and represent a range of socioeconomic conditions and levels of agroecological species and cultivar richness (see Dacks et al. 2018, 2020; Ticktin et al. 2018, McGuigan et al. 2022). Each of five farmers per village were asked to participate in a mapping exercise to determine the number, size, use, and location of all agroforest areas the farmer manages. We then identified parcels used at least partially for

subsistence, between 0.25 to 5.00 hectares, and which were within one hour's walk of the village and, of these, randomly selected one parcel per farmer to survey. Agroforests outside of these specifications were often used exclusively for commercial farming. With each farmer we recorded all species observed, including trees, understory crops and their cultivars. Any unknown species we identified at the South Pacific Regional Herbarium, Suva, Fiji.

We were granted permission to carry out this research by the Fiji national and district governments, village leadership (village headmen (Turaga ni Koro)), and the University of Hawai'i Institutional Review Board (2018-30418). The research team included University of Hawai'i at Mānoa and Indigenous Fijian (iTaukei) researchers, the latter of whom were well versed in iTaukei village protocols and ceremony, and fluent in Fijian and English languages. Informed oral consent was obtained from all farmers.

For all the species recorded, we identified origin as either native, introduced (post-European/Spanish contact), or indigenous introductions (Austronesian voyagers) from species records in Smith's Flora Vitiensis Nova volumes (1979, 1981, 1985, 1988, 1991, 1996), and CABI (https://www.cabi.org/ISC). We identified all edible species using biogeographical descriptions of Fiji and the Pacific's food environment (Thaman 1982, 1990, 1995, 2008), including if an edible plant was commonly consumed, an emergency food plant, or a potential food plant (i.e. not eaten in Fiji, but consumed as an emergency food in other places). This information can be found in the Data Statement.

Measures of functional diversity

Biodiversity has long been assumed to be fundamentally connected to ecosystem health, but over the past two decades functional trait ecology has emerged to explain the mechanisms underpinning this relationship. Functional diversity indices measure the diversity of species' ecological traits that influence one or more ecosystem functions (Petchey and Gaston 2002; Laliberte and Legendre 2010). Together, these traits mediate ecosystem processes (Hooper et al. 2005), services (Díaz et al. 2007), and their capacity for resilience (Folke et al. 2004). An ecological community with more similar functional trait combinations will have lower functional diversity than a community with more distinct traits, irrespective of species diversity (Folke et al. 2004).High functional diversity of effect traits - those regulating function - has been shown to increase ecosystem function, while high functional diversity of response traits - those mediating responses to environmental change - is expected to increase resilience to disturbance (Nock et al. 2016). Indices to measure and describe ecological functional diversity were initially introduced by Petchey and Gaston (2002) and expanded on by multiple scholars (see Mason et al. 2005; Villéger et al. 2008; Laliberte and Legendre 2010). Declerck et al. (2011) and Remans et al. (2011); and then this concept was extended to nutrition using nutrient content as traits (i.e. protein, vitamin C, iron, etc.), important for human nutrition which, in the diet, support human health and resilience to disturbances such as communicable diseases (i.e. COVID-19) and NCDs (Birgisdottir 2020).

Here we apply Laliberte and Legendre (2010)'s methods to calculate three multidimensional indices of ecological and nutritional functional diversity: richness, evenness and dispersion. Functional richness is a measure of the range of trait values in a community and is estimated by the number of functional trait combinations (Villéger et al. 2008). In multivariate analyses with diverse trait types such as ours, the measure becomes the volume of the convex hull (Laliberte and Legendre 2010). Functional evenness is a measure of the distribution regularity of unit traits in the sample volume (Villéger et al. 2008). To date, most studies on nutritional functional diversity has focused exclusively on richness and evenness (Declerck et al. 2011; Remans et al. 2014; Luckett et al. 2015). However, function dispersion, the average distance measure in trait space of each unit from the centroid derived from all units (Laliberte and Legendre 2010), is another ecologically important measure. It was included by Wood (2018) for nutrition and we include it here to identify its relevance for nutrition. These components are positive and the greater the value of each measure, the greater the component of functional diversity they quantify is. A fourth index that is important in ecology, functional divergence, is a measure of how close to the centroid traits are, where high divergence indicates more extreme functional trait values (Villéger et al. 2008). Ecologically, functional divergence translates to niche differentiation where high divergence, or polar trait combinations (traits are clustered together but functionally opposite), may lead to increased ecosystem function because of more efficient resource use (Mason et al. 2005). We consider this measure uninformative for human nutrition however and do not consider it here.

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Ecological functional diversity

We standardized species' taxonomic nomenclature using accepted names from the World Flora Online (http://www.worldfloraonline.org). We then created a species presence/absence matrix by agroforest and an ecological trait matrix of the recorded species. Ecological traits, hypothesized to be important in an agroecological system, include whole plant, leaf, root, and reproductive functional traits (Martin and Isaac 2015) and should relate to functions concerning nutrient cycling dynamics, pest management (Blesh 2018), biomass contributions (Shennan 2008), contributions to soil retention and water regulation, reproduction (Pakeman 2011), and light interception (Garnier and Navas 2012; Milla et al. 2014). Given that resilience to disturbance (human and natural) is a key concern in agroecological systems, we focused on nine response traits associated with these functions: nitrogen fixation, photosynthetic pathway, pollinator type, dispersal mechanism, clonality, leaf phenology, growth form, life form, and species height. All traits were weighted evenly (1), except pollinator type which is composed of 7 possibilities and each was thus weighted as 1/7.

We first searched the TRY database (Kattge et al. 2020) for species traits, and where information was absent, we retrieved information from alternative sources (i.e. Kew Seed Information Database (https://data.kew.org/sid/), World Flora Online (https://www.worldfloraonline.org/), Flora Vitiensis Nova (Smith 1979-1996), and others). If these databases yielded no results, we searched primary literature for trait data (see Data Statement for trait table).

Nutritional functional diversity

To assess the nutritional functional diversity of agroforests we created a food plant by nutrient matrix based on 15 key macro and micronutrients available from food composition tables and necessary in human nutrition including energy, protein, fat, carbohydrate, fibre, Na, Mg, K, Ca, Fe, Zn, thiamin, riboflavin, niacin, and vitamin C. We obtained this data primarily from the Pacific Islands Food Composition Tables (Dignan et al. 2004), and where necessary, additional FAO, WHO, and country level food composition tables from the FAO/INFOODS databases (FAO and INFOODS 2020). If information could not be found in these resources, we consulted primary literature. We obtained nutritional trait info by plant part of 97 species of the 111 edible species recorded.

We standardized nutrient content per 100g of edible plant matter and weighted values according to the percent recommended dietary intake (Remans et al. 2011; Luckett et al. 2015) for an active woman between 19 and 50 years old requiring a 2200 calorie diet composed of 35% protein (192.5g), 45% carbohydrates (247.5g), and 20% fat (48.8g) (Institute of Medicine 2011; Lourme-Ruiz et al. 2021). Fibre was not included in the carbohydrate calorie calculations (25g). We used compositions of boiled foods where possible, as this is a common preparation method in Fiji (Ravuvu 1983), or raw where unavailable or inappropriate. We base our nutritional trait standardizations on women's recommended dietary intake specifically because of their vulnerability to malnutrition as compared to men (Arimond et al. 2010; Torheim and Arimond 2013), defaulting this demographic as the baseline nutrition necessary.

We calculated multidimensional component indices of both ecological and nutritional functional richness, evenness, dispersion of the biodiversity recorded in the agroforests using R package 'FD' (version 1.0-12) (Laliberte et al. 2014).

Regression models

To assess if multidimensional indices of ecological diversity predicted their correlate indices in nutritional space, we used general linear mixed models (Zuur et al. 2009) in R package 'glmmTMB' (version 1.1.2.3). We used the log of each of the indices and included village nested within district as a random effect to account for possible spatial autocorrelation. We examined model residuals for normality and homogeneity of variance.

RESULTS

Species richness of agroforests

Fijian agroforests have high species richness: across all agroforests we recorded 171 species, including 111 edible species and 147 edible plant parts. The mean richness (number of species) per agroforest was 24.4 ± 1.1 se. Mean richness of edible plants was 18.7 ± 0.9 se and that of edible plant parts was 31.7 ± 1.3 se (Fig 4.3a).

There were similar proportions of native (including endemic and indigenous) and introduced species in the agroforests (Fig 4.3b). More than half of edible species recorded were

considered commonly consumed (Fig 4.3c) with about half as many used as emergency foods. On average, less than 20% of the edible species were potential foods (i.e. foods not eaten in Fiji but edible).

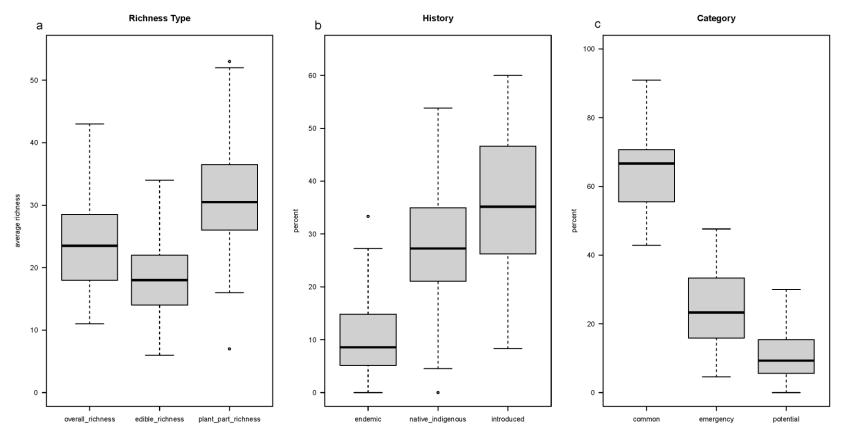


Figure 4.3: The overall richness across all agroforests of total species richness, edible species richness, and the richness of edible plant parts (a). The average proportions of strictly endemic, otherwise native or indigenously introduced, and recently introduced species present across all agroforests (b). The average percent of species classified as either commonly consumed, emergency foods, or food of potential edibility across all agroforests (c).

Relationship between ecological and nutrition functional diversity indices

Ecological functional richness and ecological functional evenness were significant positive predictors of nutritional functional richness (p<0.0001) and evenness (p<0.0001) respectively (Fig 4.4a, b). We found a significant negative relationship between ecological functional dispersion (p<0.0001) and nutritional functional dispersion. However, in contrast to the measures of richness and evenness, we found that the agroforests with the highest nutritional functional dispersion consisted of groups of species that were in within the same or similar food groups, and were therefore nutritionally limited; for example, they contained a small number of fruits and vegetables that were nutritionally diverse, but lacked starch crops. As such, nutritional functional dispersion was not an appropriate indicator of diverse dietary sources of nutrition in this context.

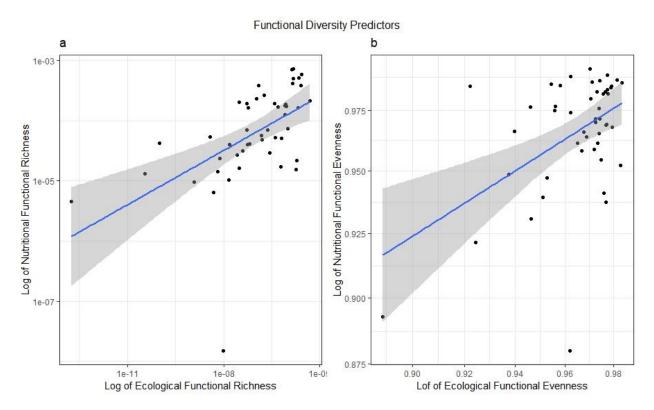


Figure 4.4: Regressions of ecological and nutritional functional richness (a) and evenness (b) across all agroforests. Ecological functional richness and evenness were significant predictors of nutritional richness and evenness. Models include village as a random term.

DISCUSSION

Two of the largest challenges facing the world today, biodiversity loss due to agricultural expansion (Tscharntke et al. 2012), and the rise in diet-related noncommunicable disease mortality (Tilman and Clark 2014), are both exacerbated by climate change and growing populations, and are inextricably linked through our food systems (Tilman and Clark 2014; Wittman et al. 2017; Willett et al. 2019). Resilience in food systems requires multifunctionality resulting from functional diversity at multiple scales (Hodbod and Eakin 2015). This includes considerations of local on-farm diversity, national spatial-temporal diversification of food producing regions, global governance actors involved in the economic and socio-economic elements of food trade, distribution, access, and finally undergirding this, cultural dimensions of utilization and nutrition (Hodbod and Eakin 2015). Therefore, identifying and managing for agroecological systems that provide diverse ecological and nutritional functional functional diversity relevant to complex, multifunctional agroecological systems and demonstrates that ecological functional diversity predicts nutritional functional diversity, with implications for improved human and environmental health outcomes, and food system resilience.

Relationship between nutritional and ecological functional evenness and richness

We found that nutritional functional richness and evenness, the two functional trait measures that when considered together are most important to nutritional diversity in the diet (Declerck et al. 2011; Remans et al. 2014; Luckett et al. 2015), were predicted by ecological functional richness and evenness. Functional richness measures the total range of trait values in a community and therefore reflects the most extreme trait combinations (Legras et al. 2018). However, this space may or may not be filled with species composed of intermediary trait combinations. Functional evenness describes the regularity of trait combinations within this functional range (Villéger et al. 2008). Taken in tandem, they provide an important measure of a system's ability to provide a range of robust and diverse functions. Ecologically, this is exemplified as ecosystem multifunctionality through resource partitioning, synergisms with other traits, and inhibitory effects towards deleterious ecological actors, such as pathogens (Le Bagousse-Pinguet et al. 2021). In the context of disturbance and loss of species, the redundancy of species filling similar trait spaces allows the ecosystem to continue performing its services with the remaining species' functional traits. Nutritional functional richness describes the range of nutrients present in a system and available for consumption. As in ecological functional richness, this does not describe the regularity, or density of nutritional traits within this range. Therefore, nutritional functional evenness must also be present. The consumption of all vital nutrients in requisite quantities is necessary for human health and resilience to disease (Birgisdottir 2020) and represents nutritional quality (Béné 2020), the utilization component of the four pillars of food security (Food and Agriculture Organization of the United Nations 2008). Food security supports food system resilience (Tendall et al. 2015), and while we do not measure consumption here, the availability of these nutrients is pivotal for an agroecosystems to be considered a potential actor in food system resilience (Hodbod and Eakin 2015).

Our finding that ecological functional richness and evenness are significant predictors of nutritional functional richness and evenness can be explained by the multiple ways in which they may be linked in agroecosystems. For example, in the same way plant primary metabolites are macronutrients in the human diet (Fig 4.1), plant secondary metabolites also provide micronutrients for humans (Guerriero et al. 2018) and serve medicinal functions (Wink 2015). Plant secondary metabolites include vitamins (Barański et al. 2014), as well as phenolics, alkaloids, terpenoids, and sulfur containing compounds (Guerriero et al. 2018). Plants also assimilate minerals from their environment that we utilize in our diets. These secondary metabolites and seed dispersers, moderate biomass production, and mediate other species interactions (Nishida 2014; Briat et al. 2015; Wink 2015; Guerriero et al. 2018). Therefore, systems with high functional richness and evenness of these ecological functions can have high functional richness and evenness in the nutritional traits that enable those ecological functions.

Although agrobiological species richness and diversity have oft been associated with ecosystem health (Johns et al. 2013) and dietary diversity (Akrofi et al. 2010; Lourme-Ruiz et al. 2021), our results indicate that a functional trait approach can be more informative than one based only on species identity. While the number of species is correlated with functional richness (Villéger et al. 2008), we found no correlation with functional evenness, indicating that the combined indices capture additional information that species richness alone cannot quantify.

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Functional dispersion and nutritional dietary diversity

We found functional dispersion was not an appropriate indicator of nutritional diversity of the diet in our study, suggesting that its value is context specific. Ecologically, functional dispersion relates to niche complementarity (Schellenberger Costa et al. 2017), whereby differences between species in their functional traits allow greater complementarity in resource use and enhances ecosystem function (Mason et al. 2012; Mason and Mouillot 2013). Functional dispersion is also an important component in response diversity to disturbance and helps ecosystems buffer against functionality loss and enhance recovery (Laliberte et al. 2010).

In some contexts, nutritional functional dispersion may be an appropriate indicator of nutritional diversity of the diet and also positively correlated with ecological functional dispersion. For example, one of the most well-known examples of niche complementarity in agroecosystems comes from the Mesoamerican practice of planting maize (*Zea mays* L.), bean (*Phaseolus vulgaris* L.) and squash (*Cucurbita* spp. L.) together (Declerck et al. 2011). Ecologically, maize capitalizes on light resources as the tallest crop (plant height, growth form), beans then utilizes this growth for structural support while also fixing nitrogen in the soil (nitrogen fixation), and finally squash thrives in the shade provided by the corn and bean (leaf size) (Powell et al. 2015). This assemblage is also complementary nutritionally. Maize is an important carbohydrate source, while beans provide important amino acids that when combined with those also provided by the maize, grants the full set off essential amino acids, or the building blocks of protein (Powell et al. 2015). Beans also provide a swath of vitamins and minerals, which the squash augments, particularly with vitamin A (Powell et al. 2015).

However, while it may be appropriate in certain contexts, the fact that we found that nutritional functional dispersion values may be higher for a subset of species within a single food group than for a larger number of species that contain the subset but also span additional food groups, suggests that it is not appropriate in complex systems such as agroforests.

Applications to fostering linked environmental and human health

We found that in agroforest systems with a combination of native and introduced species, measures of ecological functional richness and evenness are strong predictors of nutritional functional evenness and richness. Given that ecologically diverse agroforests also play key roles in biodiversity conservation (Thaman 2008; Ticktin et al. 2018), this research highlights their capacity to directly support linked environmental and human health. Our findings have local, regional, and global applications for conservation, nutrition, agroecology, and food systems as a whole.

For example, gaining a better understanding of how agroforestry practices could improve both ecological and nutritional function is critical in the Pacific Islands, where women are constrained by gendered socioeconomic responsibilities (cooking, childcare, laundering) (Ravuvu 1983) that limit their physical activity, increasing their risk of nutrition related NCDs (Kessaram et al. 2015). In Fiji specifically, where 84% of deaths are from NCDs (WHO 2020), women are consistently more likely to have hypertension, diabetes, and be overweight and obese (Kessaram et al. 2015). Furthermore, urbanization has decreased reliance on agroforestry in exchange for resources available in the city (Phillips et al. 2019), leading to lower agrobiodiversity in agroforests close to urban areas. This urbanization is associated with lifestyle and dietary changes that increase NCD incidence (Carter et al. 2011; Taylor et al. 2013). From an ecological perspective, national-level biodiversity is at risk due to changing agroecological practices (Thaman 2008) and the presence of few terrestrial conservation areas (Keppel et al. 2012). Collaborative efforts between organizations that focus on biodiversity and human health could promote and support the maintenance of diverse agroforests, which would accomplish both missions.

At the global level, while up to 33% of the world population depend on forested areas for their subsistence needs (FAO and UNEP 2020), policy decisions to enhance agroforestry have largely misunderstood the importance and interconnectedness of agroforests to human wellbeing, in part due to their inherently complex nature (Zomer et al. 2014). Indeed, agroforests in our study were not only composed of mostly edible species, more the 20% of them on average were native (endemic or indigenous introductions), underlining their combined importance in the conservation of plants that are both edible and locally-adapted, which often provide unique and important nutritional contributions (Hunter et al. 2019). This framework quantitatively elucidates those connections and demonstrates the need for policy makers to prioritize and fund efforts to restore and maintain these complex systems.

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Future directions

We provide a first attempt to quantitatively test the linkages between ecological and nutritional functional diversity. Future research can provide further insight. For example, our results are based on presence/absence data and the inclusion of species and edible plant part abundance data could potentially provide more information. However, simulations have shown that presence/absence data and abundance data yield similar results (Laliberte and Legendre 2010). Consideration of more ecological and nutritional traits would also be important. We were also limited to 9 ecological and 15 nutritional traits, for which information was not always complete. Information about agricultural and rare species (Kattge et al. 2020), and of nutritional traits for uncommon food species and crop cultivars (FAO/INFOODS 2013) is especially scarce. Moreover, there is important significant variation in nutrient content between cultivars of food plants in the Pacific, such as in banana (Musa L.) (Englberger et al. 2003), sweet potato (Ipomoea batatas (L.) Lam.) (Huang et al. 1999), and bele (Abelmoschus manihot L.) (Rubiang-Yalambing et al. 2016) that is seldom recorded in food composition tables. In the face of climate change induced reductions in nutritional quality (Myers et al. 2014; IPCC 2019), and associated declines in species and cultivars (Hooper et al. 2005), future research must prioritize this data collection and nutrient analysis.

Finally, assessing the relationships between ecological and nutritional functional diversity at additional scales, such as at the local and global food system scales will provide a greater understanding of the interrelationships between biodiversity and nutrition. In terms of scaling up, identifying if and how the relationships between nutritional and ecological functional diversity indices vary over space and time, to account for food seasonality and microclimate differences, and when measures such as functional dispersion may be important, will allow for broader application. Downscaling the application of the nutritional functional diversity assessment to the level of the plate (treating the plate as a system), may also provide additional novel insights not only of nutritional dietary quality, but also in the relationship of diets to agroforests. This could be achieved by comparing the nutritional functional diversity of farmer diets to that of their agroforests and would provide currently missing quantitative links between many different types of agroecosystems and their direct contributions to diet (Remans and Smukler 2013; Powell et al. 2015) that can then be used to inform and motivate policy decisions that promote agroforestry and other sustainable, nutrition-focused agroecosystems.

APPENDIX

Nutrient	Minimum	Maximum
Protein (g)	0.052	15.273
Fat (g)	0.143	204.713
Carb (g)	0.081	34.707
Fibre (g)	0.400	122.800
Na (mg)	0.040	59.333
Mg (mg)	0.315	110.141
K (mg)	0.194	41.921
Ca (mg)	0.060	111.000
Fe (mg)	0.030	66.296
Zn (mg)	0.271	60.000
Thiamin (mg)	0.909	327.273
Riboflavin (mg)	0.909	163.636
Niacin (mg)	0.714	67.286
Vitamin C (mg)	0.013	320.000

Table 4.1: Table of nutrients used in functional diversity analysis and the minimum and maximum values recorded per 100g of food.

			dispersal	pollination	photosynthetic	height	seedmass	wood	nitrogen	
growth form	leaf phenology	life form	mechanism	syndrome	pathway	(m)	(g)	density	fixation	clonality
climber_herb	annual	chamaephyte	ballistochory	insect	c3	0.15	0.00001	0.16	1	1
climber_strangler	deciduous	geophyte	endozoochory	wind	c4	45	83.333	0.8411	0	0
climber_wood	evergreen	hemicryptophyte	human	bird	cam					
herb_elongated	perennial	phanerophyte	unassisted	bat						
herb_extensive	semi_deciduous	therophyte	water	apomixis						
herb_rosette			wind	not required						
herb_tussock										
semiwood_bambusoid										
semiwood_palmoid										
semiwood_succulent										
wood_shrub										
wood_subshrub										
wood_tree_deliquescent										
wood_tree_excurrent										

Table 4.2: Table of ecological traits used in functional diversity analysis and the possible data values. Numerical trait examples for height, seed mass, and wood density represent minimum and maximum values per species. For binomial trait values of nitrogen fixation and clonality 1 indicates yes, 0 indicates no.

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DATA STATEMENT

Data and the reproducible R code is available by request from the author. It will also be made available in a public repository. The two data files include:

- 1. Nutritional Trait Table
- 2. Ecological Trait Table

CHAPTER 5. CONCLUSION

SYNTHESIS OF FINDINGS

There are three main findings in this dissertation: 1) agroforestry practices in Fiji are changing with global change, yet remain resilient to catastrophic disasters and suggest food system resilience is present (Chapter 2); 2) trees in agroforests are highly resilient against catastrophic wind disturbance, due in part to human management practices that may improve survival and reduce damage vulnerability (Chapter 3); 3) complex agroforestry has the capacity to simultaneously provide diverse ecological functions, as well as nutritional functions, important to social-ecological resilience (Chapter 4).

Global changes have important implications for agroforests and associated food systems at the local level and can often lead to deleterious downstream effects. A common understanding exists that part of this is due to a loss of biodiversity, especially of traditional foods (Kahane et al. 2013; Mijatović et al. 2013). This loss is associated with a decline in traditional knowledge and related management practices that maintained important ecosystem functions (Vogliano et al. 2021). Chapter 2 shows that while some levels of food crop biodiversity have been lost and continue to be replaced by modern cultivars in agroforests in Fiji, the system remains highly resilient against cyclone disturbances. This is facilitated by a resistance to starch crop species losses, the introduction of new crops and crop cultivars, and the presence and increase in emergency crops in agroforests. A clear decline in overall cultivar richness was observed however, and in addition to threatening overall resilience, this also has important implications for nutritional diversity and function.

Chapter 3 then assesses the resilience of the trees in agroforests to cyclone disturbance. We found that trees and tree stems in agroforests in Fiji generally resisted cyclone induced wind damage and suffered very low mortality overall. We found that survival was positively related to wood density, and that damage severity increased with stem size (dbh). These effects were separate from agroforest management subtype (managed or unmanaged) and suggests that management practices in subtype have a synergistic, facultative (or facilitative?) role in the other, and supports resilience. For example, the management (pruning, pollarding, or purposeful planting) of trees on forest-plantation/fallow edges likely reduces edge effects of fragmentation that may otherwise leave trees vulnerable to wind damage. Finally, Chapter 2 explores the relationship between ecological and nutritional functions of complex agroforests in Fiji today. Important correlations between ecological and nutritional functions were found, suggesting that agroforests have the capacity to support linked human and environmental health. We identified ecological and nutritional function richness and evenness as particularly important in the context of food system resilience. These indices indicate that the system is able to provide the full range of necessary nutritional and ecological functions, and to provide them in enough volume to support the functions they represent. Importantly, we show that agroforestry is able to support these functions in the same physical space and presents a viable, and scalable option to modern industrialized agriculture.

AGROECOLOGICAL MANAGEMENT RECOMMENDATIONS

The results of this dissertation have important implications for agroecological management and planning in the face of multiple global challenges. First is that, while agroforestry in Fiji is still highly resilient to disturbance, threats remain to native species and traditional crop and crop cultivar richness that must be addressed if the food system is to remain resilient. Many farmers are specifically requesting planting materials of old and traditional food crops, citing their resistant and resilient qualities to major disturbances, which are projected to increase. However, many disaster mitigation plans and agricultural management plans promote and facilitate the cultivation of crop cultivars that have been highly selected for market qualities such as mass and palatability, at the expense of resilient qualities such as salt tolerance or nutritional content, that jeopardize food system resilience ecologically and nutritionally. A global shift to a cash economy has underpinned this movement, yet has failed to provide the benefits promised and cannot insure against projected increases in natural disasters or socio-economic disturbances such as covid-19, which halted tourism in Fiji. Therefore, it is critical that local food systems be re-vitalized and prioritized in strategic plans to allow for greater autonomy and security against these shocks. Specifically, germplasm and seed stock material of traditional cultivars of important crop species should be distributed to farmers in Fiji to facilitate this rediversification. Much of this material is housed in seedbanks within the South Pacific Secretariat and research stations in the Ministry of Agriculture. Conservation and distribution plots could then also be established at regional locations throughout Fiji so farmers have greater access to

planting materials and decisions about distribution can be made more effectively based on local needs.

To ensure the success of these crops at markets and other consumer locations, marketing interventions can be employed to promote sales and consumption in multiple sectors, including tourism, education, and agriculture. However, perhaps the most important sector with which to target today is the health sector. The importance of these crops to dietary health can be included in established health interventions at the Ministry of Health and Medical Services. Workshops that detail the nutritive qualities of traditional crop and crop cultivars may be useful in helping to educate about NCDs and ways to combat them through dietary and lifestyle changes. This not only helps facilitate better dietary patterns, but also traditional knowledge transfer. Additionally, because these crops and foods are not foreign, there is a lesser barrier to use and consumption.

Building on this, a consideration of the trees composing the overstory in agroforests is also important in planning for resilience. Trees that are adapted to local conditions and able to withstand or recovery quickly from disaster and disturbance are critical. As described in Chapter 3, these qualities are often place-specific as storms and socio-economic conditions vary across space. However, emphasis should be placed on using native trees, and on management of those trees. Our research suggests that part of the enhanced resistance to damage may be a product of management practices such as pruning and purposeful planting that help reduce wind damage and may aid in resisting uprooting.

Last, chapter 4 describes how agroforests are not only viable systems for crop production in general, but also spaces where multiple functions necessary for linked environmental and human health and resilience may be maintained. These systems are scalable and have the capacity to feed large populations (Clough et al. 2011; Kiptot et al. 2014; Kurashima et al. 2019; Hastings et al. 2020). Contrarily, modern industrialized agriculture is a high intensity system that requires significant pesticide and fertilizer applications to be productive. The food produced is also less diverse at the species and nutrition levels. As global populations rise and nutritionrelated disease rise in tandem, agroforestry could be more widely adopted as an alternative to modern agriculture to meet environmental and nutritional needs. Considerations when planning an agroforest system should include local food culture and preferences, microclimate and edaphic conditions, and other socio-economic and environmental factors. Additionally, proposed plant lists can be assessed using the functional diversity metrics prior to planting to ensure that both ecological and nutritional functions and goals are being met.

These results can inform responses to natural disasters, where ensuring there is adequate and stable nutrition available and accessible, is critical to recovery success. To do this, multiple food sources must be available to communities both locally in agroecosystems, and through governmental assistance programs. The foods in these programs should be energy and nutrient dense and local where possible, to ensure that food reaches communities quickly. In agroecosystems, this may be promoted by increasing the abundance of emergency food species that withstand cyclone damage, as I documented here. In Fiji, as it often the case elsewhere, emergency foods require less maintenance than commonly consumed foods and therefor is a low cost investment practice. Furthermore, governmental programs can institute workshops that facilitate knowledge transfer around the cultivation and preparation of these foods to increase their use. These workshops may also help facilitate germplasm exchange and redistribution to increase food biodiversity in these agroecosystems. Shelf stable foods are also important immediately post-disaster, and while many of these products are high energy, some are also energy dense but nutrient poor, such as sugar, which may exacerbate symptoms in people already suffering from NCDs. Therefore, government assistance programs should eliminate energydense, nutrient-poor foods from food assistance recovery plans. These foods should be replaced with energy and nutrient dense foods, tailored to local needs, and where possible, be sourced from local farmers and food producers not affected by the disaster, thus also supporting the local economy.

LIMITATIONS

While these studies included multiple sites and almost 50 farms, the biodiversity surveys were limited to species richness measures and we could not account for species or cultivar abundance due to time and labor limitations. We therefore could not apply measures of biodiversity to our various assessments; however, they would have strengthened the findings and provided greater depth to the interpretations. We also were unable to revisit every site on every visit. In some cases, farmers no longer had access to their old planting sites due to damage from Cyclone Winston. Occasionally, farmers may have also been ill, deceased, or passed on their

land to the next of kin. In these cases, management practices may have changed and caused changes in species richness and agroforest land area.

In addition to limitations in data collection in the field, collection of functional trait data was particularly difficult as many of the plants in this study are either rare, endangered, or agricultural which are all classes of plants with documented gaps in trait knowledge, including nutritional traits. Although we conducted exhaustive literature reviews to source trait data, some data could not be obtained. This also limited the number of different trait types we could include in the analyses.

OPPORTUNITIES FOR FUTURE RESEARCH

Numerous avenues for future research became evident through this dissertation. The limiting factor across all chapters was a lack of trait data across ecological, agricultural, and nutritional realms. Research on plant traits, especially of rare, endangered, emergency, and agricultural species and cultivars is a critical next step to providing a greater depth of understanding around agroforestry and associated functional trait diversity. Specifically, a greater understanding of root and leaf traits important for soil retention would benefit the ecological trait literature, as well as complete nutrition composition information for composition tables. This information will aid in planning and designing multifunctional agroforestry systems on larger scales.

Planning for agroforestry at larger scales should also consider the different cultural, socio-economic, environmental, and climatic factors at play for success. While agroforestry is still widely practiced in the tropics, in terms of implementation in other regions, future research may need to focus on more base-line information around production capacity and crop seasonality in this type of system prior to execution. These needs assessments in new areas should consider local food and cultural needs, socio-economic factors, as well as environmental concerns (soil degradation, water pollution, etc.) that could be addressed through agroforestry. This information could be gathered from local stakeholders such as food producers and consumers, government leadership and policy makers, and nutritionists. Furthermore, consultation, collaboration, and co-leadership with Indigenous farmers and landholders practicing various traditional farming practices in these places would be critical to these

initiatives. As market and economic factors become more complex with greater global integration, research should also examine the various global actors on local farming systems.

While there is great potential to increase nutritional diversity in our food systems through agroforestry, there are significant and complex barriers to improved diet and health outcomes. Nutrition interventions seek to influence dietary preferences and eating patterns, yet the success of these interventions is often context specific. These types of nutrition interventions and recommendations must take into account culturally appropriate dietary patterns and customs, and be led by local communities and community members. More research around the practices and efficacy of nutrition interventions in communities vulnerable to NCDs should be carried out. This may also include assessment at different scales. For example, using the nutritional functional diversity scores at the scale of the food plate compared to that of the agroforests, to assess if the potential nutritional functional diversity of the agroforest is realized in diets.

Overall, future research that links ecological and nutritional outcomes in agroecosystems can help inform sustainable and nutrition-focused agriculture, as well as social-ecological resilience. This research is critical in the combating the global NCD epidemic, climate change, and in supporting food system resilience.

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