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Abundant Lands, Thriving People: Examining the Socio-Ecological Web of Kānaka ʻŌiwi Agroecosystems

By

Leslie Lee Hutchins III

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Committee in charge:

Professor Rosemary Gillespie, Chair
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ABSTRACT

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Biodiversity conservation has long pitted “natural” landscapes against human-managed landscapes. However, biodiversity has long interacted with human-shaped landscapes, starting with Indigenous management thousands of years ago. As the impacts of climate change and biodiversity loss take hold on our ecosystems, the need to see the whole landscape as a partner in biodiversity conservation, rather than nature reserves as the only solution, is imperative. Agricultural landscapes are particularly noted for their ability to bolster biodiversity while producing food, though this largely depends on their management and level of homogenization. Heterogeneous agricultural landscapes over space and time can sustain native biodiversity, even on a scale outpacing non-managed landscapes. Agricultural landscapes do not form independently but are shaped by the hands of farmers and communities. Therefore, understanding the social factors that shape farmer and community decision-making is crucial, along with an examination of how to ethically and responsibly conduct research with communities.

In this dissertation, I utilize a socio-ecological framework to examine if and how Kānaka ʻŌiwi (Indigenous Hawaiian) agroecosystems can conserve native arthropod biodiversity. First, I describe a framework to identify what mechanisms shape the ability of agroecosystems globally to conserve different taxonomic groups. Second, I present sociological findings based on interviews showing that Indigenous and non-Indigenous farmers have other motives for engaging in agriculture, with ramifications on crop diversity and community impact. Next, I utilize empirical findings based on DNA metabarcoding and Next Generation Sequencing data to showcase how arthropod alpha and beta diversity trends shift between simplified and diversified farms within an agroforestry system on Hawaiʻi island. I then examine the research process I undertook for this chapter through an Indigenous Data Sovereignty framework. Lastly, capitalizing on advances in DNA metabarcoding, Next Generation Sequencing, and information theory, I construct bipartite networks between predators (spiders) and their prey to illustrate how the structure and stability of networks change depending on agricultural landscape composition.

I dedicate this work to my kūpuna and ‘ohana.

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INTRODUCTION

We face a triple threat of biodiversity loss, climate change, and food injustice (Perfecto, Vandermeer, and Wright 2019). To address biodiversity loss, scholars have long promoted isolated reserves tucked away from society as a primary conservation tool (Claire Kremen 2015). In this view, biodiversity can be best conserved when separated from anthropogenic disturbance. However, while these reserves are essential for conserving some of the rarest and most vulnerable taxa, they have limitations and leave the potential of the much more expansive surrounding landscape unrealized (Mendenhall 2020). A few limitations of reserves include not providing adequate long-term refugia as range shifts occur due to climate change (Lim et al. 2022), creating isolated metapopulations of taxa with deleterious effects on fecundity and fitness (Frishkoff et al. 2014), and being expensive to maintain with little recognition of them and the taxa they conserve by the public (Karp et al. 2013).

A new biodiversity conservation model has emerged that emphasizes the landscape around nature reserves as an essential partner in conserving taxa (C. Kremen and Merenlender 2018). In particular, agroecosystems have been proposed as systems that can conserve and bolster biodiversity while providing benefits like food to society (Perfecto et al. 1996). However, not every agroecosystem is the same, as there is tremendous heterogeneity within them due to management practices that either increase or decrease crop and non-crop diversity over space and time (Hutchins, Guzman, and Ponisio 2024), as well as other considerations such as herbicide and pesticide application. While many have come to view agroecosystems as biodiversity hotspots only recently, Indigenous communities have tended to these systems since time immemorial (Stiegler 2019).

Indigenous agroecosystems are biodiverse, climate-adapted systems (Kurashima, Fortini, and Ticktin 2019). In Hawaiʻi, where this dissertation is based, Kānaka ʻŌiwi community members cultivate agroecosystems from mountainous high-elevation slopes and forests to the coastline. Many of these agroecosystems utilize a wide diversity of crops such as ʻuala (sweet potato), ʻulu (breadfruit), kō (sugarcane), kalo (taro), and niu (coconut) (Lincoln and Ladefoged 2014). This diversity is managed in various ways, from shifting cultivation following rainfall patterns to agroforestry (i.e., incorporating trees into cropping systems). The empirical ecological work in chapters 3 and 4 is based on the Kona Field System (KFS) on the Leeward side of Hawaiʻi Island. The KFS is an agroforestry system developed around 1400AD that has shifted in the present day to a complex mosaic primarily based on coffee, a cash crop introduced in the islands by foreign businessmen and missionaries in the mid to late 1800s (Hutchins et al. 2023). However, several ʻōiwi organizations have maintained and cultivated agroforestry systems to perpetuate culture and produce much-needed culturally relevant crops.

To understand biodiversity pattern shifts between agricultural systems, I focus on arthropods, an extraordinarily diverse and robust phylum with many taxa having essential roles in ecosystem functioning (e.g., pollination and pest control), which are particularly vulnerable to environmental change, especially for native and endemic arthropods in Hawaiʻi (Graham et al. 2023). I utilize a DNA metabarcoding pipeline coupled with Next Generation Sequencing (NGS) to rapidly and cost-effectively characterize arthropod diversity. DNA metabarcoding and NGS allow for high throughput processing of whole communities of organisms on a scale unlike ever before while also helping to uncover interactions between organisms through parasitism and gut content studies (Kennedy et al. 2020).

Studies on biodiversity patterns in agroecosystems have been limited to the Neotropics and continental systems. However, species responses differ significantly between regions (Karp et al., 2018). Therefore, investigating questions across different systems, such as islands, is essential. Island systems are unique in comparison to continental systems for numerous reasons. However, I will only highlight a few. First, island biotas are depauperate, with islands only holding a subset of genera present in continental systems (Gillespie 2016). Second, island biotas evolve without predators and disturbance, often leading to loss of critical defenses and, in the case of birds, becoming flightless. This can make them vulnerable to invasion and disturbance (Graham et al. 2017). Lastly, island systems host high species endemism rates.

Though I have mainly focused on the ecological components of conservation and agriculture, the systemic issues discussed and the actions shaping them are not purely ecological. Instead, they are coupled with human systems. Therefore, it takes an understanding of social mechanisms to fully understand issues such as biodiversity loss and food injustice and tackle them (Berkes 2017). Socio-ecological work leads to more applied interventions in resource management and policy. For example, recent efforts in coastal marine conservation efforts in Hawaiʻi to include community input and governance models have led to a substantial increase in public education and fish stock abundance (Vaughan, Thompson, and Ayers 2017).

How we choose to conduct our work as researchers has consequences that matter. Research with Indigenous communities and on Indigenous lands has long been extractive and harmful. Indigenous Data Sovereignty (IDS) has risen as a movement and field to combat extractive research and usher in a new research paradigm (Carroll et al., 2020). IDS frameworks emphasize proper alignment of the research process with relevant Indigenous governance structures and partnership with appropriate entities. The CARE principles, which stand for Collective Benefit, Authority to Control, Responsibility, and Ethics, are a particularly prominent set of guidelines dictating many scholars' approaches to IDS. While CARE is an excellent guidepost, it does not provide exact instructions on operationalizing IDS. Therefore, IDS can often seem to be a grand goal that is hard to achieve.

In this dissertation, I utilize a socio-ecological framework to identify the mechanisms that determine whether native arthropods can utilize an agroecosystem as a habitat, determine whether Kānaka ʻōiwi agroforestry can conserve native arthropod biodiversity, and highlight what motivates farmers to engage in certain agricultural management practices. This dissertation spans four chapters, with each briefly introduced below.

In Chapter 1, I provide a broad understanding of how human-mediated management shapes the agricultural ecosystems millions of species utilize as habitats. I present a framework to organize global agricultural ecosystems into three categories: coupled, hybrid, and novel. The framework examines to what extent human-mediated management homogenizes resources over space (i.e., one crop in a field vs. 5) and time (e.g., one crop flowering for two months vs many crops flowering over a year), with coupled systems having low homogenization and novel having high homogenization. High homogenization negatively affects biodiversity, especially native species, while low homogenization provides habitat for a diverse assemblage of native species.

In Chapter 2, I investigate what socio-cultural values drive farmers' management decisions. Utilizing sociological data based on semi-structured interviews with Hawaiian and non-Hawaiian farmers, I describe that Hawaiian farmer decision-making is firmly rooted in values aligned with food sovereignty. In contrast, non-Hawaiian farmers' decisions are rooted in values aligned with food security. Hawaiian farmers produce more Polynesian crops and see their farms as a space for community members to connect to culture and land. They see their actions as enacting and perpetuating Hawaiian political sovereignty. Non-Hawaiian farmers frame their actions in a more economic light and see themselves as a safety line during instability.

In Chapter 3, I present empirical arthropod DNA metabarcoding data from various diversified and simplified farm sites in Hawaiʻi. I examine alpha and beta diversity patterns and their correlation to on-farm management and landscape-level measurements. I show that landscape composition determines whether a diversified or simplified farm can support native arthropods. Additionally, I highlight that Polynesian crops shape a unique assemblage of native arthropods. Using this DNA metabarcoding data, I also provide one of the first case studies of applying an Indigenous data sovereignty framework along with the CARE principles to genomic biodiversity data.

In Chapter 4, I zoom in from a broad understanding of species composition shifts between agroecosystems to look at specific interactions between taxa and how these interactions shift based on on-farm and landscape-level measurements. Utilizing a dataset set comprised of the gut content of over 1,000 spiders, I construct bipartite feeding interaction networks between predators (spiders) and their prey. Drawing from calculated network structure and stability metrics, I present findings that landscapes comprised mainly of agriculture structure bipartite networks differently from vegetated landscapes, with consequences on stability. Moreover, on-farm measurements such as canopy cover and crop diversity uniquely shape the structure and stability of networks.

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CHAPTER 1

AGRICULTURAL ECOSYSTEMS

INTRODUCTION

This paper, now published in the *Encyclopedia of Biodiversity*, describes a framework my colleagues and I created to categorize species responses to agricultural management across the globe. We also highlight that agroecosystems are not just a matrix in which biodiversity passes through but are indeed key habitats in it of themselves. This reorients the common rhetoric of the role agroecosystems play in biodiversity conservation. It also emphasizes the need to examine the heterogeneity within agroecosystems and how temporal or spatial management changes can have cascading impacts on biodiversity. This work enabled me to do dive deeper into the global agroecosystem biodiversity literature and elucidate what mechanisms can drive species responses to management. Through writing this paper, I applied its concepts when writing about and conceptualizing my empirical ecological work in chapters 3 and 4.

AGRICULTURAL ECOSYSTEMS

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Abstract

A majority of landscapes across the globe have been shaped by human-mediated management for food and material production over the span of tens of thousands of years, beginning with Indigenous land management. The world's biodiversity must persist within these agricultural ecosystems and utilize them as habitat. Management actions determine the spatial (patchiness) and temporal homogenization (magnitude and duration of resource pulses) of an agricultural habitat, and thus affects the presence of biodiversity. The vast range of agricultural ecosystems across the globe can be organized along a gradient of spatial and temporal homogenization, and classified as coupled, hybrid, and novel systems. The degree of homogenization will determine what proportion of the pre-agricultural biodiversity a system can support. We present examples of these different agricultural systems from around the globe and highlight that these ecosystems act as habitats for organisms spanning from plants to insects to mammals.

1. Introduction

As of 2019, half of the earth's habitable land surface is agriculture (Ritchie and Roser, 2013; Ellis et al., 2010). Humans have transformed landscapes for agricultural production for tens of thousands of years. Biodiversity's first intimate interaction with humans was often through Indigenous land management, including cultural burning and food plant promotion within natural systems, dating back some 40,000 years ago in regions such as Australia (Jones, 2012). However, so-called "natural" systems were long conceptualized as the only systems in which biodiversity can persist. This perception is rooted in a pervasive ideology that sets agricultural systems apart from natural systems (Perfecto et al., 2009) often resulting in agricultural systems being overlooked as potential habitats. However, at both global and local scales, agricultural systems can be heterogeneous, spanning most biomes and utilizing various crops and management practices that create diverse habitats.

Depending on heterogeneous characteristics over space and time of the agricultural habitat, evidence suggests many species across diverse taxa can persist in these systems (Kremen et al., 2019; Kremen and Merenlender, 2018; Perfecto et al., 1996; Mendenhall et al., 2014; Kennedy et al., 2010; Nicholls and Altieri, 2013). We define three distinct habitat agricultural habitat types, building on terms commonly employed in restoration biology (Hobbs et al., 2013): coupled, hybrid, and novel (Figure 1). To distinguish between agricultural habitats, we consider whether a habitat supports species that are similar to preagricultural management species, which we term "native". Consequently, "non-native" species are species that were not present pre-agriculture. Here, we consider coupled systems support a large proportion of native species. Hybrid systems support native and non-native species and can transition to systems with a coupled or into novel systems. Finally, novel systems to be systems that disproportionately support non-native species and cannot transition back to supporting a large proportion of pre-conversion native species.

We consider the impact of agricultural management on native species for a few key reasons. Native species can be particularly vulnerable to the biotic and abiotic shifts that occur with a change in management, especially given their evolutionary history, which may impact their dispersal, reproduction, and overall fitness. Therefore, native species can act as baseline of change due to agricultural management and, thus, be great indicators of a system type (e.g., novel, hybrid, and coupled). However, we would like to honor that whether a species ”belongs” in an ecosystem goes beyond natalism (Cordell et al., 2021). For example, Polynesian wayfinders brought a collection of crop cuttings (e.g., taro, breadfruit, and candlenut) to each new island they found in the Pacific. In Hawai'i, these crops were incorporated into agroforestry systems (Lincoln and Ladefoged, 2014) that resembled the structure of the pre-agriculture forest system it replaced (Winter et al., 2020). Some of these canoe crops provide similar ecosystem functions to native flora (Ostertag et al., 2015) and also provide habitat for numerous arthropod species (Swezey et al., 1954). When managed, these crops were not invasive, rarely expanding beyond the range of the agroforestry system (Ostertag et al., 2015). In addition, canoe crops are incorporated into 'Olelo Hawai'i, the Indigenous K¯ anaka '¯ Oiwi (Native Hawaiian) language,¯ and have been given their own species status independent of the native and non-native binary (Cordell et al., 2021).

Through manipulating resource availability, agricultural management determines whether a habitat is a coupled, hybrid or novel system. Specifically, agricultural management can lead to high resource diversity within an area (spatial heterogeneity) and over a given time (temporal heterogeneity) (Figure 2a). The degree of spatial homogenization will depend on the patchiness and diversity of agriculture management (Figure 2b). Similarly, the level of temporal heterogeneity will depend on variation in the duration and magnitude of resource pulses caused by agricultural management (Figure 2c).

Temporal and spatial management that shapes the degree of heterogeneity, in turn, will determine the diversity and distribution of ecological filters—abiotic and biotic factors that prevent the establishment or persistence of species in a particular location (Chase, 2007; Kraft et al., 2015). For example, changes in water, light, and nutrient availability, as well as the dominant plants and animals within an agricultural habitat, will determine how suitable it is for a species, given its biology. Agricultural homogenization (the opposite of heterogeneity) modifies ecological filters such that only species with limited physical, functional, and life-history traits can persist (Ponisio et al., 2016*a*; Gamez-Viru´ es´ et al., 2015; Duflot et al., 2014; Estrada-Carmona et al., 2022). The higher the agricultural temporal and spatial homogenization, the more significant the shifts in habitat filters, and the lower the proportion of native biodiversity that can persist (Figure 2d). Conversely, many decades of ecological theory have found that the more heterogeneous the habitat, the more biotic diversity it can support (the "diversity begets diversity" hypothesis, Rosenzweig, 1995). In agricultural habitats where pre-agricultural ecological filters have not been homogenized, a higher proportion of native species will be more likely to be supported (hybrid or coupled systems). In contrast, a highly homogenized habitat will be less likely to support native species (novel systems).

Box 1: Agricultural management terminology

- Agriculture: cultivating soil, producing crops, raising livestock, and selectively managing landscapes to increase food resources.
- Crop and non-crop diversification: a variety of techniques that add plant and animal diversity to a system.
- Crop rotations: different crops are planted in succession on the same land. Rotations can be seasonal.
- Monoculture: the cultivation of a single crop in a given area.
- Polyculture: the cultivation of multiple crops in the same row or bed, or in rows or strips that are close enough for biological interaction.
- Cover cropping: non-crop plants cultivated under or between the rows of crop plants. Also known as green manure when plowed back into the soil.
- Wildflower strips: perennial and annual flowers mixed planted between rows of crop plants or along the borders of crop fields.
- Hedgerows: rows of native shrubs planted along field borders.
- Livestock integration: co-locating plant crops and livestock.
- Mixed pasture: two or more forage crop species (grasses and legumes) grown in pasture to control insect and weedy pests.
- Tillage: the turning of the soil to control for weeds and pests and to prepare for seeding.

- Surface soil scraping: mechanical scraping of surface soil to remove debris and flatting soil, often in preparation for harvest.
- Agroforestry: trees and shrubs are grown intentionally among crops and pasture.
- Cultural burn: the utilization of prescribed burning practices to promote culturally significant food and material species.

Three agriculture practices significantly determine the degree of spatial and temporal homogenization: crop and non-crop spatial diversification, crop rotations, and the addition of external inputs (e.g., fertilizers, pesticides, Box 1-2). Crop and non-crop diversification directly affect spatial homogenization, and because plants vary in their timing of flowering, fruiting, and senescence, diversification also impacts temporal homogenization. Adding non-crop plants, such as cover crops, green manure, wildflower strips, trees or hedgerows, can also add spatial and temporal resource heterogeneity (Figure 3a-b). Livestock and bison integration can promote floral and forage species heterogeneity by limiting grass species that tend to dominate landscapes without grazing. With the increase in diversity in these integrated systems, invertebrate and bird diversity tend to increase (Manning et al., 2017; Bruninga-Socolar et al., 2022). Monocultures are more spatially and temporally homogenized than polycultures (Figure 3e-f). For example, the synchronized mass-flowering of monoculture crops creates a pulse of pollen, nectar, and temporary habitat for wildlife (Westphal et al., 2003; Jauker et al., 2012; Cohen et al., 2021) at dramatically high levels in a given area, but only for a short duration (Figure 2c). The lower the local (i.e., within a crop field) and landscape (i.e., between many crop fields) crop and non-crop diversification, the further an agricultural habitat will shift toward a novel system. Similarly, the more rotations within a field and across a landscape (i.e., different crops planted in a staggered rotation), the lower the temporal and spatial homogenization (Figure 2). Conversely, the fewer the rotations (with no rotations being a single monoculture crop) at the local and landscape scale, the further an agricultural habitat will shift toward a novel system (Figure 2).

Adding external inputs can act synergistically with the other drivers of homogenization. For example, fertilizers are intended to homogenize natural spatial variation in soil nutrient content to promote synchronous plant growth. Fertilizers also increase the duration and magnitude of crop resource pulses. In addition, herbicides and other techniques (e.g., tillage, surface soil scraping) are intended to increase the spatial homogenization of plants by killing non-crop plants. Insecticides kill insects, therefore homogenizing those communities directly, and may also indirectly homogenize other species that interact with insects or are exposed secondarily (Tooker and Pearsons, 2021; Bot´ıas et al., 2016; Hladik et al., 2016). Similarly, fungicides are targeted at preventing the growth of fungi, but can also affect higher trophic levels (David et al., 2016; Fisher et al., 2017). Irrigation, moving water from one location to another to standardize soil moisture, can alter local and landscape-level hydrology (Alter et al., 2018). Lastly, selectively releasing insects to a landscape is an input. For example, European honey bees (*A. mellifera*) are brought into agricultural habitats for intensive pollination where wild bees are in short supply to pollinate crops (Kremen et al., 2002; Klein et al., 2012).

Box 2: Agricultural inputs terminology

- Fertilizers: any material (naturally occurring or synthetic) applied to soil or plants to supply nutrients to crop plants. Common fertilizers include nitrogen, phosphorus, and potassium.
- Pesticides: chemicals (naturally occurring or synthetic) intended to kill specific pests. Pesticides include herbicides (plant-targeted), insecticides (insect-targeted), fungicides (fungus-targeted).
- European honey bees (*Apis mellifera*): managed colonies are brought to fields to provide pollination and then often removed once the crop is finished blooming.

We next describe examples of agricultural habitat from coupled, hybrid, and novel systems, focusing on practices shaping their spatial and temporal homogenization and the ramifications for supporting native biodiversity. We would like to emphasize that these examples are set in the context of specific regions and not every type of agriculture can take place in any given biome nor will biodiversity respond in the same way.

2. Coupled systems: Low temporal and spatial homogenization

Coupled systems are highly diverse and have low temporal and spatial homogenization at a given time (Figure 11a-c). The management and structure of coupled systems creates more heterogeneous biotic and abiotic conditions for flora and fauna to use as habitat than either novel or hybrid systems. Management in coupled systems often promotes flora diversity with varying life history traits and phenology that range during a given time (Manning et al., 2017; Nickell et al., 2018). These systems can have similar species diversity to the natural landscape typical of the region they are located within (Quazi and Ticktin, 2016), or in some circumstances, even exceed that diversity (Armstrong et al., 2021; Schuster et al., 2019). Coupled systems can retain native and endemic taxa, including rare and endangered taxa (Figure 5a-c, Ticktin et al., 2018). Therefore, these systems can support a diversity of vertebrates and invertebrates with varying life history traits (Winter et al., 2020; Ponisio et al., 2016*b*; Boyce et al., 2021).

Many coupled systems have been shaped over the span of thousands of years through intimate and continued interaction with Indigenous communities (Nelson, 2008). The template ecosystem Indigenous communities first encountered influenced the development of their knowledge systems, such as Traditional Ecological Knowledge, the body of environmental knowledge held by Indigenous communities and passed down through generations, and cultures (Nelson and Shilling, 2018). Using their various knowledge systems, Indigenous communities applied a wide array of agricultural management practices to produce abundant resources while maintaining culturally and ecologically important biodiversity (Anderson, 2005).

Here we highlight three examples that exemplify coupled systems as habitats for native biodiversity in relation to spatial and temporal homogenization. These systems utilize fire, bison (*Bison bison*), and agroforestry management to produce abundance and sustain communities in North America and Bangladesh (Figure 4a-c, 5a-c, 6a-c). Some of the systems described in the following paragraphs are often not included in mainstream agricultural conversations. This is often due to misconceptions that management by Indigenous communities is passive or simply ’hunting and gathering’ (Norgaard, 2019; Settee and Shukla, 2020). However, the direct tending of these landscapes through fire, seed dispersal, selectively enhancing some crops, and promotion of favorable biotic and abiotic to produce food can be encapsulated by numerous definitions of agriculture, including our provided definition (Settee and Shukla, 2020).

2.1 Bison Grazing in the Great Plains, U.S.A.

The Great Plains stretch across a vast extent of North America from Northern Texas through Montana and North and South Dakota into Canada. This region is comprised of a gradient of tall, mixed, and short grassland covering some 366 million acres (Samson et al., 2004). While still expansive, this represents a fraction of its historical coverage, as much grassland has transitioned to novel agricultural habitat for wheat, corn, and soybean production (Lark et al., 2019). Historically, the system provided habitat for large herds of Bison (*Bison bison*) numbering an estimated 30-60 million (Flores, 2021). Being a primary food and material source for Tribal nations in the region, they utilized an array of management strategies, including fire and temporal hunting strategies, to expand the range of the plains and consequently Bison populations (Morgan, 1980). Over the span of thousands of years, bison and Tribal nations shaped the prairie and each other. However, bison kill drives conducted by European colonists moving westward led to the sharp decline of bison, with only 723 bison remaining by 1902 on primarily privately owned land (Shamon et al., 2022). However, beginning as early as the 1970s, Tribal nations in collaboration with federal agencies (e.g., National Park Service), non-government agencies (e.g., Nature Conservancy), and private entities have been raising bison and reintroducing them. Today there are 20,000 bison on Tribal lands (Shamon et al., 2022).

2.1.2 Spatial heterogeneity

Bison are considered ecosystem engineers, organisms that physically alter their surrounding environment to an extent that affects other organisms and ecosystem functions (Nickell et al., 2018; Geremia et al., 2019). The grazing in which bison engage is one of the most important factors impacting the functioning of the grass prairies of North America (Ratajczak et al., 2022). Grazing alters nutrient cycling and availability along with light availability (Knapp et al., 1999). Grazing can also affect the composition and texture of the soil, which combined with the effect of altered nutrient and light availability on primary productivity, can determine the structure of the plant community, with cascading effects on the structure of consumer communities (arthropods) (Singer and Schoenecker, 2003; Joern, 2005; Bruninga-Socolar et al., 2022).

2.1.3 Temporal heterogeneity

Historically, large herds of bison in the Great Plains made immense seasonal migrations in concert with new plant growth during the spring that propagates from low to high elevations. Recent studies have shown the aggregate grazing pressure bison exert on grasslands, commonly referred to as the Green Wave Hypothesis (Geremia et al., 2019) , can enhance productivity by 40% and modify the green wave by elongating the proliferation of high-quality young vegetation shoots (Frank et al., 2016; Geremia et al., 2019). This in turn prolongs a low temporally homogenized landscape for other species to utilize.

2.1.4 Current Tribal Management Efforts

Tribal-run programs implore strategies for raising and conserving Bison, with an understanding of the tremendous social, cultural, and ecological ramifications a healthy bison herd can exert. Here we summarize the findings of Shamon et al. (2022) of four Tribal run programs using two different management strategies–continuous and rotational grazing– to raise bison in the Northern Great Plains (Figure 4). Each program sets aside herds of bison for commercial and conservation purposes. Bison are culled based on herd dynamics, gender, health, maintenance of genetic diversity, and economic considerations. Each program sees raising bison as a way to spur economic opportunity while revitalizing their cultural lifeways and the health of their communities and landscapes. The Fort Belknap Indian Community (Fort Belknap) is the home of the Nakoda and Aaniiih Nations. The Fort Peck (Fort Peck) Reservation is the home of the Assiniboine and Dakota Sioux Tribes. Fort Belknap has 93 km^2 of pasture with 900 bison while Fort Peck has 97 km^2 of pasture with 670 bison. Fort Belknap and Fork Peck utilize continuous grazing over a large pasture area. Little intervention is used while bison graze. Their main management intervention is to keep the stocking rate, the number of bison grazing in a pasture area, low enough to not overgraze the pasture and decrease forage quality. In comparison to cattle, bison move rhythmically covering a larger area. Bison raised in expansive fenced parcels under continuous management can still surf and modify the green wave to a certain degree (Figure 4c). In these continuous systems, the full range of beneficial ecosystem effects of bison is more likely to be seen (Hillenbrand et al., 2019).

In addition to Fort Belknap and Fort Peck, the Blackfeet Nation, and Rosebud Sioux Tribe have some of the largest Tribal bison management programs in the Great Plains. The Blackfeet program has 625 bison in 36 km^2 of pasture while Rosebud has 112 km^2 of pasture with 800 bison. Both programs utilize rotational grazing as a primary management tool. A large fenced-off area is subdivided into paddocks through inner fences (Figure 4b). Bison are moved between paddocks on time intervals ranging from days to months based on paddock size, grass height and quality, and season. In the early spring, bison enter paddocks with various grasses and sedges measuring a foot high which bison are left to graze on until they measure a few inches high. The bison are then led to adjacent paddocks where the process is restarted over and over again.

2.1.5 Impact on biodiversity

Bison are graminoid (grass and sedge) specialists. By selectively grazing on dominant graminoids, they have been shown to increase native plant diversity and heterogeneity (low spatial homogenization), thus allowing less competitive rarer native species to coexist (Manning et al., 2017). In a 29-year study of the effect of bison reintroduction on grassland diversity, native plant species richness increased by 103% at local scales (10 m^2) and 86% at the landscape scale (Ratajczak et al., 2022). In grasslands, native herbivorous insects are the most abundant food base for predatory insects. Grazing patterns heavily mediate the interaction between these two functional groups through the removal of vegetation for prey to hide in or plant quality for herbivory. In addition, bison create wallows through repeated rolling on the ground (Nickell et al., 2018). This creates a compacted depression in the soil that supports unique assemblages of plants, including native taxa, and soil characteristics. Due to the compacted soil, wallows have greater water retention than the surrounding landscape, and thus filled with water can be utilized as amphibian habitat. Nickell et al. (2018), utilized transect sampling to measure arthropod communities in active and abandoned wallows (2-3 years since active) in the Tallgrass Prairie Preserve in Oklahoma, U.S.A. While active wallows had a lower abundance and diversity of arthropods than non-wallow control plots, abandoned wallows are distinctive microhabitats that support higher arthropod richness, especially for herbivorous species, and seasonally, with the early season (late spring) having much higher abundances. The spatially heterogeneous plant and insect communities formed due to grazing have been shown to support grassland obligate native songbird species as well (Boyce et al., 2021; Williams and Boyle, 2018).

2.2 Cultural Burns in California, U.S.A.

California is a fire-adapted landscape (Keeley and Brennan, 2012). For 13, 000 years California Native Tribes used fire to shape the various ecosystems across the state into what early explorers described as an "Eden", marveling at the diversity and abundance of resources present (Anderson, 2005). Early explorers also gazed at a landscape smoldering with fires set by California Native Tribes to promote the growth of culturally significant flora and fauna as far as the eyes could see. These cultural burns altered the natural fire regime, the frequency, severity, patch size, extent, and season of fire, across the state (Knight et al., 2022). Around 1.8 million hectares burned annually in California before 1800 (Stephens et al., 2007). As a result of the fire adapted landscape, about 54% of the state's flora and fauna requires fire to persist (Barbour and Major, 1988). For example, the cones of the Sierra Lodgepole Pine (*Pinus contorta var. murrayana*) only open to disperse seeds when exposed to intense heat (Wall, 2008).
In the Klamath River Basin in Northern California, the Karuk and Yurok Tribes ignited cultural burns for 9, 000 years (Figure 5a-c, Tushingham et al., 2013). These burns produced rich Oak woodlands that provided the primary staple foods for the Yurok and Karuk–Acorns, berries, deer and elk–in addition to materials needed for regalia and cultural items (Norgaard, 2019). Deliberate policies supporting genocide, land tenure shifts, and the disruption of cultural lifeways enacted by the United States Federal Government and the State of California led to a steep decline of Karuk and Yurok people, the contraction of land under their authority, and the disruption of cultural fires (Norgaard, 2019; Madley, 2016; Norgaard and Reed, 2017). In 1905, the USDA Forest Service initiated fire exclusion policies that went on to be codified throughout the State of California to include the exclusion of cultural burning (Marks-Block et al., 2021). Fire suppression led to an ecosystem transition from oak woodland to the encroachment of dense stands of conifer trees, which impacted the food sovereignty and security of the Karuk and Yurok Tribes (Norgaard, 2019). Moreover, the loss of frequent fires to the landscape has allowed a buildup of dry biomass that fuels large destructive wildfires (Odion et al., 2004). However, since 2013, after years of resistance, community building, and cultural revitalization, the Karuk and Yurok Tribes have led efforts to reintroduce cultural burning to California in collaboration with federal and state fire agencies along with non-government organizations such as the Nature Conservancy (Long and Lake, 2018).

2.2.1 Spatial heterogeneity

The Karuk and Yurok Tribes utilize cultural burns to increase the productivity and functionality of culturally important habitats. The Tribes utilize prescribed burns to prevent and thin single-species stands of trees. Through this managed disturbance, they increase the amount of sunlight reaching the forest floor, as well as increase soil carbon and nitrogen (Wang et al., 2005; Eisenberg et al., 2019; Hamman et al., 2008). This management creates a spatially heterogeneous landscape with an increase in flora diversity, such as shrubs, forbs, ferns, fungi, along with browsing vertebrate diversity, such as deer and elk, all of which are important food and cultural resources (Lawrence and Biswell, 1972; Connor et al., 2022; Halpern, 2016; Long et al., 2021; Tribe, 2010). For example, in post-burn sites, native shrub and forb abundance and richness have increased (Pollak and Kan, 1998; Hankins, 2013). In particular, after a fire, hazelnut (*Corylus cornuta Marsh var. californica*), an especially important basket-making material, becomes more abundant and has a favorable stem width and elasticity for basket-making (Figure 5c, Smith, 2016; Marks-Block et al., 2021).

2.2.2 Temporal heterogeneity

The Yurok and Karuk Tribes apply two types of burns to the landscape: Patch burns (<10 ha) and broadcast burns (>10 ha) (Figure 5b). At the local scale, the frequency at which these burns occur varies from annually to 3-12 year intervals and differs across a landscape (Knight et al., 2022). At both the local and landscape scale, this diverse fire history, also known as pyrodiversity, influences the biotic and abiotic in space and time leading to habitat heterogeneity (Collins et al., 2007; Martin and Sapsis, 1992). This heterogeneity can generate diversity in ecological niches across space and time, thereby allowing a greater number of species to coexist (Stephens et al., 2021). Species that benefit from diverse fires (reviewed in, Stephens et al., 2021) includes understory plants (Wilkin et al., 2021), pollinators Ponisio et al. (2016*b*), birds (Tingley et al., 2016), bats (Steel et al., 2019), small mammals (Roberts et al., 2015); endangered California spotted owls (*Strix occidentalis occidentalis*) (Hobart et al., 2021; Kramer et al., 2021) and even trees (Blomdahl et al., 2019).

The timing of burns and their severity is seasonal. Drawing from a base of traditional ecological knowledge, these communities observe seasonal trends associated with rainfall in order to determine when to burn and what type of burn to pursue. For example, Bill Tripp, Director of the Karuk Tribe Department of Natural Resources, in Norgaard (2019) describes seasonal burns used by his family:

> Right here in the valley, my grandfather, he burned this whole slope that you can see on that side of Orleans, over on the redcap side. He burned that whole slope every three years. He [would] burn it in early October and the rain always put it out. Some years the rain came sooner, some years it came later...But ultimately the rains always put it out.

The emergence of pest species and the planned promotion of beneficial ones also determines the timing of a burn. The understory vegetation and litter in oak-dominated acorn gathering areas is burned in the late summer to late fall to reduce populations of pest frugivorous insects (*Cydia latiferreana, Curculio occidentalis*) that infest the acorns of endemic tanoaks, a culturally important food species (*Notholithocarpus densiflorus*) (Halpern et al., 2022; Manos et al., 2008). The reduction of these highly frugivorous insects has cascading effects on the composition of the oak woodland insect community while leading to the proliferation of tanoak (Bruck and Walton, 2007; Halpern et al., 2022).

2.3 Betel Agroforestry in Bangladesh

In the Northern upland forests of Bangladesh, a plethora of Tribes have managed agroforests for centuries (Alam and Mohiuddin, 1995). The region is dominated by hills with interspersed valleys and classified as subtropical wet evergreen/semi-evergreen that covers 6,700 km^2 of the country (or 44% of total forest land). The annual rainfall is typically around 4,000 mm and primarily falls during the monsoon season between May-October (Quazi and Ticktin, 2016). Agroforests are multi-structured and multi-functional (Mukul and Saha, 2017). These systems have been shown to provide similar abiotic and biotic conditions to forests and thus provide habitat for native biodiversity (McNeely and Schroth, 2006; Perfecto et al., 2009). Agroforests span a wide range of management intensities from clearing an entire understory and replacing it with crops to more specific minimal alterations (Sinclair, 1999). In the case of the Khasia people of northern Bangladesh, the latter minimal alteration type of agroforestry management is utilized to produce betel leaves and nuts (*Piper betle*), a native evergreen perennial vine.
The Khasia have been in the division of Sylhet in northeastern Bangladesh for 500 years practicing various forms of agroforestry (Nath et al., 2003). In the 1940s, Khasia members were employed by the Bangladesh Forest Department to carry out logging and plantation operations in Lawachara National Park which covers 1,250 ha (Figure 6c, Riadh, 2007). When the operations ceased, the Khasia stayed in the national park and each villager was allotted 1.5 ha of forested land in which to live and make a living (Nath et al., 2003). From these allotments sprang various forms of agroforestry utilizing pineapple and lemon. However, betel leaf agroforestry has particularly expanded in the past 50 years due to market forces (Riadh, 2007). Almost all members of a village will engage in betel leaf and nut cultivation as it is the primary economic driver due to its popularity as a chewing stimulant throughout Asia and the Pacific (Figure 6b, Nath et al., 2003).

2.3.1 Spatial heterogeneity

The Khasia grow betel in agroforests under mixed native forest canopies in a practice called “bri”. When preparing a new agroforest, farmers uproot shrubs and ground flora only keeping trees and their saplings. Having beliefs that the betel plant has a strong connection with natural forest, farmers use at least 30 different tree species and their saplings, a majority of which are native, as trellises for the betel vine (Figure 6c, Alam and Mohiuddin, 1995). Betel grows best in moist, cool shade with high soil moisture. Therefore, farmers prune canopy trees annually, but do not fell large trees, and all pruned materials and weeds are used as mulch to maintain soil moisture and maintain fertility (Quazi and Ticktin, 2016). Bri patches are periodically abandoned if there is high crop disease prevalence. While abandoned, these systems see the regeneration of native understory plants and begin to transition back to a pre-agriculture habitat. The selective management of farmers for tree saplings and the inclusion of canopy species creates spatially heterogeneous habitats with similar vegetation richness and abundance in comparison to nearby secondary forests of the same age (Quazi and Ticktin, 2016). Bri have avian species density and richness equal to secondary forests (Mukul, 2014). Moreover, these systems have a higher species richness of common birds and mammals than old-growth secondary forests (Mukul and Saha, 2017). A majority of plant species in the bri systems are animal dispersed. Therefore, bri can be a key native seed source for dispersal to surrounding forests.

2.3.2 Temporal heterogeneity

Khasia management supports the growth of trees of different heights and life stages at various times which provides diverse habitat for birds, mammals, and pollinators (Nath and Inoue, 2009; Quazi and Ticktin, 2016; Mukul and Saha, 2017). In addition, soil moisture and fertility management maintain optimal tree-growing conditions during Bangladesh's dry season. Therefore, through Khasia management, there is a prolonged growing, fruiting and flowering season that can benefit a host of species (low spatial homogenization).

3. Hybrid systems: Intermediate temporal and spatial homogenization

Management in hybrid systems utilizes higher spatial and temporal homogenization than coupled systems. However, hybrid systems defy the the persistent trend towards the spatial and temporal homogenization reflected in novel agricultural habitats, as they still maintain some degree of temporal and/or spatial resource diversity (Martin et al., 2019). The level of spatial homogenization can be similar or distinct to temporal homogenization on hybrid systems, which creates complex and varied resource diversity patterns across space and time. The shift in these patterns will have combined effects on native biodiversity. As a result, as hybrid agricultural habitats move towards novel or coupled systems, they will support more or less native biodiversity. In this section, we will describe four systems that have at least some resource diversity in space or time.

3.1 Rice paddy fields, Sado Island, Japan

Terraced paddy fields stretch upwards on the mountainous slopes of Sado Island (in central Japan) creating a green staircase of interconnected rice fields (Figure 7a-b). These hundreds of paddy fields, of different shapes and sizes, were created for rice production and have now been in rice cultivation since the Edo Period (1603-1867) (Koohafkan and Altieri, 2016). The long history of rice cultivation across Japan transformed landscapes through a network of paddy rice fields connected to adjacent ponds, creeks, and rivers as well as fallow fields, grasslands, and woodlands (Kobori and Primack, 2003; Natuhara, 2013). This mosaic matrix of habitats is part of the "Satoyama" landscape, which comes from the Japanese words "sato" meaning village and "yama" which means hill or mountain to describe landscapes that were formed through centuries of small-scale agricultural and forestry use (Morimoto, 2011; Indrawan et al., 2014; Takeuchi et al., 2016). Since rice farming is one of the major industries on Sado Island, much of the agricultural land is dedicated to rice-producing paddy fields occupying approximately 12.6% of land (Maharjan et al., 2022). The long-standing, traditional management of these paddy fields was built on the sustainable use of resources and has also functioned as surrogate habitats for numerous organisms (Kobori and Primack, 2003; Bambaradeniya et al., 2004).

3.1.1 Spatial heterogeneity

Management of water is one of the main ways rice paddy fields alter resource availability across landscapes. Rice cultivation requires a constant and abundant supply of water (Figure 7b-c). Across the landscape, the traditional rice paddy area is composed of rice paddy fields, ponds, reservoirs, and streams for irrigation or drainage. Therefore, beyond the paddy fields, the cultivation of rice provides spatially heterogeneous sources of water habitat across the landscape. In this way, rice paddy fields can form alternative aquatic habitats to natural water sources that provide refuge for a wide range of aquatic fauna (Natuhara, 2013; Dias et al., 2014; Herring et al., 2019).

3.1.2 Temporal heterogeneity

Throughout the year, farmers also alter the amount and availability of water in rice paddy fields. Paddy fields are flooded for almost a third of the year (spring to summer) and intermittently during summer after a brief mid-summer drainage (Morimoto, 2011; Natuhara, 2013; Usio et al., 2014). Then, they are drained from fall until the following spring (Morimoto, 2011; Natuhara, 2013; Usio et al., 2014). The flooding period consists of shallow water levels mimicking features of wetland habitats. In contrast, the drained periods of the rice paddy fields limit the availability of water to small puddles or none.

3.1.3 Impact on biodiversity

Together, the spatially and temporally heterogeneous availability of water throughout the year influences the presence and movement of organisms, including the Japanese brown frog (*Rana japonica*), grey-faced buzzard (*Butastur indicus*), grey-headed lapwing (*Vanellus cinereus*), and skylark (*Alauda arvensis*), to and from the paddy fields. Likewise, the varying amount of water retained in the paddy fields (e.g., shallow water during the growing period and drained before harvest) creates habitats for different organisms at different times (Amano et al., 2008; Amano, 2009; Katayama et al., 2015*a*). Between spring and summer, the vast amount of flooded paddy rice fields supports a highly diverse and abundant community of wetland species (Natuhara, 2013). For example, various frog species lay eggs in wet paddy fields, and the tadpoles metamorphose into frogs during the rice planting period. Afterward, some of these frog species move onto woodlands or other habitats while some frog species (e.g., Nagoya-daruma pond frog, *R. porosa brevipoda*) stay in paddy fields (Natuhara, 2013). After the flooded period (fall to spring), the drained paddy rice fields provide a suitable habitat for birds, seed eaters, and invertebrates for invertebrate feeders (Jiao et al., 2019). For example, the grey-headed lapwing and skylark make nests in dry paddy fields before flooding, and herons (*Ardea* spp.) prey on aquatic animals and insects after flooding when the height of rice plants is low (Fujioka et al., 2001).

Altogether, nearly 5,000 wildlife species, including birds, amphibians, fish, invertebrates, plants, fungi, and viruses have been recorded in or around paddy fields, including several endangered species (Usio et al., 2014). Of these species, more than 30% (135 species) of 430 native avian species use paddy fields, and 24% (32 species) of 135 species that use paddy fields are designated as threatened at the global or national scale (Fujioka et al., 2010). However, in the past decades, urbanization, modernization of rice production, consolidation of paddy fields, and abandonment of rice cultivation negatively impacted the wildlife that depended on these habitats (Yoshikawa et al., 2010; Natuhara, 2013; Katayama et al., 2015*b*; Osawa et al., 2016*b*,*a*).

Sado Island was the home of the last populations of the Japanese Crested Ibis (*Nipponia nippon*, called “Toki” in Japanese), a species endemic to east Asia, which was historically widespread throughout Russia, China, Korea, Taiwan, and Japan (Figure 7d). The presence of Japanese Crested Ibis declined severely in the middle of the last century because of changes in land use and human activities, such as using fertilizers and pesticides, direct hunting, and the abandonment of paddy rice fields (Li et al., 2009; Yu et al., 2015). In 2008 Japanese Crested Ibises were reintroduced onto Sado Island, Japan, and a rice certification initiative was central to the island-wide efforts. As part of the certification initiative, farmers had to grow Koshihikari rice plants and implement various eco-friendly practices, including strategic flooding and reduction of agrochemical use. Recent studies suggest that the re-introduction efforts on Sado Island have been positive: while the reproductive success of the Crested Ibis is low, its population and number of mature individuals are increasing due to the high survival rates with no extinction probability in the short term (Okahisa and Nagata, 2022). In contrast, reintroduction efforts in the Qinling Mountains of central China (Okahisa and Nagata, 2022) have been less successful (i.e., lower survival rates than Sado Island) due to the deterioration of habitat quality, which is mainly attributed to the abandonment of rice farming (Okahisa and Nagata, 2022) (Wang et al., 2017).

3.2 Milpa system of Mesoamerica

From intentionally burned parcels of land, the Mayas grow food in the lowlands of southern Mexico and northern Central America. This swidden system is called the “milpa” and was developed by Indigenous communities across Mesoamerica, which extends from mid-Mexico to Guatemala, El Salvador, Belize, and western Honduras and Nicaragua (Figure 8a), over 7,000 years ago (Rodr´ıguez-Robayo et al., 2020, 2021). The word milpa roughly means “maize field” and is derived from two Nahuatl words: “milli”, which is a cultivated plot, and “pan”, which is the adverb upon (Rodr´ıguez-Robayo et al., 2020). Milpa is referred to as “kol” in the Mayan language (Silvia and Rasmussen, 1994). Farmers adapt the milpa system to the local environment. The milpa system can take various forms since it is used across Mesoamerica, from sea level to highlands above 2000 m with dynamic differences topography, wind exposure, and moisture patterns (Nigh and Diemont, 2013).

3.2.1 Spatial heterogeneity

The Mayas developed many of the agroecological practices used in the milpa system and, in one form or another, the milpa system has remained a central part of Maya culture and their traditional management of environmental sustainability for millennia (Bernsten and Herdt, 1977; Nations and Nigh, 1980; Gomez-Pompa,´ 1987; Steinberg, 1998; Diemont and Martin, 2009; Isakson, 2009; Nigh and Diemont, 2013). Milpa is a multi-stage cropping system where the cultivation of maize is managed together with fields at various successional stages, from fallow to short-term perennial shrubs and trees to mature closed forest, on the once-cultivated parcels of land (Nations and Nigh, 1980; Silvia and Rasmussen, 1994; Xolocotzi, 1995; Nigh, 2008), which creates a landscape of fields composed of different vegetative resources. Maize is at the basis of the milpa system. It is typically grown in polyculture with beans, squash, and other domesticated, semi-domesticated, and tolerated species (Xolocotzi, 1995; Nigh and Diemont, 2013). Beyond these annual crops, farmers also actively cultivate multiple tree species in the milpa fields for food, wood, and medicine (Nations and Nigh, 1980; Falkowski et al., 2016). In this way, the milpa system is spatially heterogeneous across a landscape, with fields at different stages of the milpa cycle, and within a field, with the simultaneous cultivation of maize, beans, squash, and other plants.

3.2.2 Temporal heterogeneity

Through the multi-stage process of the milpa system, farmers also alter the availability of resources over time. The milpa system begins with burning small patches of land to establish crop fields, in which maize is rotated with other annual crops, and culminates in the re-establishment of the vegetation on land that was previously cultivated(Figure 8b-c, Ben´ıtez et al., 2014; Vallejo et al., 2014; Velasco-Murgu´ıa et al., 2021). In some cases, the successional rotation cycle of crop fields and woodland vegetation can be about 10 to 40 years (Nigh and Diemont, 2013). Farmers only burn and re-establish the maize polyculture when farmers believe the soil has recovered from the previous cultivation (Nigh and Diemont, 2013). Integrating the milpa cycle into the local environment has allowed farmers to intervene in the processes of ecological succession to shape the ecosystem and, thus, form the contemporary woodland habitats across Mesoamerica (Nigh and Diemont, 2013).

3.2.3 Impact on biodiversity

While the milpa system harbors high amounts of crop and non-crop diversity, farmers also provide a rich source of biotic and abiotic resources that allow native biodiversity, including some rare and threatened species, to persist within these agricultural habitats. For example, for the Lacandon Maya, one of the many Indigenous groups residing in southern Mexico, the milpa system has been at the center of their management of the rain forests of Chiapas, Mexico, which also provides habitat for wildlife. As typical of the milpa system, Lacandon farmers establish polycultures dominated by maize on small swidden patches of secondary forest (Nations and Nigh, 1980; Diemont et al., 2006; Martin et al., 2010; Falkowski et al., 2019). Some granivore bird species (e.g., *Sporophila*) consume the maize on these fields (Cook, 2016). While some various frugivore bird species (e.g., *Amazona farinose*, figure 8d) and bats (e.g. *Alouatta palliata*, figure 8e) are also attracted to fruiting tree species (e.g., *Tabernaemontana amygdalifolia*) (Cook, 2016), other tree species can enhance soil fertility (e.g., *Ochroma pyramidale*) (Figure 8f, Falkowski et al., 2016). When fields are fallowed, the soils serve as a seed bank to re-establish the forest, and the early successional vegetation provides new habitat for wildlife (Nations and Nigh, 1980).

The role the milpa and other agroforestry systems can play in biodiversity conservation has been questioned. Some studies suggest that agroforesty can have both ecological, via wildlife conservation, and socioeconomic benefits (Vandermeer and Perfecto, 2005; Philpott et al., 2008; Weisser et al., 2017) while others assert that agroforests are unable to support threatened species as successfully as protected forest areas (Green et al., 2005; Bhagwat et al., 2008; Hulme et al., 2013; Chandler et al., 2013) and could negative impacts on the soil ecology when agroforests are established on burned parcels of land. In the Lacandon rain forest, the bird community across the various stages of the milpa system is structurally similar to the bird community in surrounding protected areas (Falkowski et al., 2020). This provides evidence that the mixture of open areas and trees in the milpa system are important habitats for bird species; it may also affirm that the thousand years of management by the Lacandon Maya has had lasting impacts on the biotic communities present in across the region (Fernandez-Vega et al., 2017). East of the Lacandon rain forest, overwintering migratory bird species in the Yucatan peninsula also appear to be preadapted to the contemporary landscapes formed by the milpa system, which includes open fields dedicated to maize polycultures and other parcels of land at various stages of vegetation succession (Lynch and Whigham, 1995). Despite the ecological importance of milpa systems, they are increasingly being abandoned, which could impact their potential role in conservation (Falkowski et al., 2020).

3.3 The dehesa system of the Iberian Peninsula

The "dehesas" of the Iberian Peninsula are human-made ecosystems with two strata: a sparse canopy of various species of oak trees and a herbaceous understory that is periodically grazed by livestock, such as cattle, goats, pigs, and sheep, and sometimes removed for crop fields. The word "dehesa" is derived from the Latin word "defensa" meaning fenced to refer to land that was enclosed by fences to defend against intruders (Paleo, 2010). The origins of the dehesas date as far back as 4000 BCE (Stevenson and Moore, 1988) and were integrated into Palaeolithic and Mesolithic cultures of South-west Spain (Davidson, 1980) with the development of livestock breeding (Edmondson, 1992). Today, dehesa habitats are distributed across the woodlands of the southwestern Iberian Peninsula (Figure 9a) occupying 2.3 million hectares in Spain and 0.7 million hectares in Portugal, where they are also called "montados" (Moreno and Pulido, 2009). Dehesas are adapted to the Mediterranean forests and shrubland, the highly variable climate, the low fertility of soils, and the usually undulating topography that make arable farming unprofitable in this region. The adaptive management of the dehesa system contributes to its long-standing presence as a dominant habitat across the Iberian Peninsula.

3.3.1 Spatial heterogeneity

The emblematic feature of dehesas is the rearing of traditional livestock breeds at low stocking densities through the careful utilization of various tree species in the highly variable Mediterranean climate (Figure 9b-d, Joffre et al., 1999; Plieninger and Wilbrand, 2001). Dehesas are formed by simplifying the structure of Mediterranean forests and shrublands in favor of a grassland understory and low tree density (Montero et al., 1998; Plieninger, 2006). The type of trees maintained is integral to the dehesa system. Trees belonging to the genus *Quercus* (oak), such as the holm oak (*Quercus ilex sp. ballota*) and cork oak (*Quercus suber*), are often used although other tree species such as beech and pine trees may also be present. The trees are strategically scattered across space to maximize light availability for the understory grasses (Joffre et al., 1999) and cultivated cereals (oats, barley, wheat), both of which are used as grazing resources (Montero et al., 1998; San Miguel Ayanz, 1994). Different types of livestock (cattle, sheep, goats, pigs, horses) are also common, but their presence in the dehesa varies by season, climate, and management goals (Figure 9b,d Moreno and Pulido, 2009; Kaonga, 2012). Apart from oaks and livestock, the dehesa system also supports the production of wild game, mushrooms, honey, and firewood. In this way, the management of the dehesa system generates fine-scale mosaics of resources due to differences in stand composition, density, and structure and the variety of grazed, shrubby, and cultivated herbaceous plants (D´ıaz et al., 1997).

3.3.2 Temporal heterogeneity

The management of oak trees is an especially integral part of the dehesa system's ability to support biodiversity. For centuries, purposeful planting and pruning system has been implemented in a way that supports biodiversity rather than reduces it. For example, several prunings are done during the life of the oaks to maximize acorn production, which is a high-quality stock feed (Ruperez, 1957; Joffre et al., 1999; Kaonga, 2012). Despite regular pruning, oak trees are managed to persist for about 250 years whereas the understory is typically cleared every 7-10 years to prevent shrubland habitat or unintended oak seedlings from establishing. The integration of livestock is also temporally heterogenous. For example, pigs are introduced in late fall to early winter when acorns are abundant (Moreno and Pulido, 2009).

3.3.3 Impact on biodiversity

The dynamic changes of resource availability and diversity in the areas between isolated trees in the dehesa system (Moreno et al., 2016) have positively affected biodiversity (Manning et al., 2006; Maran˜on et al.,´ 2009; D´ıaz et al., 2013) supporting a rich diversity of plants and animals. Long-standing evidence has shown that even a single 220 ha dehesa habitat can support approximately 264 fungi, 75 bryophytes, 304 vascular plants, and 121 vertebrate species (Moreno and Pulido, 2009). Several globally threatened species also depend on the dehesa system because it provides a variety of resources across the different microhabitat types that can be used for feeding or breeding purposes (Carrete and Donazar,´ 2005) Some of these species include the Imperial Eagle (*Aquila adalberti*), Black Vulture (*Aegypius monachus*), Black Stork (*Ciconia nigra*), Common Crane (*Grus grus*), and Iberian lynx (*Lynx pardinus*). In fact, the dehesa system has become a focal point for the conservation efforts of the Iberian lynx (D´ıaz et al., 2013).

The Iberian lynx is a medium-sized carnivore endemic to Spain and Portugal (Gaston´ et al., 2019; Garrote et al., 2020) that was once distributed throughout most of the Iberian Peninsula (Figure 9e). By the beginning of the 20th century, its range began to contract disappearing from much of its original distribution by the end of the century. In the first years of the 21st century, its range had contracted to only 100 individuals between two isolated areas (Gaston et al.,´ 2019; Garrote et al., 2020). Recent conservation efforts have focused on the dehesa because the Iberian lynx is more likely to establish home ranges within permanent crops and heterogenous agricultural lands, which are characteristic of the dehesa system, but avoid intensively managed agricultural habitats, such as strawberry fields (Gaston et al.,´ 2016). Recently, a habitat suitably model predicted that over half of the potential area suitable for the Iberian lynx is outside of protected forest areas (Garrote et al., 2020). Therefore, the dehesa system throughout the Iberian Peninsula will continue to be a critical habitat for the long-term survival of Iberian lynx populations.

3.4 Transitioning to and from hybrid habitats

The rice paddy fields in Sado Island, milpa in southern Mexico, and the dehesas of the Iberian peninsula demonstrate that hybrid agricultural habitats can support biodiversity. Hybrid habitats still retain some degree of resource heterogeneity, which is key to the persistence of several species, including those considered endangered (e.g., the flooded paddies for the Japanese Crested Ibis (*Nipponia nippon*), the fruit-bearing trees in milpas for multiple bird species, and the sparse oak tree canopy for the Iberian lynx (*Lynx pardinus*.

3.4.1 Transitioning from hybrid to novel systems

Many of these agricultural habits continue to be transformed into habitats that are more spatially and temporally homogeneous through a combination of agricultural simplification (via a reduction in spatial and temporal diversity of crops) and farmland abandonment (e.g., paddy rice fields in Japan, milpas in Mexico, and dehesas in the Iberian Peninsula). While paddy rice fields in Japan are experiencing a resurgence with positive impacts on the endangered Japanese Crested ibis, other hybrid agricultural habitats continue to be homogenized, consolidated, or simply abandoned. For example, the Chianti agricultural region of Tuscany was once largely cultivated as an agro-sylvopastoral system (Figure 10a-b, Gualandi and Gualandi, 2016). Then, beginning in the 1950s, crop fields were increasingly homogenized and consolidated due to, in part, the pressures of increasing specialization and standardization of marketable varieties (Santoro et al., 2020). The conversion to large extensions of farmland devoted to monocultural crops and reduction of other adjacent vegetation, such as the presence of hedgerows known to function as ecological corridors, created agricultural habitats that were no longer suitable for farmland birds and also for reptiles (Simoncini, 2011; Santoro et al., 2020). As the large monocultures extended into hill slopes, the lack of water run-off control increased the sediment in the surrounding streams. This impacted species that required clear, cold water such as the fish vairone (*Leuciscus souffia*) and the crab (*Potamon fluviatile*) (Simoncini, 2011; Santoro et al., 2020).

Likewise, the formation and presence of the Iron Curtain (1948–1990) between Eastern and Western European drove agricultural land-use changes with two opposing farming strategies (Figure 10c-d). During this period, the West maintained farms smaller in size and retain much of its on-farm heterogeneity (Batary et al.,´ 2017; Clough et al., 2020). In contrast, to increase production, farmland consolidation in the Eastern bloc transformed small, diversified farms into large-scale operations by removing minor field roads, field margins, hedgerows, and any semi-natural habitat (Batary et al., 2017; Clough et al., 2020).´ The result was a dramatic loss of farmland biodiversity, and it continues to impact wildlife to this day (Happe et al., 2018). In some cases, bird diversity decreases 1.5-fold on farms in Eastern versus Western Europe (Austria versus Czech Republic) (Sˇalek et al.,´ 2021).

3.4.2 Inhibiting the transformation of hybrid systems to novel systems

To counteract the negative impacts homogenizing agricultural habitats, practices that increase on-farm heterogeneity have had promising effects on biodiversity. Crop rotations, crop diversity, the introduction of cover crops, and crop-livestock integration could have important and positive impacts on biodiversity even in landscapes that have been drastically homogenized over the years. In a meta-analysis, Beillouin et al. (2021) demonstrated that the use of agroforestry, cover crops, crop cultivar mixtures, intercropping, and crop rotations can have positive impacts on the associated biodiversity in agricultural habitats. Cover crops, for example, when used can provide a pulse of resources for wildlife between cash crop production (Figure 10e). The midwestern U.S.A. is dominated by a monoculture of maize and soybean and has negatively impacted native biodiversity. Yet, recent studies suggest cover crops can provide habitat for several bird species (Wilcoxen et al., 2018). On the western coast of the U.S.A., farms with integrated livestock supported a higher diverse community of native birds than crop-only farms (Figure 10f, Smith et al., 2020). Even for more specialized organisms, such as the squash bee (*Eucera* spp., formerly *Peponasis* spp.), crop diversification can improve their abundances, especially when surrounded by homogeneous agricultural habitats (Figure 10g, Guzman et al., 2019). However, the effectiveness of the agri-environment schemes in Europe, which were focused on increased farm biodiversity through various management practices, has had inconsistent results (Kleijn et al., 2011). While farmers are adopting diversification practices, studies that examine how reducing homogeneity on agricultural habitats (e.g., via crop rotations, crop diversity, cover crops, crop-livestock integration) on native biodiversity remain scarce.

3.5 Novel systems: High temporal and spatial homogenization

Novel systems have altered the diversity and distribution of pre-agricultural biotic and abiotic conditions so drastically that it is improbable that they can support a high proportion of native species again. Though many so-called “conventional” or “industrial” agricultural systems are locally homogenized, few reach the degree of conversion where a shift back to a hybrid system is impossible. To be a novel system, agricultural management must have created widespread spatial and temporal homogenization due to limited crop diversification and limited restored or preserved non-crop habitat. In addition, significant use of fertilizers has altered nutrient cycling, and pesticides have contaminated the soil and water. Soil disturbance and water redistribution can also change the hydrological cycle. For example, corn cultivation in the “Corn belt” of the central U.S.A. has altered the hydrological cycle of the region (Alter et al., 2018). Other examples of novel systems include almond cultivation in California, U.S.A., (Durant, 2019), Concentrated Animal Feeding Operations in North America and Europe (CAFOs) (Spellman and Whiting, 2007) and oil palm cultivation in Southeast Asia, Latin America and West Africa (PALM, 2016; Potter, 2015). Interestingly, few of these systems have detailed records of the pre-agricultural biodiversity, and studies on contemporary biodiversity focus on agriculturally-relevant species such as pollinators and natural enemies. Here we use almond cultivation in California, U.S.A., as an exemplar of novel systems in agriculture.

3.5.1 Almond orchards in California, U.S.A.

Almond (*Prunus dulcis*) orchards in California are a spatially and temporally homogeneous habitat, covering 1.37 million acres in 2022 (Figure 11a-c, USDA, 2021). The almond orchard area in California exceeds that of many countries, including Trinidad and Tobago and Luxembourg. Orchards are concentrated in the Central Valley, a flat valley ringed by the Sierra

Nevada Mountains to the East and the Coast Range to the West (Figure 11a). California almond growers now produce 99% of all almonds in the United States and 80% of the global supply (Boriss and Brunke, 2005). We hypothesize that almond orchards are a novel ecosystem, as evidenced by a higher degree of local and landscape-level spatial homogenization, temporal homogenization, and high external inputs relative to hybrid or coupled systems.

Before its conversion to agriculture, the California Central Valley was a heterogeneous, highly biodiverse coupled system, managed, in part, by cultural burning (See Section Cultural Burns in California U.S.A.). It was composed of a mixture of prairie, seasonal vernal pools, oak savanna, marsh, and riparian forest (Katibah, 1984; Anderson, 2005; California State University, Chico Department of Geography and Planning and Geographic Information Center, 2003; Garone, 2020). John Muir, in *The Mountains of California*, paints a picture of what the habitat was in the 1890s before industrial, agricultural conversion:

> The Great Central Plain of California, during the months of March, April and May, was one smooth, continuous bed of honey bloom, so marvelously rich that, in walking one end to the other, a distance of more than four hundred miles, your foot would press about a hundred flowers at every step...When I first saw this central garden, the most extensive and regular of all the bee pastures of the state, it seemed all one sheet of plant gold, hazy and vanishing in the distant, distinct as a new map of the foothills at my feet...Sauntering in any direction, hundreds of these happy sun-plants brushed against my feet at every step, and closed over them as if I were wading in liquid gold.

These grasslands supported diverse and abundant wildlife. Hundreds of thousands of endemic tule elk (*Cervus elphanus nannodes*) grazed the valley alongside flocks of California quails (*Callipepla californica*) each with thousands of individuals (Anderson, 2005). Waterfowl including ducks and geese overwintered in the valley’s waterways, and while millions of salmon (*Oncorhynchus keta, O. kisutch and O. tshawytscha* ran up every major river or creek (Anderson, 2005). Before European colonization, the native peoples of California—speaking as many as 100 different languages—managed the valley (Anderson, 2005) (See Section Cultural Burns in California, U.S.A.). The transition from a coupled to a novel system began with the genocide of the native peoples of California and the cessation of cultural burning and then the conversion of land to more homogeneous land uses including industrial agriculture (Anderson, 2005; Olmstead and Rhode, 2017).

3.5.2 Spatial homogenization

Though almonds were planted in California as early as 1853 (Geisseler and Horwath, 2014), it was not until the 1960s that acreage began expanding from 100, 000 bearing acres to over a million acres in 2017 Geisseler and Horwath (2014); USDA (2016). Studies attribute expansion to market expansion and an increase in the irrigated area in the center of the Central Valley—the San Joaquin Valley—where soils and climatic conditions are ideal for almond production (Geisseler and Horwath, 2014; Durant, 2019). In the leading almond-growing counties of California, a person can drive for hours up the N-S interstate 5 and see nearly uninterrupted almond orchards on either side of the highway (Figure 11a, USDA, 2021). Almonds now occupy ∼ 14% of harvested agricultural land in California (Figure 11a, USDA, 2021).

At a local scale, almonds are grown in monoculture rows of alternating varieties; the orchard floor is most often kept bare (Figure 11b, Haviland et al., 2017). However, in a 20192020 survey of almond growers, 35% self-reported that they grew cover crops within the last five years (Durant and Ponisio, 2021), suggesting some small-scale, pulsed diversification of flora.

Only 19% of growers reported they grew permanent habitat, defined in the survey as "year-round herbaceous and/or woody plant species (e.g., hedgerows, perennial or re-seeding wildflower strips, riparian forests, filter strips) that are maintained along at least some of the edges of the orchard" (Durant and Ponisio, 2021). Adoption rates of these diversification practices varied by region, potentially because of differences in water availability (Durant and Ponisio, 2021).

3.5.3 Temporal homogenization

Almonds begin to bloom around Valentine's day (February 14) and usually finish within two weeks, depending on tree age, variety, and latitude (Traynor, 2017). In 2021, the yield per acre was 2, 200 USDA (2021). Therefore, based on the total acres in production, we can estimate 3 billion almond flowers bloom within a few weeks each year. This scale of a floral resource pulse is unprecedented in natural systems (Figure 11c). Beekeepers from around the nation bring thousands of colonies into almond orchards on flatbed- and semi-trucks (Figure 11e) to pollinate these flowers (Figure 11d). Currently, two colonies per acre are recommended by crop experts (USDA, 2018), which translates to needing two million European honey bee colonies to pollinate almonds—nearly 88% of all managed colonies in the country (Goodrich and Durant, 2020).

3.5.4 External inputs

Along with being spatially and temporally homogeneous, almond orchards require high external inputs. Almond orchards require approximately 9.5% of the state's agricultural water (The Almond Board, 2017). The extraction of groundwater for almond and other crop cultivation is causing land subsidence, evidenced by the positive relationship between the density of wells in the Central Valley is positively related to the amount of subsistence (Jeanne et al., 2019). Fungicides are applied in the spring to avoid the blooms being destroyed (USDA, 2018). These chemicals have been shown to affect *A. mellifera* worker survival (Fisher et al., 2017). Pesticides to kill insect pests, including organophosphates and pyrethroids—the latter of which has increased in use since the 1990s (Liu et al., 2012)—runoff into waterways (Weston et al., 2004; Amweg et al., 2005), are detectable in fog (Seiber et al., 1993), and volatilize to be transported to the neighboring Sierra Nevada (Aston and Seiber, 1997; LeNoir et al., 1999). Herbicides are also used to limit vegetation between orchard rows (USDA, 2018). In addition, according to a study conducted in 1999, 90% of growers apply nitrogen fertilizer (Geisseler and Horwath, 2014). Finally, commercial honey bee colonies are another currently necessary input because wild pollinator populations are limited by semi-natural habitat proximity (Klein et al., 2012) and therefore cannot provide sufficient pollination given the current conditions. Honey bee importation is therefore needed for crop production.

3.5.5 Impact on biodiversity

The conversion of Muir's "central garden" to intensively managed agriculture in combination with urbanization and other drivers of land-use change have come at the cost of the region's biodiversity. Species that were once common are now considered threatened or endangered across many taxa, including fish (e.g., Chinook salmon, *O. tshawytscha*), mammals (e.g., San Joaquin kangaroo rat, *Dipodomys nitratoides*; San Joaquin kit fox, *Vulpes macrotis mutica*), reptiles (e.g., giant garter snakes, *Thamnophis gigas*), invertebrates (e.g., Midvalley fairy shrimp, *Branchinecta mesovallensis*) and plants (e.g., Solano Grass, *Tuctoria mucronata*) (California Department of Fish and Wildlife, 2022*b*,*a*). The once dominant tule elk (*C. elphanus nannodes*) was saved from the brink of extinction in the midnineteenth century, but its population is still largely extirpated from the valley (Huber et al., 2011). Using a public database of endangered and threatened species occurrences in the Central Valley, Liu et al. (2012) found that species occurrence was negatively related to pesticide use in agricultural areas suggesting these chemicals limit persistence in and/or recolonization of these areas. Field surveys within almond orchards are limited to agriculturally relevant ecosystem service providers, including pollinators and natural enemies (Eilers and Klein, 2009; Klein et al., 2012). Studies found that the native pollinators and natural enemies populations are related to semi-natural habitat proximity, suggesting almond orchards alone, given current management, may be unable to support these communities (Eilers and Klein, 2009; Klein et al., 2012). Surprisingly, the only comparison of historical (1920s) and 20*th*-century bird communities found that species occupancy and richness have remained remarkably stable over the past century (MacLean et al., 2018). Given that this is the only study of community-level change in this system, it is impossible to know which other taxa may be similarly able to persist. More broadscale biodiversity surveys, in addition to specific surveys for threatened and endangered species, are needed in almond and other agricultural habitats to assess current, native species distributions. Assessing the extent of extinction, however, may be hindered by the lack of historical surveys of many species groups, such as insects.

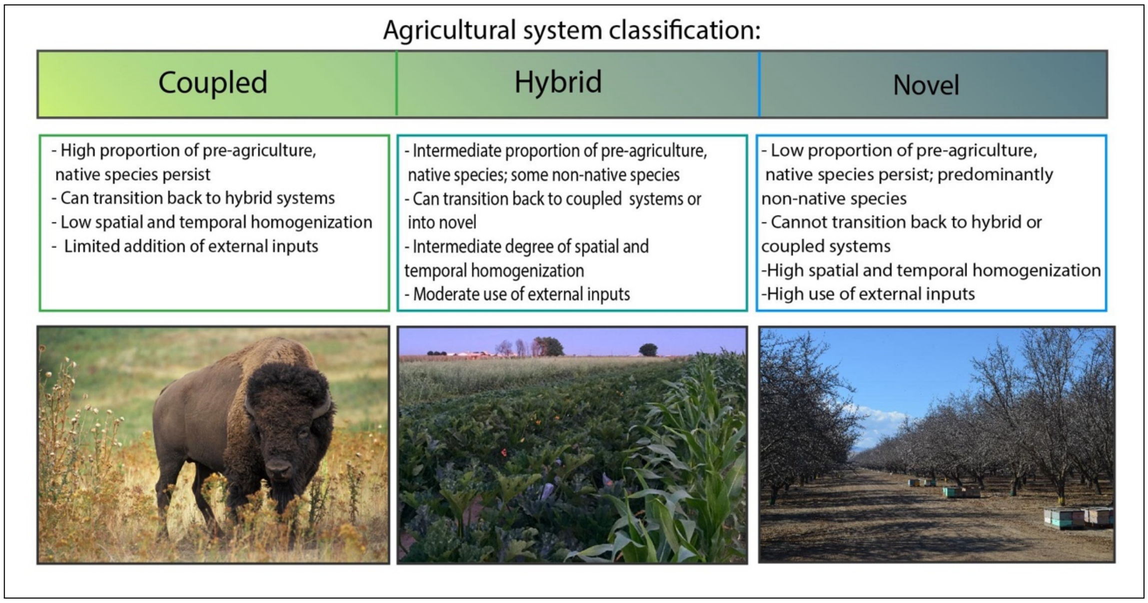
4. Concluding remarks

Agricultural habitats, regardless of their degree of homogenization, are unarguably part of the landscape matrix that biodiversity interacts with. Shifts in the homogenization of these agricultural habitats will considerably impact the biodiversity that encounters these patches in the landscape. Novel systems, such as almond orchards, have high spatial and temporal homogenization, and have experienced high species loss. In addition, any biodiversity that may remain in these systems may be affected by intensive inputs like insecticides and fungicides. Novel systems are unlikely to support a high proportion of native species. Hybrid systems encompass a wide array of agricultural systems, such as the Rice paddy fields of Sado Island or dehesa system of the Iberian Peninsula. They have some degree of temporal and spatial heterogeneity that may be more similar to novel or coupled systems. Therefore, hybrid systems can support a higher proportion of native species or a lower proportion. coupled systems, such as the bison grazing in the Great Plains, have low spatial and temporal homogenization. Novel and hybrid systems support the highest proportion of native species.

Socio-cultural, economic, and political factors have shaped the management of agricultural habitats in the past, present and into future. For example, coupled systems are tended by communities with certain cultural value systems that prioritize community health, biodiversity, and food sovereignty (Hutchins and Feldman, 2021). Economic factors also play a role in coupled systems, as is the case with the expansion of almond orchards (see novel systems section). A history of colonization, which came with population decline, land tenure, and value system shifts, led to the transition of many coupled systems to hybrid, novel or pre-agricultural systems. In addition, political barriers exist. In northern California, policies enacted by the state and federal governments severely limited the use of cultural burns for many decades. However, the revitalization efforts of members of communities such as the Karuk and Yurok are leading to the expansion of coupled systems once again.

Decades of biodiversity conservation initiatives have ignored the habitat agriculture systems provide, nor the diverse and deep-rooted hands that tend landscapes (Perfecto et al., 2009). However, as we have shown, agricultural systems, especially below high levels of temporal and spatial homogenization, can provide a habitat for a whole suite of species. In an era rife with increased food production demand, climate change, and biodiversity loss, we must reconcile society's bleak perspectives of agriculture and biodiversity with the opportunities these landscapes have and can continue to have in addressing these pressing issues.

5. Figures



Coupled	Hybrid	Novel
- High proportion of pre-agriculture, native species persist - Can transition back to hybrid systems - Low spatial and temporal homogenization - Limited addition of external inputs	- Intermediate proportion of pre-agriculture, native species; some non-native species - Can transition back to coupled systems or into novel - Intermediate degree of spatial and temporal homogenization - Moderate use of external inputs	- Low proportion of pre-agriculture, native species persist; predominantly non-native species - Cannot transition back to hybrid or coupled systems -High spatial and temporal homogenization -High use of external inputs

Figure 1. Classification of agricultural habitats using modified terminology from restoration biology (Hobbs et al., 2013). Examples are bison grazing in the Great Plains, U.S.A., high diversity polyculture in California, U.S.A., and almond orchards in California, U.S.A. Photos by J. Dykinga (a), A. Guzman (b) and L. Ponisio (c).

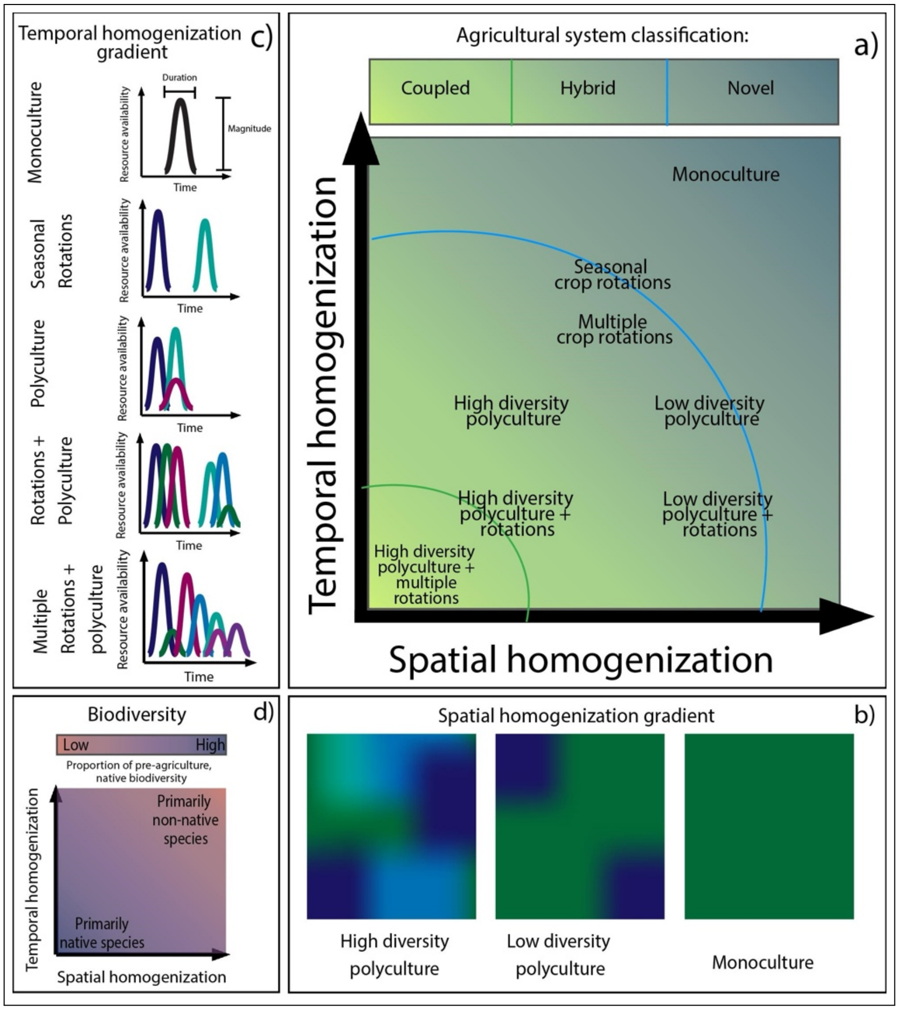


Figure 2. (a) Agricultural habitats vary in their degree of temporal and spatial homogenization, which, combined with the amount of external inputs added to the system, determines whether a habitat is novel, hybrid, or coupled system (z-axis, color gradient). Different agriculture management practices, such as crop rotations and polyculture, determine the degree of temporal and spatial homogenization. Exemplar agricultural systems are placed on the spatiotemporal homogenization gradient. Here, polyculture is an example of local crop or non-crop diversification. The placement of the divisions between novel, hybrid or coupled systems is illustrative and not exact. (b) Spatial homogenization will depend on the patchiness of the habitat. Different colors represent the spatial distribution of different crops. (c) Temporal homogenization will depend on the magnitude and duration of resource pulses, such as flowers, nutrients or water, in the system. Different colored curves represent the resource pulse of different crops. (d) The degree of spatial and temporal homogenization will determine the proportion of pre-agricultural native species (z-axis, color gradient) an agricultural habitat can support. The higher the degree of homogenization, the lower the proportion of native species that can persist.

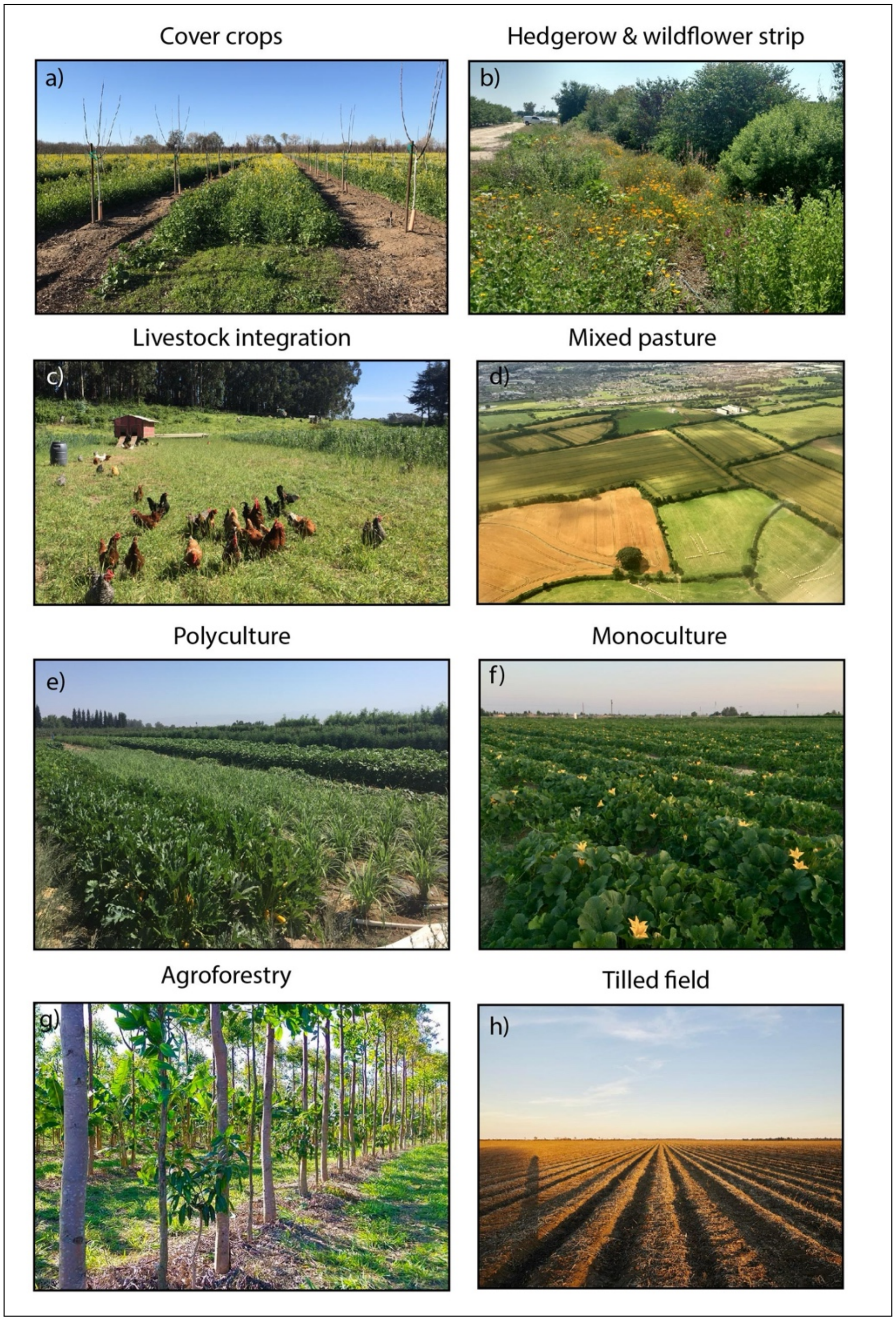


Figure 3. Examples of agricultural management practices. Photos by: A. Guzman (a, c, d, e, f), L. Ponisio (b), GrowCycle Creative Commons License (g), C.M. Highsmith, Creative Commons License (h).

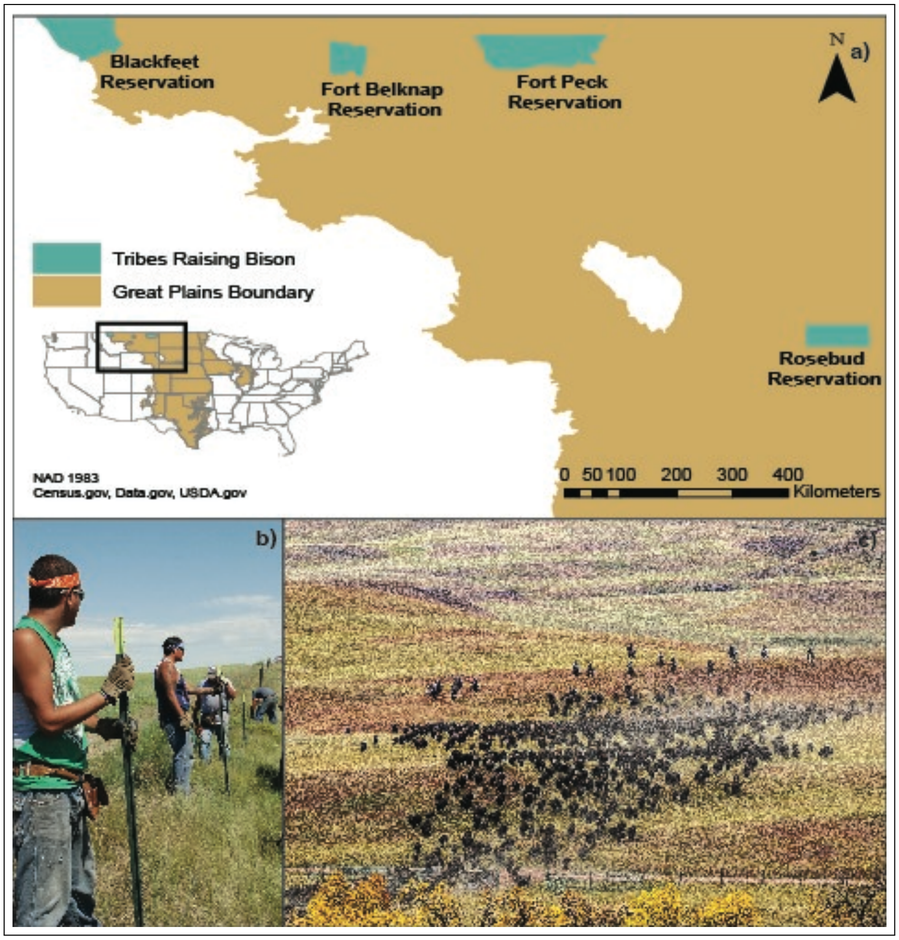


Figure 4. The four Tribal nations with the largest bison herds in the Great Plains (a). Tribal members construct fences (b) to raise bison in paddocks or continuous grazing (c). Photos by Wikimedia Commons (b-c).

Figure 5. The Karuk and Yurok Tribes lead cultural burn revitalization efforts in California (a). Tribal members use drip torches to ignite low-intensity fires (b) to promote the growth of culturally significant plants such as hazel for basket cap making (c). Photos by Wikimedia Commons (b-c).

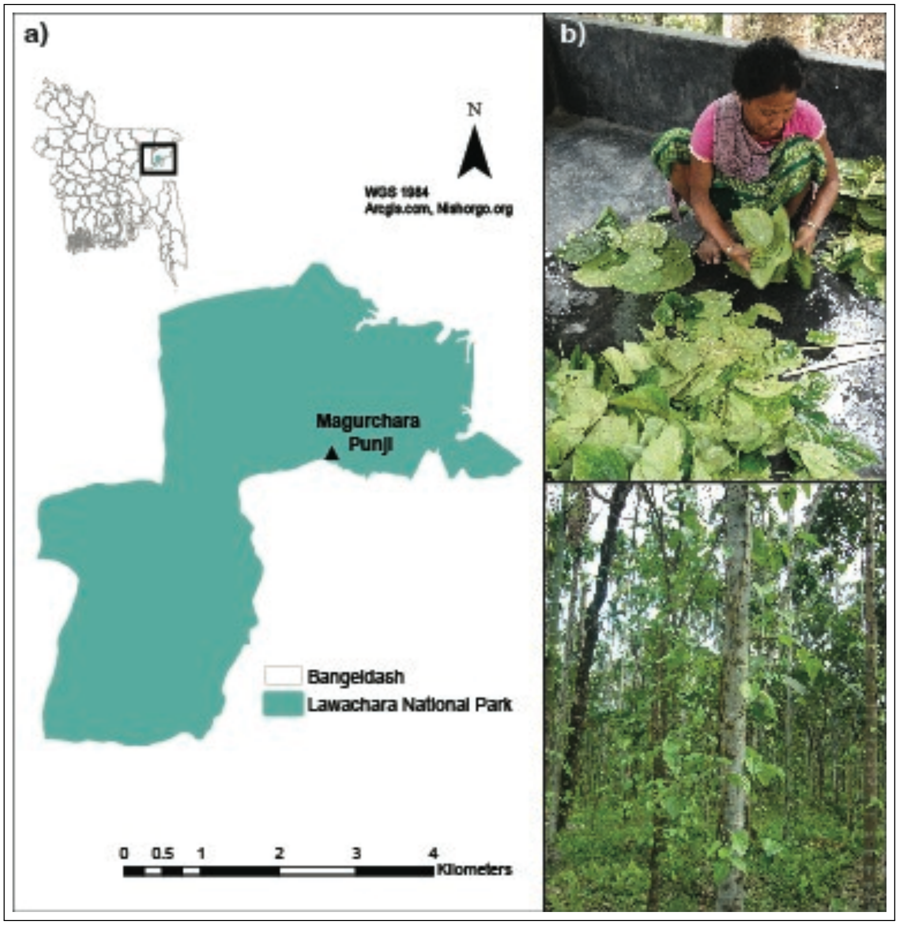


Figure 6. Magurchara Punji is the primary Khasia village engaging in betel agroforestry in Lawchara National Park, Bangladesh (a). Almost all villagers engage in growing and processing betel leaves and nuts (b) due to their popularity as a stimulant in many countries in Asia and the Pacific. Villagers manage tree and sapling density to utilize in order to utilize them as trellises for the betel vine (c). Photos by Wikimedia Commons (b-c).

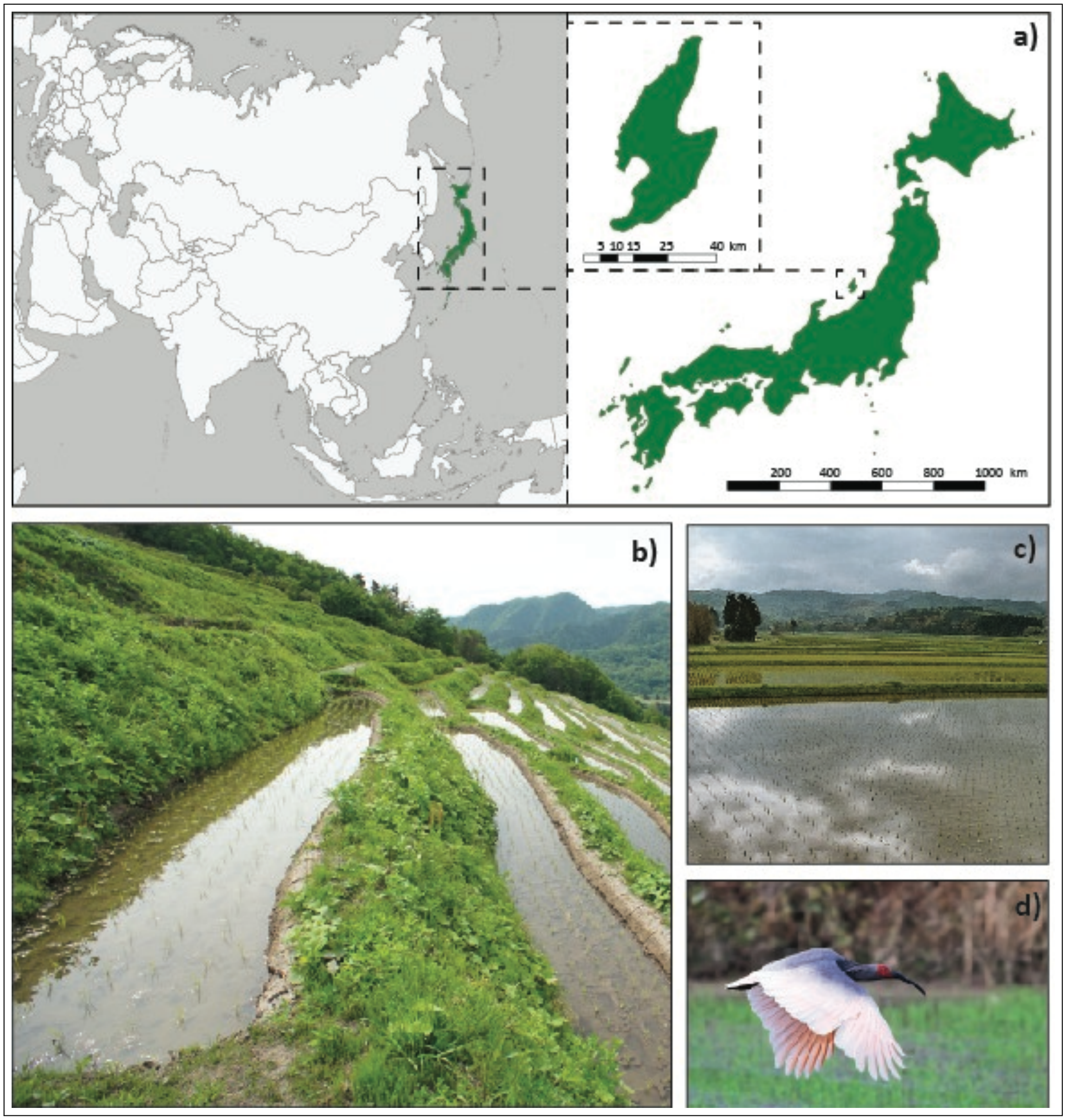


Figure 7. On Japan's Sado Island (a), rice paddy fields paddy fields (b-c) provide essential resources to wildlife. In recent years, the rice paddy fields have been crucial to reintroducing the Japanese Crested Ibis, called Toki in Japanese (d). Photos by Wikimedia Commons (a-d).

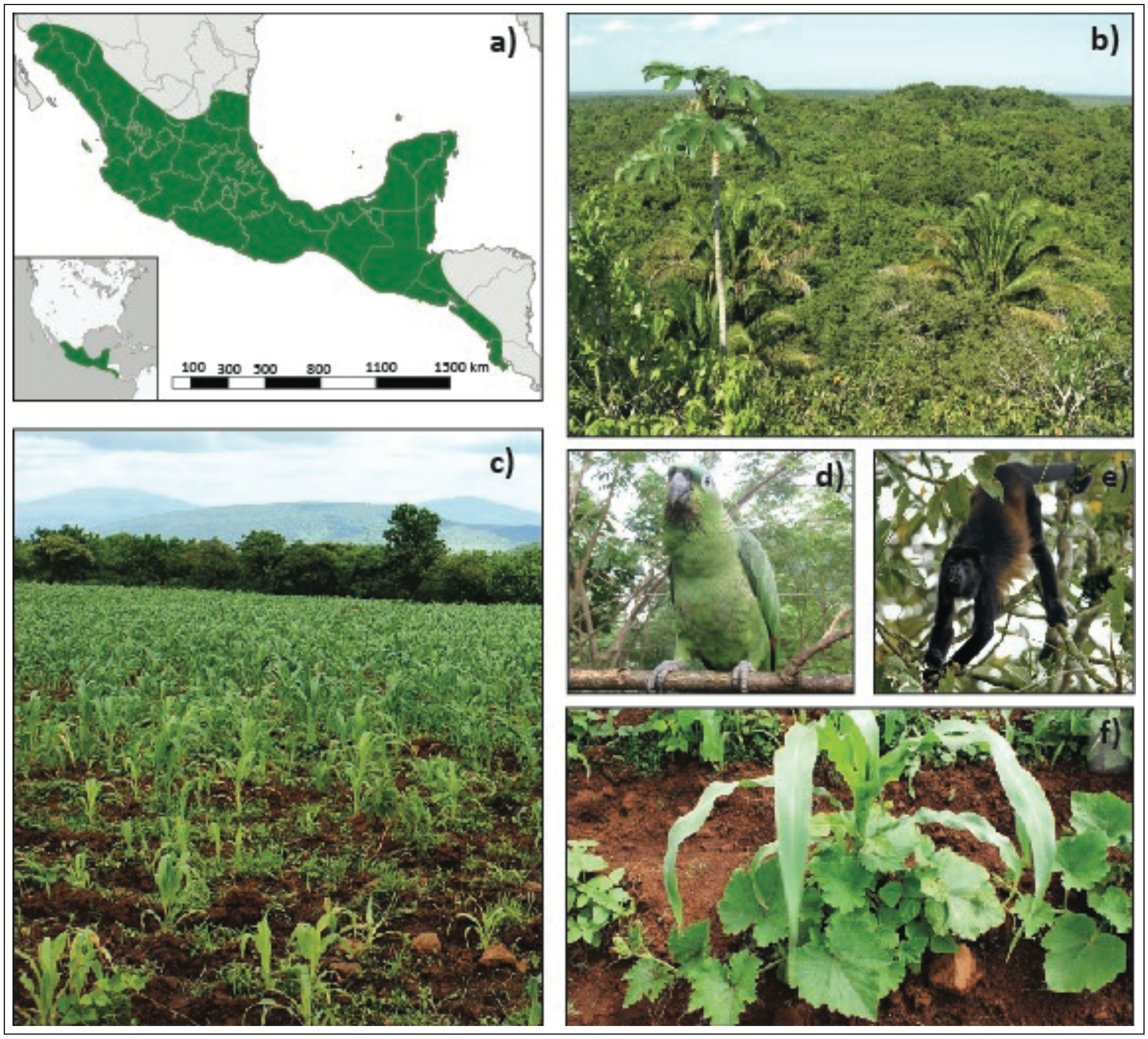


Figure 8. Across Mesoamerica, which encompasses mid-Mexico, Guatemala, El Salvador, Belize, western Honduras, and Nicaragua (a), the milpa systems (b-c) were developed thousands of years ago. Milpa is an itinerant cropping system that begins with burning small patches of land to establish crop fields (c) and culminates in the re-establishment of the vegetation on land that was previously cultivated (b). The management of high plant diversity provides important food sources for several bird species, such as the southern mealy parrot (*Amazona farinose*) (d), and mammals, such as the howler monkeys (*Alouatta palliata*) (e). It also has positive impacts on the soil ecology (f). Photos by Wikimedia Commons (a-f).

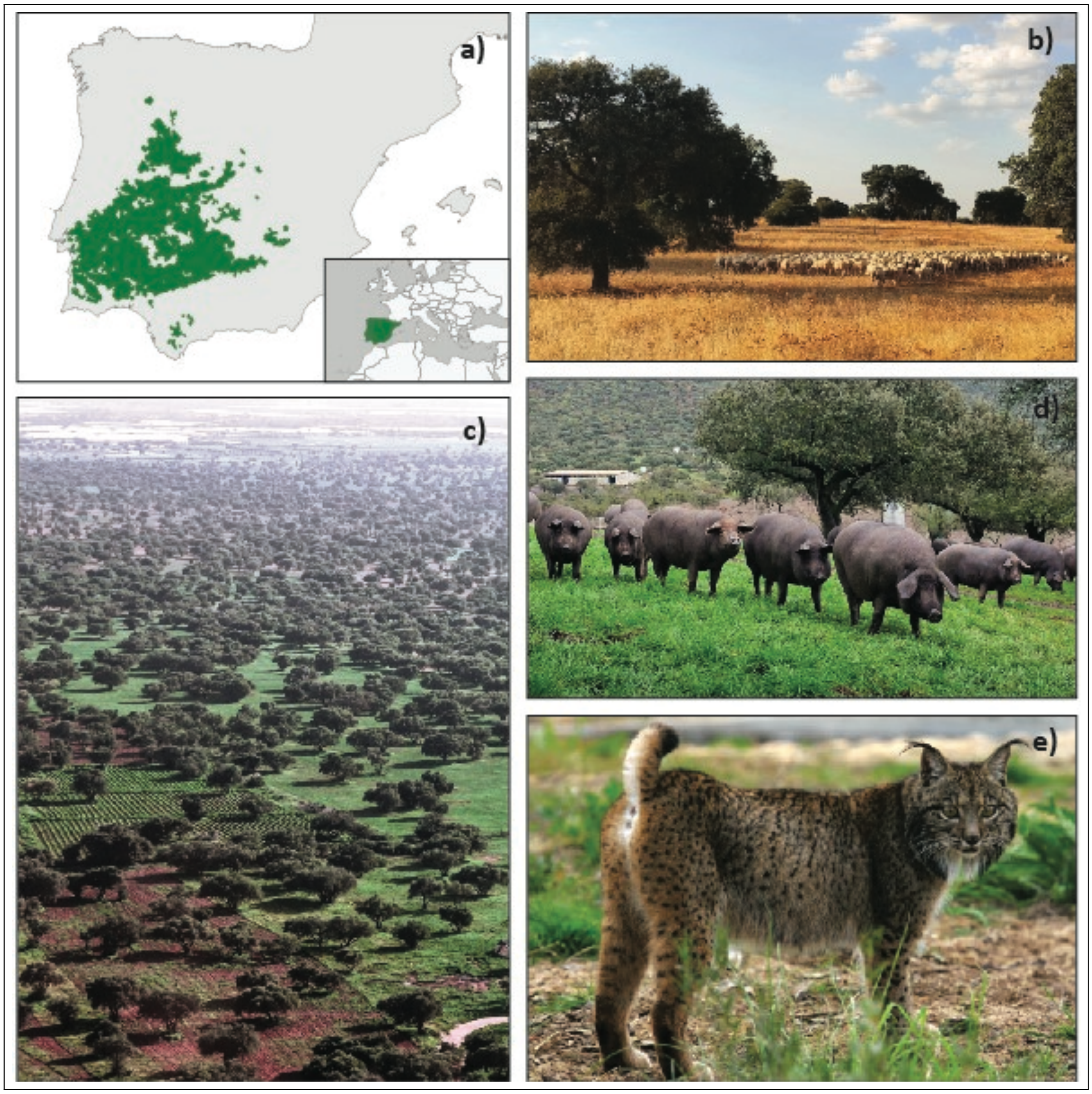


Figure 9. In the Iberian Peninsula, which covers Spain and Portugal (a), dehesa systems are a dominant form of agriculture. The emblematic features of the dehesa systems are its management of two strata an herbaceous understory that is periodically grazed by livestock, such as cattle, goats, pigs, and sheep, and sometimes removed for crop fields (b) and a sparse canopy of various species of oak trees (c) that also provide acorns for the Iberico pigs (d). Photos by Wikimedia Commons (a-e). Recent conservation efforts for the endangered Iberian lynx (*Lynx peardinus*) have focused on the dehesa as a critical habitat to maintain lynx populations. Photos by Wikimedia Commons (a-e).

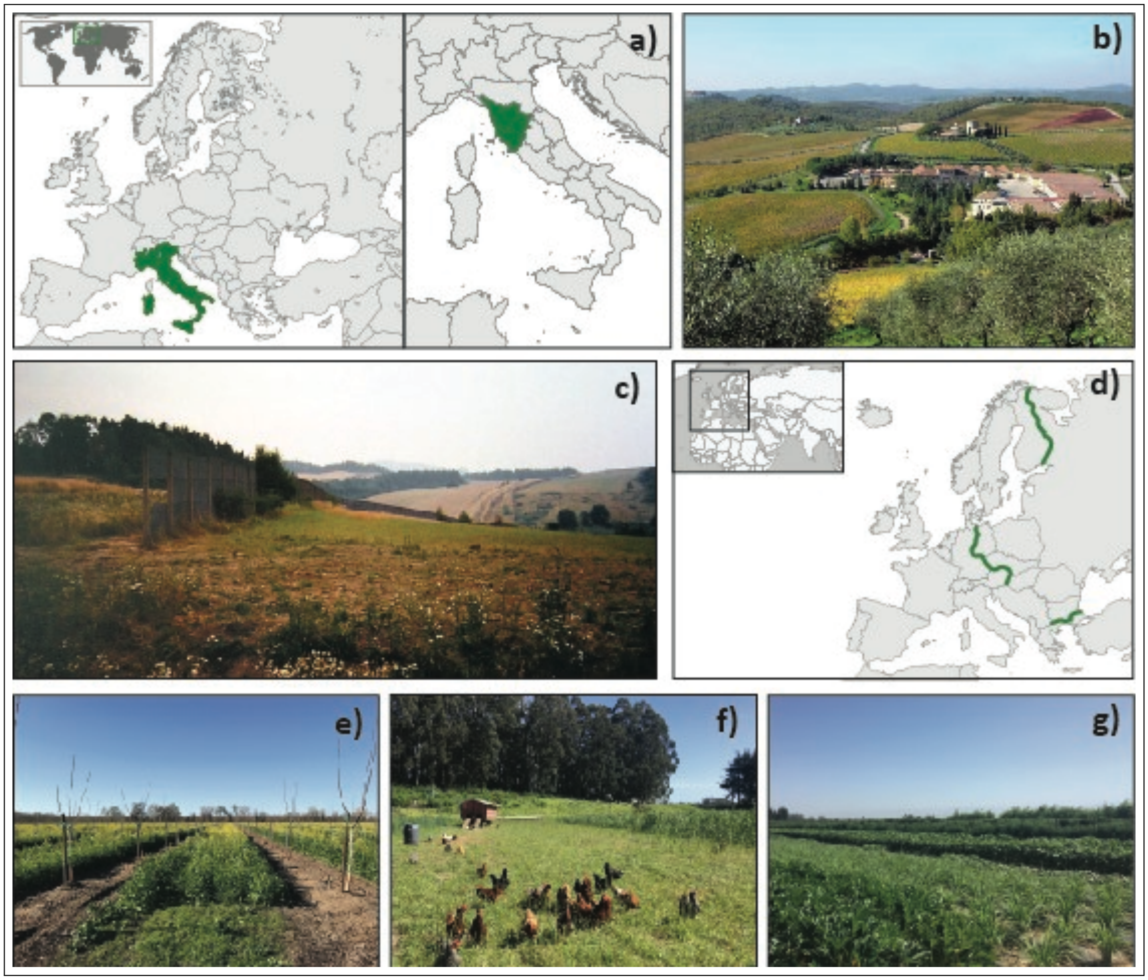


Figure 10. While hybrid systems are key to the persistence of native biodiversity, shifts to greater spatial and temporal homogenization can occur. For example, the Chianti region of Tuscany, Italy (a-b) used to be largely cultivated as an agro-sylvopasotral system but much of the farmland was consolidated over the past century. Similarly, the formation and presence of the Iron Curtain (1948–1990) between Eastern and Western European led to the simplification of agricultural land in the West (c-d). Efforts to reduce the homogeneity of agricultural systems, such as cover cropping (e), crop-livestock integration (f), and crop diversification (g) have been shown to have positive effects on native biodiversity.
Photos by Wikimedia Commons (a-d) and A. Guzman (e-g).

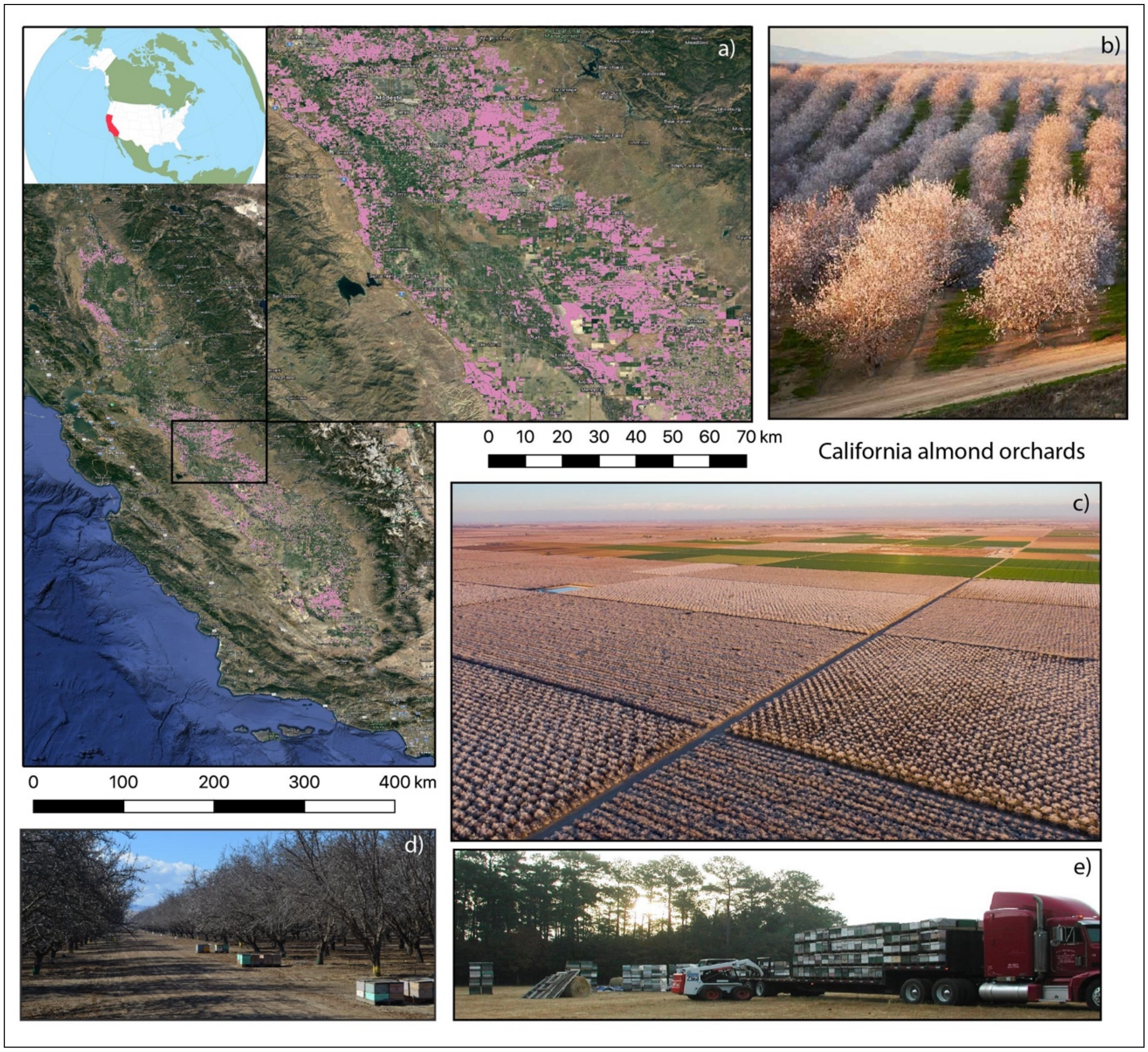


Figure 11. The distribution of almond orchards across the California Central Valley (pink), including a close-up of the major central San Joaquin growing counties. At the field scale, orchards are monocultures with limited vegetation between rows (b). At the landscape scale, there is also often limited crop diversity (c). An almond orchard in bloom creates a single, massive pulse of floral resources in the spring. European honey bees (A. mellifera) are stocked alongside orchards to pollinate crops (d). These colonies are brought from around the country, often on semi-trucks (e). Crop spatial distribution (a) from CropScape 2021 (NASS, 2021). Photos by the Almond Board Creative Commons Licence (b-c), L.
Ponisio (d), and Wikimedia Commons (e).

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CHAPTER 2

WHAT DO VALUES HAVE TO DO WITH IT?: EXAMINING THE RESPONSES OF TWO DIFFERENT TYPES OF FARMERS IN HAWAI‘I TO THE COVID-19 PANDEMIC

INTRODUCTION

This paper, now published in *Frontiers in Sustainable Food Systems*, is my pursuit to delve into social science methods and understand the human components of my study system. Through the assistance of Professor Louise Fortmann, I learned to craft interview questions and lead interviews. The formal interviews and casual discussions with farmers helped to shed light on the hardships and triumphs of running a farm, the attention that all farmers place on biodiversity, though not all act to foster it, and the pride that farmers have in their profession and the beautiful crops they grow. The discussions with farmers also contextualized the arthropods and their ecological value. In addition, these discussions prepared me for interactions with all types of farmers as I collected data for chapters 3 and 4. The results of this study highlight the different motivations farmers have to grow and distribute their crops within the landscape. Moreover, it highlights the resiliency of Hawaiian farmers to system shocks in the face of COVID-19.

WHAT DO VALUES HAVE TO DO WITH IT?: RESILIENCE OF TWO TYPES OF FARMERS IN HAWAIʻI TO THE COVID-19 PANDEMIC.

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Abstract

A history of agriculture and socio-cultural formation has led to a complex local food system in Hawaiʻi. Customary agricultural systems built by Kānaka ʻŌiwi (Indigenous Hawaiian) are now rested within a landscape filled with many different crops tended by farmers from a variety of ethnic backgrounds. Value systems dictating farming practices and crop selling decisions differ. In Hawai'i, values of food security or food sovereignty are of particular importance, especially as growing movements seek to increase local production and decrease the state's reliance on imported food in the wake of the COVID-19 pandemic. In this study, we systematically compare two different groups of farmers in Hawai'i and their values related to production and distribution. We then analyze the experiences of these two groups of farmers during the COVID-19 pandemic and their responses to them. The study is based on interviews with 22 Indigenous Kānaka ʻŌiwi (IF) and Non-Indigenous local farmers (LF) from the island of Oʻahu. Ninety percent of IF say values associated with both food security and sovereignty drive their production and distribution decisions, while 75 percent of LF describe food security as the sole driver. Sixty percent of IF follow a non-profit economic model and emphasize cultural and educational values in their production decisions. LF follow profit-driven models and emphasize the influence the market has in their decisions. Prior to the COVID-19 pandemic, IF sold or donated the bulk of their crops to the local community through farm pickups, while restaurants were the primary buyers of LF crops. During the pandemic, the local community continues to be the primary recipient for IF, and due to the closure of many restaurants, LF have pivoted their sales to the community as well. Farmer interviews are augmented by three interviews with Hawai'i food system experts and relevant literature to suggest multiple pathways state agencies and local organizations could implement to support farmers from different backgrounds through COVID-19 and into the future.

1 Introduction

The relationship between a farmer's values and the use of sustainable practices to foster environmental stewardship is well researched (Sullivan et al., 1996; Mccann et al., 1997; Ryan et al., 2003; Lincoln and Ardoin, 2016; Schoon and Grotenhuis). However, the role ethnic identity plays in this agricultural stewardship relationship, along with crop distribution decisions, has not received as much attention (Alkon and Agyeman, 2011). This topic is especially relevant in Hawaiʻi, where the local food system is influenced by a complex history of land tenure, agriculture, and socio-cultural formation. This history has made values associated with food security and food sovereignty particularly prevalent (Loke and Leung, 2013a; Kent, 2016). The local food system has been stressed by the COVID-19 pandemic. In response to COVID-19 spreading across the United States and the globe, Hawaiʻi State Governor David Ige issued his first emergency proclamation on March 4th, 2020 (Young, 2021). The first COVID-19 case in Hawaiʻi was subsequently reported on March 6th. On March 23rd a stay-at-home order was issued by Honolulu mayor Kirk Caldwell closing all businesses, except for those deemed essential. On March 26th a 14-day quarantine for out of state travelers was implemented. Subsequent orders were implemented, expired, and reinstated as case numbers fluctuated throughout summer 2020. These orders allowed various businesses to open at limited capacity. In the face of this shifting political and economic landscape, farmers had to display resilience, shift their operations, and pivot their sales.

Drawing from 25 semi-structured interviews with farmers and food system leaders, this paper explores the values driving crop production and distribution for farmers belonging to two different ethnic groups on the island of Oʻahu, Hawaiʻi: Kānaka ʻŌiwi (IF) and non-Kānaka ʻŌiwi local farmers (LF). In addition, we explore how these groups have responded to the COVID-19 pandemic. Specifically, we ask:
1) How do sociocultural and economic values, including the desire to strive for community food security and food sovereignty, affect the decisions IF and LF make?
2) To what extent has the response to the COVID-19 pandemic differed between IF and LF? Has one group shown more resiliency through the pandemic thus far?

Broadly defined resilience is the capacity to continue to achieve goals despite disturbances and shocks (Brown et al., 1987; Heller and Keoleian, 2003). In the context of the food system, Tendall et al. (2015) define resilience as "ensuring sufficient, appropriate and accessible food to all. By sufficient, we understand sufficient quantity and nutritional quality of food; by appropriate, we include the notions of culturally, technically and nutritionally appropriate food; by accessible, we mean physically and economically accessible." To measure their resilience, we examine: the degree to which a farmer's pre-pandemic farming operations, consumer base, sales shifted; and how well positioned they are to continue operating through the pandemic and into the future.

This article proceeds in four parts. First, we outline the history of agriculture and movement building that has led to an agricultural landscape composed of farmers from many different backgrounds. Second, we present quantitative and qualitative findings demonstrating the ways in which IF and LF interact with subsets of consumers and seek out varied means by which to maintain their farming operations. Third, we argue that certain attributes of each value system provided unique opportunities and obstacles in trying to achieve resiliency through the COVID-

19 pandemic. Last, we suggest multiple pathways state agencies and local organizations could implement to support farmers from different backgrounds through COVID and into the future.

2 Study system background

2.1 Historical Foundations of Hawaiʻi's food system

Beginning at their first arrival to the Hawaiian Islands, Kānaka ʻŌiwi established expansive systems of food production that ranged from offshore fisheries to mountainous agroforestry systems (Vaughan and Vitousek, 2013; Lincoln and Vitousek, 2017). These systems were embedded in socio-political institutions at the personal (religious, see Kameʻeleihiwa, 1992), local (ahupuaʻa, see Minerbi, 1999), and landscape scale (moku, see Winter et al., 2018). Kānaka ʻŌiwi socio-political institutions relied on cultural frameworks emphasizing familial and spiritual connections to land and crops and an understanding of overall community well-being and health (Goodyear-Kaʻōpua et al., 2014; Winter et al., 2020). The act of eating was spiritual, and great significance was attributed to the cultivation of crops (Kamakau and Barrère, 1992). The crop diversity, multi-tier structure, and use of altitudinal and seasonal shifts in these food production systems coupled with the socio-political institutions enabled high productivity and resiliency (Kagawa and Vitousek, 2012; Lincoln and Ladefoged, 2014; Kurashima et al., 2019). For example, Kurashima et al. (2019) concluded that terrestrial cropping systems could have sustained a population of 1.2 million people.

The actions of missionaries, their descendants, and the United States government have had a far-reaching impact on Kānaka ʻŌiwi society. With the first arrival of foreign traders in 1778 and missionaries in 1820, came disease and population decline. Along with a diminished population came shifts in socio-economic, cultural, and religious institutions. To further their religious agenda, missionaries pressured local chiefs to dismantle the customary Kānaka ʻŌiwi spiritual system. Soon many Kānaka ʻŌiwi were enveloped in an entirely new religious system, Christianity, that was not rooted in relationships with the community, land, aliʻi and akua (gods). Missionaries exploited their new power and Kānaka ʻŌiwi were coerced into becoming the primary labor force, producing resources for growing settler colonialism on the island of Oʻahu, which often came at the expense of their own daily food needs (Steele, 2015).

The 1848 Māhele, a property right and land redistribution act, further affected Kānaka ʻŌiwi land tenure and subsequently food production. Land that had been held in common by communities and produced abundant food was commodified and divided into parcels to be managed on an individual level. Not accustomed to Western land ownership practices, many Kānaka ʻŌiwi did not file claims to any parcel of land (Kameʻeleihiwa, 1992). Western businessmen soon bought up and controlled large swaths of the island.

The illegal overthrow of the Kānaka ʻŌiwi Kingdom in 1893 by American businessmen backed by the United States Navy furthered the loss of Kānaka ʻŌiwi food production systems and knowledge. The foreign businessmen established a government that suppressed Kānaka ʻŌiwi cultural practices, access to land, and the use of ʻōlelo Hawaiʻi (Kānaka ʻŌiwi language) in public and at home (Warschauer et al., 1997). Kānaka ʻŌiwi food production systems and cultivation practices faded with the diminishment of cultural transmission and land access.

Moreover, the Kānaka ʻŌiwi worldview and diet shifted under the pressures of colonialism (McMullin, 2016; Silva and Ngũgĩ wa Thiong'o, 2017).

Eurocentric notions of environmental management took hold as well. Government regulation and bureaucracy has also limited the ability of Kānaka ʻŌiwi communities to regain formal management and oversight of traditional food producing regions (Vaughan et al., 2017). Finally, many famous historical native food producing landscapes have been paved over to make way for single family homes, shopping centers, and military bases, or are used for the seed corn industry (Gupta, 2015; Fujikane, 2021).
The result of this history of land and cultural loss has led to a sharp decline in self-sufficiency with Hawaiʻi importing almost 90% of its food. The Kānaka ʻŌiwi population in comparison to the rest of the Hawaiian state has a higher prevalence of hypertension, heart disease, diabetes, and obesity (McMullin, 2016). In addition, a disproportionate number of the Kānaka ʻŌiwi population is enrolled in the SNAP benefits program (U.S. Department of Agriculture, Food and Nutrition Service, Office of Policy Support, 2019) and experience a higher poverty rate (13.5) than the averages in the state (9.5).

Seeking to capitalize on a booming need for sugar in the US, and with ample land resources, foreign businessmen established sugarcane plantations in 1835 and imported workers as cheap labor from countries around the world: China, Japan, Philippines, Korea, Portugal, and Germany. These workers brought seeds of new crops as well as cultural traditions with them. While living on plantations, workers exchanged food, recipes, and traditions, ultimately giving rise to what is now known as local food and culture in Hawaiʻi (Yamashita, 2019). As the sugar industry shifted to South America and the Hawaiian plantations closed, these workers began farming their own plots across the state with polyculture cultivation including rice, taro, and pig (Takaki, 1984).

2.2 Movement building and food system transformation in Hawaiʻi

The birth of the Kānaka ʻŌiwi sovereignty movement is built on the struggles of Kānaka ʻŌiwi farmers and community members who sought to maintain access to their lands and farming practices (Trask, 1987). A group of Kānaka ʻŌiwi farmers and community members facing eviction from their agricultural lands changed the narrative in 1969 by occupying Kalama Valley. Although the subdivision was ultimately built, the stand the Kalama Valley farmers took ushered in a wave of Kānaka ʻŌiwi activism and cultural resurgence that continues to this day. Therefore, the roots of the Kānaka ʻŌiwi sovereignty movement are firmly planted in land access and agriculture but evolved to include cultural revitalization in forms such as language, hula, and ocean wayfinding.

The movement has also evolved to center Kānaka ʻŌiwi conceptualizations of sovereignty and land-based relationships characterized by the terms "ea" and *"aloha ʻāina."* Like most Kānaka ʻŌiwi words ea holds multiple meanings including "life," "breath," and "sovereignty." Ea is described as "an active state of being . . . that requires constant action day after day, generation after generation . . . [It] is based on the experiences of people on the land, relationships forged through the process of remembering and caring for wahi pana, storied places" (Goodyear-Kaʻōpua et al., 2014). Ea is therefore an understanding that sovereignty and life itself is rooted in caring for and maintaining a relationship with the land. Aloha ʻāina encapsulates maintaining a righteous relationship between people and place. It has also become the name and rallying cry of the Kānaka ʻŌiwi sovereignty movement itself (Osorio, 2002).

Kānaka ʻŌiwi political scientist Noelani Goodyear-Kaʻōpua describes a plurality of sub movements in Hawaiʻi that contribute to the goals, mainly political and economic autonomy and self-determination, of the broader Kānaka ʻŌiwi sovereignty movement (Goodyear-Kaʻōpua et al., 2014). In this way, the Kānaka ʻŌiwi food sovereignty movement can be seen as a sub movement working towards Kānaka ʻŌiwi sovereignty at large. The first formal mention of this movement can be traced back to Maʻo Farm's "Hands Turned to the Soil" youth conference in 2003 (Meyer, 2014). From that conference came the proliferation of urban gardens and the rise of youth programs centered around cultural and agricultural education. A second food sovereignty conference on Hawaiʻi Island in 2007 began to define Kānaka ʻŌiwi food sovereignty as "a spiritual, physical and cognitive pathway toward greater wellbeing and self-sufficiency" (Gupta, 2015). A third conference took place in 2018 where a youth congress, comprised of Kānaka ʻŌiwi youth, crafted a future vision for Hawaiʻi's food system and expanded the definition of Kānaka ʻŌiwi food sovereignty to include the right and responsibility to ʻai pono (righteous food); co-design educational models outside of the classroom; the conscious care of resources for future generations; and uplifting of the community[i].

The values associated with the Kānaka ʻŌiwi food sovereignty movement are aligned with food sovereignty and Indigenous food sovereignty struggles across the globe. The term food sovereignty was first coined by La Via Campesina in 1996. A commonly cited definition of food sovereignty comes from the Declaration of Nyeleni, where it is defined as "the right of peoples to healthy and culturally appropriate food produced through ecologically sound and sustainable methods, and their right to define their own food and agriculture systems" (Fairbairn, 2010).

A growing body of work from Indigenous scholars across North America have begun to define Indigenous food sovereignty (see Mihesuah et al., 2019; Settee et al., 2020). Moreover, Indigenous food sovereignty is seen as continuation of anti-colonial struggles and advancement of self-determination (Grey and Patel, 2015). In this study, we draw on Kānaka ʻŌiwi, Indigenous, and the Declaration of Nyeleni definitions of food sovereignty to define food sovereignty as the right of Kānaka ʻŌiwi to culturally significant foods produced through ecologically sound methods; manage and access cultural food producing regions; and define their future outside of the purview of the State of Hawaiʻi and U.S. federal government.

The food landscape in Hawaiʻi is heavily influenced by a regional food movement started in 1991 by a group of local chefs wanting to utilize locally grown ingredients (Yamashita, 2019). The chefs pushed against a Euro-American food hierarchy stemming from plantation owning families and their descendants who looked down on local food (Laudan, 1996). Influenced by a burgeoning local food movement on the Continental United States and realization that comparable or even better food could be produced in Hawaiian Islands, these chefs began to procure food from local farmers and encouraged them to ramp up production. Since 1991, Hawaiʻi has seen an exponential rise in marketing schemes and labeling efforts for locally grown food, more farm to table restaurants, and a consumer base that demands locally grown food (Loke and Leung, 2013b).

The regional food movement is heavily aligned with the values of food security and subsequently self-sufficiency. At the heart is also a recognition that importing 90% of the island chain's food needs is unsustainable and provides little security should a natural disaster arrive. The State of

Hawaiʻi government and other local entities utilize the United Nations Food and Agriculture Organization definition of food security, "a situation that exists when all people, at all times, have physical, social and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life" (Hawaiʻi Department of Business Economic Development & Tourism (DBEDT), 2011). This is the definition of food security utilized in this study as well.

Who are Hawaiʻi's farmers? Farmer demographic trends mirror the historical shifts discussed previously. The count of Kānaka ʻŌiwi or Pacific Islander farmers declined by half from 22% in 1900 to 11% in 1959. Conversely, in 1900, Hawaiʻi's principal farmers were of Asian (56%) and White decent (22%). In 2012, the number of Kānaka ʻŌiwi or Pacific Islander farmers declined even further to 9% while Asian and White farmers held large margins at 45% and 43% respectively (Hollyer and Loke, 2014). The number of farm operators in Hawaiʻi increased from 2,273 in 1900 to 7,013 in 2012 (Loke and Leung 2013). An overwhelming majority of farms on Oʻahu are small scale tending to plots between 1-9 acres (76%) or 10-49 (15%) (United States Department of Agriculture (USDA), 2019).

3 Methods

Both authors are of Kānaka ʻŌiwi descent and a part of the food system community on the island of Oʻahu. Leslie Hutchins first became involved in the local food system while interning with Paepae o Heʻeia, a local non-profit organization restoring Heʻeia fishpond. Mackenzie Feldman entered the food system through working with local organizations on food system related policy. The conceptualization of this work was born out of numerous informal conversations with farmers of many different backgrounds prior to and during the COVID-19 pandemic. Combined purposive and network sampling approaches to identify and contact potential farmers was implemented (Blaikie, 2000). In all, 22 interviews using a structured questionnaire approach with farmers across the island of Oʻahu were conducted during the summer and fall of 2020 (see table 1). The ethnic demographic of the farmers included ten Indigenous Kānaka ʻŌiwi (IF) and twelve non-Indigenous local farmers (LF) comprised of 58 percent Asian and 42 percent White respondents. Three additional interviews were conducted with food experts and community leaders to help contextualize the interviews and relevant food movement(s). All interviews were conducted over the phone or through online video conference services and recorded for transcription. We used Nvivo 11 to identify common themes within responses. Interview text included in the article is left in its original format to allow the usage of Hawaiian Pidgin (creole langugage spoken in Hawaiʻi) spoken by several respondents. The "bipartite" package in R (version 3.6.2) was used to illustrate crop distribution between farmers and consumers (R Core Team, 2019). A review of popular, policy, and academic literature along with suggestions from farmers was utilized to write policy recommendations.

4 Results

4.1 Reasons to start and continue farming

Although similar reasons for farming were found in both groups, there were clear differences between the two groups in the value placed on Kānaka ʻŌiwi culture and people. When asked whether food security or food sovereignty influenced their decision to start and continue farming, nine out of twelve LF selected food security while nine out of ten IF selected both (Figure 1). Farmers from both LF and IF groups described environmental considerations such as sustainability and climate change as important in their decision to farm. Each farmer had specific reasons for starting their respective farm. However, the reasoning given by LF and IF tended to cluster with their respective group. For example, six out of ten interviewed IF are a part of, or lead, non-profit organizations with in-depth mission statements and goals that seek to increase the socio-economic outcomes for the communities they serve. For example, respondent 11 stated their mission is to provide "a gathering place for people in the community to connect with and care for the ʻāina (land), perpetuate Kānaka ʻŌiwi culture through the cultivation and preparation of kalo (taro, *Colocasia esculenta*), and to be a place that would ultimately bring healing to people, especially at-risk youth."

The remainder of IF suggested similar socio-economic and cultural reasons for starting to farm. Respondent 1 noted how farming kalo became a way to heal from intergenerational trauma associated with growing up surrounded by drug, alcohol, and domestic abuse. They describe working with taro as therapy: "each time my feet step into the mud, it reconnects me to my culture and myself." IF take tremendous pride in growing culturally significant crops such as taro. Respondent 13 described this best saying "our ancestors took great pride in growing the best taro. They'd want to grow the best taro to feed their children and make their keiki [children] warriors. I grow with that same pride. I want my keiki to be strong." However, IF do not solely grow culturally significant crops, but also grow to fulfil market demands and cater to new preferences. Respondent 5 noted how they grow not only taro, turmeric (*Curcuma longa*), sweet potatoes (*Ipomea batatas*), and other Kānaka ʻŌiwi crops, but kale (*Brassica oleracea*), arugula (*Eruca vesicaria*), and many others because "if our Hawaiian ancestors knew about arugula, I'm pretty sure they'd grow it too."

The market is a huge factor in determining what eight out of ten IF and nine out of twelve of LF decide to grow. Respondent 7 described how they grow different crops to cater specifically towards different community demographics represented in the farmers markets they serve: "the Waipahu market has lots of Filipino people, so I'll grow bitter melon and bring it to them. I cater towards Americans at the Kapiʻolani Community College and Mililani markets, so I grow stuff for salad like kale and lettuce." Other farmers discuss tracking what sells best at their markets and shifting their growing practices accordingly. The two out of ten IF and five out of twelve LF with grocery stores discussed the need to focus on high demand and specialty crops. Moreover, they emphasized the need to produce a consistent ample supply to provide to produce managers to keep those accounts open. Respondent 5 explained the crops provided in general are seen as an addition to the supply shipped in from outside the state as opposed to a direct substitution.

4.2 Food sovereignty

IF see food production as a medium through which larger visions of social and political change can be achieved. Respondent 20 highlighted this saying "what we're doing-- it's not only about food; it's not only about kale. We're trying to connect people to place. The food is just a byproduct of trying to get people to connect to ʻāina (land)."

4.2.1 Access and kaiāulu (community)

Cultivating food provides a way for IF and community members to get their feet in the soil again and an opportunity for Kānaka ʻŌiwi crops to spread their roots once more. Eight out of ten interviewed IF host community workdays and cultural activities on their farms, where participants can harvest kalo, learn how to prepare traditional foods, and engage in various ceremonies. Their farms become key gathering places where Kānaka ʻŌiwi community members get to connect and reconnect with others. Moreover, three out of ten IF highlighted how community members often interact with and eat Kānaka ʻŌiwi crops for the first time while visiting.

Many of these organizations are nested within landscapes dominated by other uses—urban, large scale agribusiness, private access— not conducive for many cultural practices. Therefore, their farms can be considered cultural kīpuka (safe, regenerative places to be Kānaka ʻŌiwi). Many of their farms feed the community both spiritually and physically by growing and distributing Kānaka ʻŌiwi culturally significant, nutritious crops and engaging in cultural practices they might not be able to access otherwise. Respondent 17 solely started offering educational programs to the community because they noticed a lack of resources about how to grow and prepare Kānaka ʻŌiwi culturally significant crops. In addition, they sell culturally significant crops at a discounted price. They noted that many individuals can only gain access to their ancestral foods because of their programs.

4.2.2 Identity and place

Food and the landscape it's grown in are intertwined into the identity of the people belonging to that place. Respondent 5 captured this relationship well: “there's a story behind all food and a lot of indigenous people are tied to that. It's embedded in our culture and our DNA. Food is not only something that gives you life. Food is the resilience of our people, our knowledge, and our ancestor’s actions.”

Community members participating in workdays are often reminded of the rich history of the landscape and its identity. For example, respondent 11 teaches community volunteers that their ahupuaʻa (socioeconomic subdivision of land) was once a famous “taro breadbasket” that provided abundance for the entire region. Respondent 6 said they share similar sentiments with volunteers about the fish grown in their fishpond: “Pauahi [a revered Kānaka ʻŌiwi aliʻi] called the mullet of our fishpond the sweetest mullet she ever tasted, and I would take her word for it more than mine, ‘cause she’s probably ate way more mullet than me in her lifetime than how much I’ve eaten. . . . the water quality and limu [seaweed] specific to our pond is probably behind the sweetness.” Therefore, reclaiming Kānaka ʻŌiwi cultural identity is rooted in revitalizing the cultural landscapes across Oʻahu and ensuring their health and abundance. As Respondent 12 puts it “if we have a healthy ahupuaʻa, we have a healthy community. It takes conscious everyday actions by us and those in the community to restore the abundance of our island home.”

4.2.3 Education

The non-profit model of IF makes education a cornerstone of their operations. By providing hands-on education with a focus on community and culture, IF hope to inspire youth to learn more about themselves and how they can uplift others. Respondent 6 described the goal of their efforts:

“The fishpond feeds us spiritually and educationally. Our job is to try to spark interest in the kids that visit. And, we do. Sometimes those kids that come here and just don’t wanna step in the mud, by the end of the day, they do catch on to something. Maybe they’re gonna see a fishpond in their community, and they’ll be like, “we can do this. We can start somewhere. We can start building this pond.” Soon enough, that pond will be feeding people. And then another pond, and then another pond, and that’s how we’re gonna change communities.”

Education is vital to ensuring that the next generation is prepared for a successful future. Using Kānaka ʻŌiwi crops and farming practices as a model, IF offer a robust set of internship programs and funding pathways for personal and professional development. For example, respondent 11’s organization offers programs for youth between ages twelve and twenty-three. Their entry level program focuses on improving social functioning and cultural connection for at-risk youth through taro farming and mentorship from life coaches. Their advanced programs offer paid internships and apprenticeships for those in high school and college to gain value-based job preparedness.

4.2.4 Self determination

Kānaka ʻŌiwi food sovereignty leads to overall Kānaka ʻŌiwi self-determination and sovereignty. Respondent 20 noted how their individual actions contribute to the greater community, “it's all about aloha ʻāina. If we can do our own part for our community and teach people about our stories, about haloa as our older brother, and build connection, then hopefully the end result is self-determination.” Respondent 13 described food sovereignty and self-determination being achieved through daily actions to grow, gather, and eat traditional Kānaka ʻŌiwi foods: “you can’t fight for sovereignty by waving a hae Hawaiʻi [Kānaka ʻŌiwi flag] just one day. You have to take action all seven days. True sovereignty is gained each time a kanaka plants taro. Each time they plant taro, they’re planting a hae Hawaiʻi.”

4.2.5 LF on food sovereignty: From allyship to “sounds nice”

Three out of tweleve LF respondents mentioned food sovereignty inspired their farming operations. Two out of the three see themselves as allys to Kānaka ʻŌiwi food sovereignty. For example, respondent 4 leads an innovative extension program from their farm that buys excess harvested fruit (e.g., mangoes and breadfruit) from primarily low-income Kānaka ʻŌiwi households in the surrounding community and sells it at a discounted rate to those in the community. The program provides a secondary source of income for these Kānaka ʻŌiwi households while providing access to crops others across the island could not afford. In this way, although the farm is not operated by nor solely focused on Kānaka ʻŌiwi, respondent 4 described the programs work specifically as being rooted in some Kānaka ʻŌiwi values: “we're creating great abundance, abundance was always here. And I think it's rooted in culture. And I think it's also cultural that people don't want to waste food and that's partially why they want to share food. So our program wanted to become an extension of sharing.”

When LF were asked to expand on their reasoning for not engaging in food sovereingty, their responses clustered around having no general knowledge or interest to not wanting to engage in politics. For example, respondent 15 described their lack of knowledge of food sovereignty saying “it sounds nice. Never heard of it. I grow Polynesian crops but I ain’t Hawaiian or participate in the sovereignty movement.” In terms of the political aspect of food sovereignty, respondent 19 explained “[I’m] just looking to do the farming, not trying to get involved in any politics. I think digging my hands in the soil is an escape for me. It’s like an escape from the headlines and what not.

4.3 Food security and its interaction with food sovereignty

A majority of LF picked food security as being a primary inspiration for farming. They see their work as a means to provide consistent access to healthy foods to the local community at all times. Respondent 14 encapsulated these sentiments: “I want everyone to have access to healthy food. If the container ships stop coming in, I'll be here to provide.”

4.3.1 Community

Supporting local communities by feeding them is important to LF. Their focus on community is not primarily on Kānaka ʻŌiwi, but those on the island in general and in their specific town. Respondent 2 expressed their joy in feeding the community: “I love going to the farmers markets and seeing community members come by my stall. I’m doing what I am doing for them.” Nine out of twelve interviewed LF do not host community workdays or conduct cultural activities on their farms. Respondent 22 gave one possible reason why this might be the case: “hosting requires a lot of organizing and coordinating that I don’t have time for. I don’t know how the liability and insurance works either. Maybe I’d do it in the future though.”

Respondent 4 explained the main driver behind their work with the community is the realization that the food security model emphasized by many in Hawaiʻi does not seek out justice for all: “with food security, we're actually not even looking at that injustice of who is excluded from the marketplace. . . some food security advocates say we should bring food over here as cheaply as possible so that people can afford it and have it but then you're ignoring a lot of people's diets.” In terms of IF, respondent 18 highlighted food security is a matter of empowering a community where many do not have access to healthy food: “a lot of people in the community are stuck going to McDonalds and other fast-food places because that's what they can afford. People in my ʻohana [family] like most families here have a history with diabetes and other stuff like heart disease. I want to give them fresh and healthy food. The homeless kanaka on the beach, they need food now. They need that security.

4.3.2 Past, present and future disaster

Both LF and IF brought up the importance of being prepared for disastrous situations citing past instances of hurricanes, tsunamis, and the current pandemic as key indicators of why Hawaiʻi should increase its self-sufficiency and grow more of its own food. Respondent 15 (LF) recalled past and present anxieties to localize the food system: “after the tsunami in 2011, everyone started realizing we need to grow more food here. Everyone was worried about the ports getting destroyed. This pandemic is another good example to show how we need to grow more local. The grocery shelves are getting emptied out. Where are people supposed to turn when Costco no more supplies?”

Ensuring the island is prepared for the future disasters was discussed by 45 percent of IF and LF. Respondent 6 (IF) described the virtues of farming in ensuring food security: “The great disaster of Hawai’i is its seven days of food supply. If the disaster comes, we get seven days of food. If you can farm, those seven days don’t apply to you. That’s out the window. You’ve got a lifetime supply of food to feed you and your community.”

4.3.3 The taste and feel of local food

A common sentiment shared by LF revolved around valuing the taste of locally grown food and the pride emmitnating from growing local food. Respondent 8 explained how they favor the taste of local food over imported food: “I always try to eat my own vegetables or the stuff my friends grow. The climate and soil here just makes everything taste better. When I need to eat stuff shipped over from California, I ain’t happy. It tastes old.” Respondent 19 described how growing and eating local food makes them feel like a better citizen: “I’m doing part to help the island. Feels good. My customers tell me they feel good buying my products too. They like support too.”

The sentiments that local food tastes better and makes you feel better are used by LF to attract customers and potential vendors. These sentiments are shared through in-person conversations, the labeling of products, and advertisement. Respondent 9 explained an interaction they had with a new potential restaurant customer: “We market ourselves as fresh, never frozen. Most people eat frozen chicken imported from the mainland. But fresh chicken is so much better. We made a connection with a restaurant. Told them we had local chicken. They seemed skeptical at first, but then we sent a sample chicken, and they were hooked. At first they ordered infrequently, but now they ask for chickens every week.”

4.3.4 Two different solutions to the same problem?

Food security and food sovereignty are different food system models that LF and IF find themselves participating in. However, there are instances where these two disparate approaches intersect with each other, but only to a certain extent before widely diverging. Although nine out of twelve LF did not see their work inspired by food sovereignty, their responses nonetheless mirror food sovereignty discourse: LF want to control local food production by increasing production, and do not want to rely so heavily on importing food, which is a main tenet of food sovereignty. Their desire to control the food system, however, is less political than IF and their focus is generally not on culturally significant crops. In addition, LF see working with the State of Hawaiʻi, whose food security model relates to economics and individual buying power, to create incremental change, as the primary pathway towards a more localized food system.
IF are part of a community in which many members experience food insecurity, not even gaining daily access to basic nutritious foods. Therefore, they selected food security as a model that would serve them. They focus on both short and long-term ways to feed their communities. In the short-term, IF want to guarantee continued access to healthy food to community members. However, in the long-term, IF seek to dismantle the current food system. In its place, IF want to have the power to create a new system that centers on their cultural values and teachings to determine the future of their community and food system outside the purview of the state.

4.4 Adaptations and pivots during COVID-19

4.4.1 Pre-COVID-19 Production and Marketing Strategies

Prior to the COVID-19 pandemic, LF and IF experienced a broad range of economic realities. Four out of twelve LF and three out of 10 IF experienced a plateau in sales due to their inability to increase production due to labor or land shortages, while five out of twelve LF and two out of ten IF experienced exponential growth with an expansion into hotels and supermarkets. LF and

IF often pursued different economic avenues to make ends meet. Due to the non-profit nature of a majority of IF, they commonly seek out external grant funding from local and federal agencies/organizations. Respondent 20, who leads a non-profit, described how they feel like a “subsidized farmer” because their organization does not rely on crop production revenue but grant sources to stay afloat. IF nonprofits rely heavily on a funding model rooted in providing educational services to the community by hosting school groups and/or local companies. Therefore, the non-profit model allows for a suite of outcomes that transcend crop production, including community upliftment. The non-profit business model also allows IF to conduct the business practices most suitable to their cultural values and community-oriented goals. Respondent 13 expressed this sentiment best: “if I were to run a business, I'd be charging $7.50 a pound for taro. Who can afford taro at $7.50 a pound? Nobody in my community.” On the other hand, grant funding sources in most instances need to be reapplied to every year and provides uncertainty. This uncertainty can make long range planning and staffing difficult. In addition, when applying for funding, IF are faced with rehashing the same precarious solemn narrative about their community. Respondent 17 explained their uneasiness with this narrative: “We‘re trying to uplift our community. And we’ve made great strides in doing that, but each grant cycle, I need to talk about the poverty, the diabetes, and the dissarray. I want to start telling new stories.”

Taro and poi, the primary staple food of Kānaka ‘Ōiwi culture made of steamed and mashed taro, are at the center of six out of ten IF operations. Therefore, the price of these products heavily influences the stability and longevity of IF. For-profit IF may have trouble when selling to the same consumers targeted by non-profit IF. Respondent 1 described their personal struggle: “the non-profits [are] doing great work, but it can be hard to sell my poi with so many competitors, especially since they have all these big grants and volunteers. I’m only here supporting myself with the money in my pocket.” Respondents 11 and 13 provided more insight into the forces determining the price of taro and poi explaining that large scale commercial producers from other islands, such as the Hanalei region of Kaua‘i, use highly intensive practices and cheap labor to produce a surplus that they then sell at an extremely discounted rate (~70 cents/lb as opposed to the $3-5/lb sought by the respondents).

LF expressed similar issues with large scale commercial production as well. Respondent 7 has seen their fellow vendors at the farmers markets they serve selling produce shipped from the US and abroad instead of locally grown food. They further explained that these vendors can sell their produce at a cheaper price point. Ten out of twelve are for-profit and sell their produce at various markets.

Three out of ten IF and six out of twelve LF pursue secondary sources of income by gaining employment in establishments such as restaurants and engaging in ecotourism by leading farm tours. Engagement in these activities mainly contributes to household income and not necessarily maintaining farming operations. Those engaged in these secondary income activities emphasized the importance of these activities in allowing them to continue farming. Although 59 percent of IF and LF expressed good economic health trends, profitability and paying down debt were issues brought up. Farmers expressed that although their sales were increasing, they were still only breaking even due to farm costs and paying down existing debt taken on to purchase equipment or land.

4.4.1 Adapting to COVID-19

Prior to COVID-19, the crops produced by LF went to a wide assortment of consumers (Figure 2), with farmers markets, restaurants, and high-end restaurants being the primary recipients. However, during COVID, LF experienced a contraction in their consumer base and a pivot in where most crops went, with community-based pick-ups and CSA (Community Supported Agriculture) programs becoming a major recipient. Farmers with restaurant accounts experienced a 70-90% drop in orders. For example, respondent 3 (LF) experienced a retraction of all their restaurant accounts: “All my sales were going to a handful of restaurants in Waikīkī. I lost all of those accounts. A couple of CSA services approached me and now I got a bump in sales. I don't know how long it'll last.”

Crops produced by IF went overwhelmingly to community-based pick-ups, with farmers markets and restaurants also being significant recipients (Fig. 2). During COVID, community-based pick-ups and CSA programs became an even more overwhelming recipient of crops receiving the excess associated with the retraction of farmers markets and restaurants. Recipient 22 (LF) described farmers markets remained an important source but many of them temporarily closed: “I go to two farmers markets weekly. The busier market I rely on is temporarily closed. Hope it opens back up soon. I'm harvesting and selling less in the meantime. One market is keeping me afloat for now--barely”

The impacts of the COVID-19 pandemic required almost all farmers to innovate and change their business model. As the local population began to seek out opportunities to avoid in person contact in grocery stores and honor the idea of buying more local, farmers set up online sales platforms, “drive- thru” pick up options, and joined or created their own direct to consumer CSA programs. LF and IF both benefited from the uptick in community sales, seeing a 2-5-fold increase in CSA based subscriptions. However, the drastic increase in demand for CSA services has not been a golden opportunity seized by all. Farmers that do not already have the infrastructure in place or the resources to acquire it may be at a disadvantage. For example, respondent 7 primarily relies on a two-to-four-person work crew and could not keep up with the demand from CSA services. Since they did not have the capital to pay more workers, they had to stop production for CSA accounts all together.

Respondent 4 (LF) and respondent 17 (IF), both of whom focus on food security and food sovereignty, did not need to change their business model, they instead ramped up their pre-pandemic strategies. In addition to growing their own crops, they procure crops from other small-scale farms and act as a hub of distribution. Respondent 17 explained how their work has enabled many small-scale farmers to continue operations throughout the pandemic:
“Prior to the pandemic, we were buying from maybe eight farmers, but now we are up to around fifteen every week. That has increased our distribution from 500 pounds to 2000 per week. The farmers are from all over the island. A couple of them have said we are solely contributing to their persistence. It feels good to help out but its heavy knowing we are their lifeline at the moment.”

The pandemic proved to be troublesome for IF non-profits that rely on volunteer help and received income from education programs as well. As schools and summer programs moved to online platforms and the State of Hawaiʻi implemented restrictions on group gathering, income revenue from education sources declined. Moreover, the volunteer help often needed to complete laborious tasks disappeared. IF expressed anxiety in terms of grant money drying up due to the economic crisis, thus either eliminating significant sources of funding or making them even more competitive to receive. Respondent 12 and 21 have started to consider implementing new production-oriented funding models, such as increasing crop acreage and acquiring more land. Four out of twelve LF and eight out of ten IF mentioned inter-farm relationships became especially important to gain advice on how to adapt to and sell their crops during the pandemic. For IF, this involved relying on relationships that have been forged and tended to over many years. Prior to the pandemic, inter-farm visits between IF commonly occurred. During these visits, farmers from two or more farms would come together to complete a large task or learn how to care for a unfamilar crop. During the pandemic, these visits shifted towards picking up the extra slack from a lack of volunteer help and perpetuating a sense of community between farmers. For LF, the pandemic provided inspiration to reach out to fellow farmers they had not spoken to years or ever. Their discussions centered on discussing what markets are open, what crops are popular, and how to operate with CSAs in mind. Both IF and LF found avenues within their respective communities or between their communities to make joint value-added products or incorporate each other's products in CSA boxes.

5 Food security and food sovereignty resiliency

Throughout the pandemic, three IF have led large initiatives to give out free taro and sweet potato cuttings to the community. They have done so by organizing drive thru events and community pickups. Each person that shows up receives a handful of cuttings they can take home and grow in their own garden. Respondent 1 discussed the importance of providing cuttings: “This is to create more resilience for our Kānaka ʻŌiwi families out there. They can take the huli [taro cutting] plant them and it'll grow a corm they can eat and keiki [off shoots] they can plant. They can even give the keiki to more ʻohanas so they can grow too. It’s like that old saying: Give a man and fish and they can eat for the day. Teach him how to fish and he’ll eat forever.”

IF have experienced less of a pivot in crop distribution in comparison to LF. The focal recipient of their crops was community both before and during the pandemic. Moreover, the strong value placed on forging relationships with others in the community has proven to be an invaluable source of work aid and crop sales. However, IF with a non-profit funding model are facing some form of financial instability now and into the future. LF experienced a greater pivot in distribution in comparison to IF, as the restaurant accounts they relied greatly on closed abruptly. However, CSA programs have improved their stability through the pandemic. Three LF discussed forming a relationship with food bank programs in the State of Hawaiʻi during the pandemic. Respondent 23 pointed out the complexities in such a relationship: “The Hawaiʻi Foodbank is doing great work to get food to people. Lots of farmers I work with have been delivering crops to the foodbank. And we all want to continue to help but they want to buy their crops at a pretty discounted rate. I don't know how long they could sustainably give a bulk of produce to them at that price.”

The relationships formed between the farmers and food banks, and the formation of the food banks themselves, are centered on food security and localization. Food security on Oʻahu has and is currently keeping farmers afloat, but has not exactly enabled them to be resilient and thrive economically. Food security initiatives are essential in providing food to the community, especially during rough times, but it is more of a response to a dysfunctional system than a pathway for long term resilience. IF have deployed food sovereignty strategies and from a standpoint of crop distribution pivoting and relationship strength have shown greater resiliency through the pandemic. As the pandemic continues and as the island moves forward into the future, both IF and LF can work together to overcome challenges, become more resilient, and feed the local and Kānaka ʻŌiwi community at different time scales. Many of the aspirations of IF, and the food sovereignty movement in general, are a long-term undertaking that cannot easily be met in the short term. Food security provides a short-term solution to address some food system problems but does not meet the overall goals of LF and IF in the long term.

Future studies might include a larger respondent size and an inclusion of more for-profit Kānaka ʻŌiwi farmers. As the study went on, we found it increasingly relevant to interview non-profit IF, partially due to the sheer number of them, but also because we found it to be the model most conducive to their values and mission. However, keying in on the struggles of the for-profit IF may illuminate additional or contrasting values to the non-profit IF. In addition, since this study was conducted during the summer of 2020, future work might capture the later impacts of the pandemic on farmers and their recovery.

6 Conclusion: Integrating findings into policy

We conclude with suggestions that state and federal agencies and local organizations could implement to support farmers from different backgrounds through COVID-19 and into the future. During discussions with farmers, sentiments of wanting to see change happen through a shift in policy was brought up frequently. These policy pathways are centered on increasing food supply chain access; and mitigating financial and bureaucratic barriers. It should be recognized that these policy and broader food system shifts will require a sustained effort by all parties to be realized.

IF are currently seen as essential sources of place-based education for the local community as a whole. However, these sites should also be seen as key producers and suppliers of culturally significant foods. Legislation intended to expand the Hawaiʻi farm to school program (Act 218, Session Laws of Hawaiʻi 2015) and meet current goals to source fifteen percent by 2025 and thirty percent by 2030 of public-school meals locally should require a portion of each percentage to be acquired from IF. This would be especially helpful for IF non-profit organizations seeking to diversify their financial portfolio to focus on education and production due to pandemic related hardship. This will allow Kānaka ʻŌiwi children, who represent the single largest ethnic group in Hawaiʻi public elementary and secondary school student population, to gain access to culturally significant foods they might not otherwise encounter at home (Goodyear-Kaʻōpua, 2013). In addition, the expansion of the program will further uplift the numerous LF that already participate.

Loans and microloans are valuable to farmers looking to invest in new infrastructure, acquire land, implement innovate crop plans, and meet food safety and processing standards. However, eligibility and high interest rates have long been a barrier. Legislation to expand loan programs with increased eligibility and lower interest rates for farmers could prove pivotal to many pivoting and rethinking business plans through and after the pandemic. Likewise, partnerships between State of Hawaiʻi, federal, and private partners to expand grant programs and their scope could be especially beneficial (Croix and Mak, 2021). In addition to expanding loan and grant programs, dedicated support and education should be provided to farmers to help them understand what they qualify for and how to complete successful loan and grant applications. Respondent 9 discussed their interest in expanding their business but felt held back because of the grant application process: "I want to venture into the realm of making value added products. The opportunity is there, but I am limited by money and time. I see grants pop up here and there that could be helpful. I don't even know how to go about applying for one—what do I write?" For IF and the Kānaka ʻŌiwi community, gaining access to ancestral lands to restore cultural food producing regions and increase the abundance of culturally significant foods is a priority.

Efforts to restore abundance and gain access to sites have long faced bureaucratic barriers erected by the State. Many cultural food producing regions are zoned for conservation or exhibit a need for more formal community oversight and cultural values to ensure persistence of abundance. Therefore, communities often go through community-based subsistence fishing areas (CBSFAs), Memorandum of Understanding (MOU), or seek administrative rule changes to gain access to an area and engage in co-management. These processes often involve unequal power relations and a disregard for different world views and data types (Ayers et al., 2018). While there have been legislative wins (see Hobart, 2017; McMillen et al., 2017; Vaughan et al., 2017), the time, effort and adherence to bureaucratic red tape required to achieve those wins has often minimized their scale and efficacy (Vaughan and Caldwell, 2015). Legislation to streamline bureaucratic barriers and designate additional CBSFAs and carry out more MOU sought out by communities should be considered. In addition, amendments to conservation zoning should be done to encourage the efficient use of conservation lands for Kānaka ʻŌiwi food production now and into the future. This recommendation, however, represents incremental change within the existing governing structure of the state. The sovereignty movement that many IF and those in the broader Kānaka ʻŌiwi community engage in seeks land restitution and greater political autonomy. Therefore, for the goals of Kānaka ʻŌiwi food sovereignty to be fully realized, state and federal officals must engage in meaningful dialogue with Kānaka ʻŌiwi communities to initate pathways towards land restitution and political sovereignty. Until these actions take place Kānaka ʻŌiwi community members will find themselves in a contentious position in trying to realize feed and empower their communities.

These policy suggestions and the main findings of this study provide academics, policy makers and public servants, community leaders, and food system practioners with an up-to-date analysis of a diverse local food system comprised of Indigenous and non-Indigenous community members impacted by COVID-19, along with actionable strategies for achieving resilience and equity for all members of the community. We specifically focused on farmers values associated with food sovereignty and food security, and the degree of resiliency each provides through the COVID-19 pandemic. Both groups of farmers shared similar values when it came their reasoning to begin farming and providing food to the community, but they diverged on their specific focus, intentions, and envisioned futures. IF values are associated with food sovereignty. They are focused on revitalizing their cultural practices and crops while uplifting Kānaka ʻŌiwi communities. IF are utilizing food as pathway towards greater political sovereignty. LF values are associated with food security. They are focused on feeding local communities and are not focused on growing culturally significant crops. LF seek to work with the State to achieve greater food security. LF and IF interacted with different subsets of consumers prior to the COVID-19 pandemic, with the community being the primary recipient of IF crops, and restaurants the main recipient of LF crops. As the impacts of the pandemic took hold, both LF and IF had to adapt and show resilience. IF pivoted less of their crop distribution and relied on established relationships with other IF to adapt. LF pivoted a lot of their crop distrubution from restaurants to community based programs. Both LF and IF face barriers in continuing to operate during the pandemic and into the future. However, both groups have a vision for a better agricultural future that will require consistent participation between themseleves, political representatives, and other related programs and officials. Policies that uplift both groups and their associated values through the pandemic and into the future should be considered. These policies should be centered on food supply chain and land access, financial and bureaucratic barriers, and fostering relationships among farmers.

7 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

8 Author Contributions

LH conceptualized the study, analysed the data, and wrote the first draft. Both LH and MF conducted interviews and edited manuscript drafts.

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11 Figures

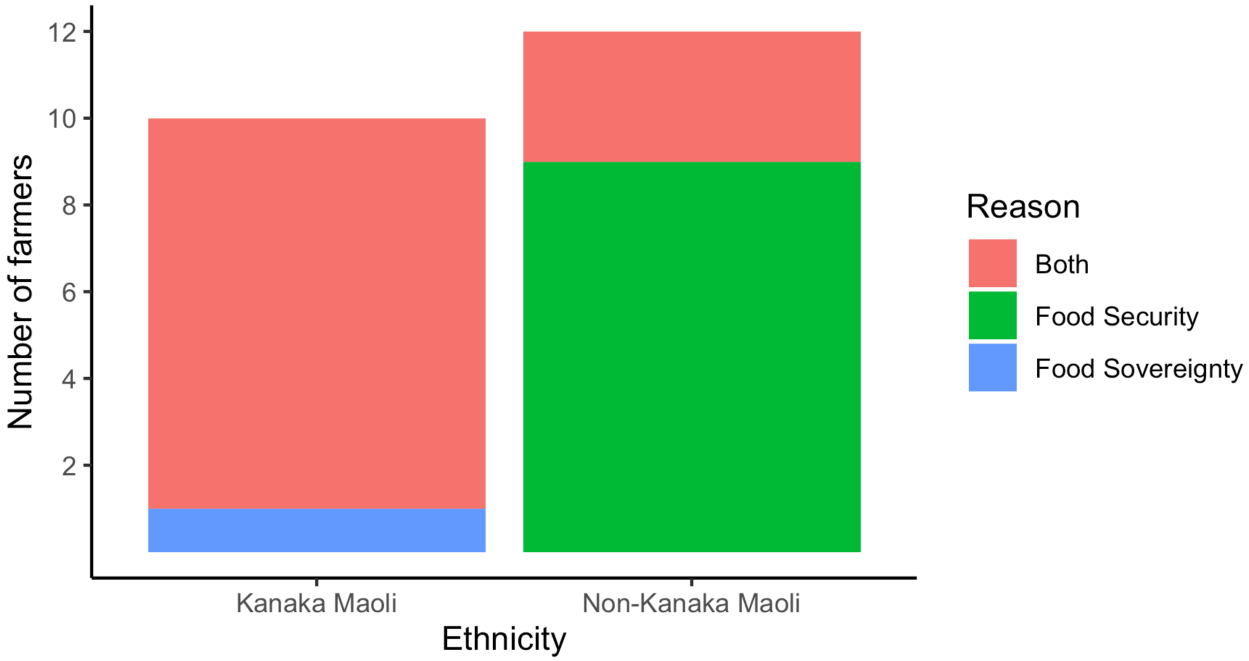
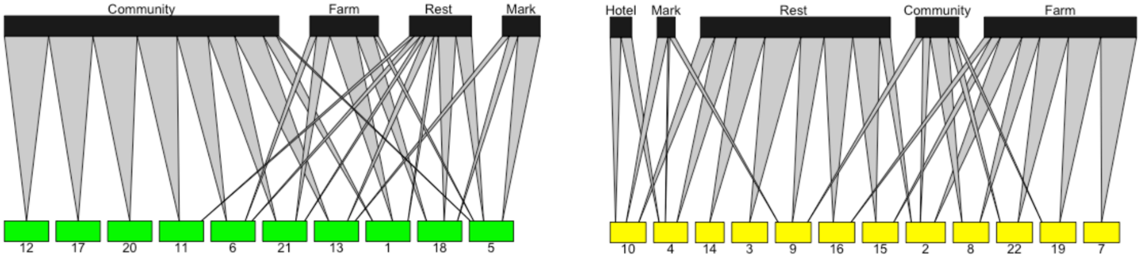
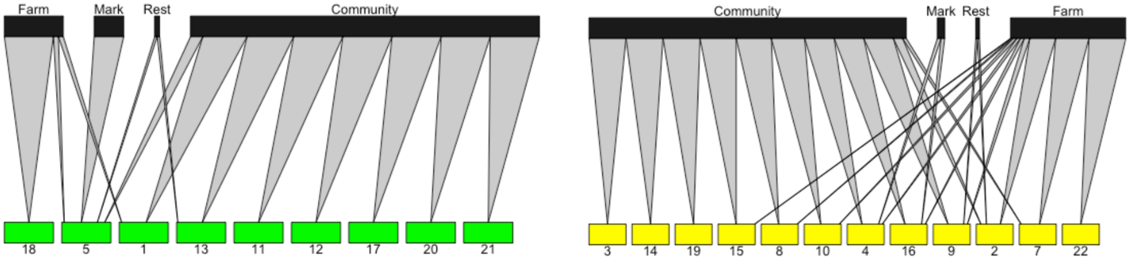


Figure 1. Number of respondents who selected food secuirty, food sovereignty, or both as areason they began and continue farming.



Prior to the Covid-19 Pandemic



During the Covid-19 Pandemic

Figure 2. The distribution of crop sales between each respondent (lower boxes; green = Kanka Maoli Farmers (IF) and yellow = Non-Kānaka ʻŌiwi Farmers) and different consumer base types (community (e.g. CSA boxes, farm pick ups, and donations), supermarkets (Mark), farmers markets (Farm), restaurants (Rest), and hotels) prior to and during the COVID-19 pandemic. The links between the two represent the proportion of pounds distributed to that consumer base relative to the overall pounds harvested by each respondent.

12 Table

Table 1. Demographic attributes of interviewed farmers (respondents).

Respondent #	**For-profit? (Yes/No)**	**Ethnic Identity**	**Years in operation (1-10 years, 10-20 years, 20+ years)**	**Location**	**Farm scale (Small (1-50 acres), medium (50-100 acres), and large (100+ acres))**
1	Yes	Hawaiian	1-10	East O‘ahu	Small
2	Yes	Asian	1-10	East O‘ahu	Small
3	Yes	Asian	1-10	East O‘ahu	Small
4	Yes	White	20+	West O‘ahu	Small
5	No	Hawaiian	20+	West O‘ahu	Large
6	No	Hawaiian	20+	East O‘ahu	Medium
7	Yes	Asian	10-20	Central O‘ahu	Small
8	Yes	White	1-10	East O‘ahu	Small
9	Yes	Asian	1-10	Central O‘ahu	Small
10	Yes	White	1-10	Central O‘ahu	Medium
11	No	Hawaiian	10-20	East O‘ahu	Small
12	Yes	Hawaiian	1-10	West O‘ahu	Small
13	No	Hawaiian	1-10	East O‘ahu	Small
14	Yes	Asian	10-20	East O‘ahu	Small
15	Yes	White	20+	East O‘ahu	Large
16	Yes	Asian	1-10	East O‘ahu	Small
17	No	Hawaiian	10-20	East O‘ahu	Small
18	Yes	Hawaiian	1-10	East O‘ahu	Small
19	Yes	White	1-10	East O‘ahu	Small
20	No	Hawaiian	1-10	East O‘ahu	Small
21	No	Hawaiian	10-20	East O‘ahu	Small
22	Yes	Asian	10-20	Central O‘ahu	Small

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CHAPTER 3

ARTHROPODS ARE KIN: OPERATIONALIZING INDIGENOUS DATA SOVEREIGNTY TO RESPECTFULLY UTILIZE GENOMIC DATA FROM INDIGENOUS LANDS

INTRODUCTION

Now published in Molecular Ecology Resources, this paper is my first chapter to utilize empirical ecological data. While collecting data for this chapter, I was able to deepen and create new relationships with farmers, fully test out field sampling methods, and identify future sites for sampling for chapter 4 and future work. Subsequently, the data analysis for this chapter unveiled key on-farm and landscape composition variables shaping native and introduced arthropod communities, such as the number of Polynesian crops and distance to a forest. These analyses and results were crucial in deciding how to best sample future sites and how to address analyses for Chapter 4. As this chapter was coming together, I became immersed in the field of Indigenous Data Sovereignty. I was inspired to operationalize the CARE principles with the genomic data I was collecting. This placed an emphasis on the importance of how I was conducting myself as a scientist. Operationalizing CARE in Chapter 3 led to revelations on how to improve several parts of the scientific process to be in alignment with the local community, which led to the co-development of research questions with a community partner for a grant that is addressed in Chapter 4 and future work.

ARTHROPODS ARE KIN: OPERATIONALIZING INDIGENOUS DATA SOVEREIGNTY TO RESPECTFULLY UTILIZE GENOMIC DATA FROM INDIGENOUS LANDS

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Abstract

Indigenous Peoples have cultivated biodiverse agroecosystems since time immemorial. The rise of metagenomics and high-throughput sequencing technologies in biodiversity studies has rapidly expanded the scale of data collection from these lands. A respectful approach to the data life cycle grounded in the sovereignty of Indigenous communities is imperative to not perpetuate harm. In this paper, we operationalize an Indigenous Data Sovereignty (IDS) framework to outline realistic considerations for genomic data that span data collection, governance, and communication. As a case study for this framework, we use arthropod genomic data collected from diversified and simplified farm sites close to and far from natural habitats within a historic Kānaka ʻŌiwi (Indigenous Hawaiian) agroecosystem. Diversified sites had the highest Operational Taxonomic Unit (OTU) richness for native and introduced arthropods. There may be a significant spillover effect between forest and farm sites, as farm sites near a natural habitat had higher OTU richness than those farther away. We also provide evidence that management factors such as the number of Polynesian crops cultivated may drive arthropod community composition. Through this case study, we emphasize the context-dependent opportunities and challenges for operationalizing IDS by uilizing participatory research methods, expanding novel data management tools through the Local Contexts Hub, and developing and nurturing community partnerships—all while highlighting the potential of agroecosystems for arthropod conservation. Overall, the workflow and the example presented here can help researchers take tangible steps to achieve IDS, which often seems elusive with the expanding use of genomic data.

1. Introduction

Global ecosystems are under siege with threats to biodiversity approaching critical tipping points. Key native taxa are disappearing (de Oliveira Roque et al., 2018), while introduced species are increasingly spreading and disrupting the functioning of ecosystems (Burnett et al., 2006). Recognition that landscapes have been anthropogenically shaped for tens of thousands of years has directed efforts to understand biodiversity patterns beyond “pristine, wild, and natural” environments. Indigenous-managed agroecosystems have been noted for their capacity to maintain and bolster biodiversity (Perfecto et al., 2019). For Indigenous Peoples, the culturally relevant biodiversity fostered by agroecosystems has shaped their identity and culture (Nelson & Shilling, 2018). Biodiversity conservation efforts have been vital to global Indigenous sovereignty movements that seek to rematriate and restore lands where biodiversity has been eroded due to colonization (Settee & Shukla, 2020; Wezel et al., 2009). However, the historical and ongoing extraction of biodiversity resources with little engagement or benefit to communities has undermined Indigenous sovereignty and caused a rightful distrust by Indigenous Peoples concerning biodiversity conservation studies and initiatives (Merson, 2000).

The growing popularity and utilization of metabarcoding and environmental DNA (eDNA) in biodiversity research has expanded the scale of data generation from Indigenous lands (Arribas et al., 2022; Kennedy et al., 2020). Moreover, in the case of many eDNA samples, a full new understanding of ecosystems can be gained in covert ways: A single water sample from a river can determine if a prized riparian species is upstream (Rees et al., 2014) or a bag of tea leaves bought from a supermarket can illuminate arthropod community composition (Krehenwinkel et al., 2022). The novelty, scalability, and covertness of eDNA-based data stress the need to understand how to respectfully use genomic data collected on Indigenous lands to support communities better and honor their sovereignty.

Consequently, efforts are underway at multiple governance scales to empower communities and protect Indigenous Data Sovereignty (IDS). For example, the United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP) (Assembly, U.N.G., 2007) and Convention on Biological Diversity and its Nagoya Protocol (Convention on Biological Diversity - Article 1. Objectives, n.d.) all affirm Indigenous Peoples have bona fide sovereignty that must be honored. Data collected within Indigenous homelands should be under the authority of relevant communities or an entity designated by each community. Initiatives such as the Global Indigenous Data Alliance (GIDA) (Global Indigenous Data Alliance, n.d.) promote the exercising of IDS through the CARE (Collective benefit, Authority to control, Responsibility, and Ethics) principles (Carroll et al., 2022) for Indigenous data governance. These human-centric principles sit alongside the more data-centric FAIR principles (Wilkinson et al., 2016) and guide researchers in operationalizing IDS through collective benefit, authority to control, responsibility, and ethics.

Global biodiversity genomics initiatives are beginning to recognize the importance of Indigenous Peoples in their mission to sequence all of eukaryotic life (Mc Cartney, Anderson, et al., 2022; Mc Cartney, Tsosie, et al., 2022). Indigenous communities are also taking agency over their data by providing guidelines for researchers. Indigenous Peoples across the globe have developed codes of research conduct to gain and retain agency over their biodiversity resources, including Māori (Hudson et al., 2016; Stats, 2020), First Nation, Metis, and Inuit Peoples (TCPS-2, 2014), the San community (Callaway, 2017), Aboriginal and Torres Strait Islander Peoples (*Guidelines for Ethical Research in Australian Indigenous Studies*, 2012)and Tribes across the United States (Carroll et al., 2022).

The breadth of emerging IDS initiatives highlights the importance and potential of halting extractive research practices in Indigenous communities. Nonetheless, to many communities and researchers, IDS still seems to be an elusive goal, especially in its application. In this paper, we build on a framework developed by Mc Cartney et al. (2023) by applying it to an empirical case study of arthropod genomic data collected along a gradient of agricultural diversification and proximity to natural habitat on Hawaiʻi Island, Hawaiʻi (Figure 2A). The McCartney et al. (2023) framework recommendations are guided by the CARE principles to work more justly with Indigenous Peoples and Local Communities (IPLC). These recommendations fit into six steps. However, for our case study, we found it best to summarize and organize our IDS workflow into the three steps presented below (and illustrated in Figure 1).

1) **Proactive Engagement and Benefit-Sharing in Research Development and Data Collection.** Researchers must invest time and resources to develop relationships with community members to gain support and permission to access sites and obtain samples. Access should be obtained legally and ethically, such as those outlined by the Nagoya Protocol or following community protocols. Community partners should provide input and be a part of the co-development of project goals throughout the life of the study. It is critical to be transparent about initial project goals and benefits with community partners and the risks and benefits of storing samples away from the community's residence (if applicable). When curating metadata, researchers should redact specific sensitive metadata fields congruent with Dublin Core and Darwin Core (Wieczorek et al., 2012).

2) **Data governance and storage.** Researchers should understand and respect the Indigenous communities' cultural sensitivities, customs, and protocols surrounding the governance of the data life cycle. A responsible data management plan should be developed to prioritize long-term sustained community access and perspectives.

3) **Research Communication and Dissemination.** Researchers should design a research communication and dissemination plan that considers a breadth of appropriate audiences, such as community members and partners, land managers, or researchers. Researchers should consider further project and partnership continuity through funding opportunities if possible and mutually desired.

2. Case study: ʻUpena of Pilina: Revitalizing Connections Between Kānaka ʻŌiwi Food Systems and Arthropods

In Hawaiʻi, Kānaka ʻŌiwi (Indigenous Hawaiian; referred to as ʻōiwi hereafter) established vast agricultural systems spanning elevational ranges from the coast to upper-elevation mountainous areas (Kagawa & Vitousek, 2012; N. K. Lincoln & Vitousek, 2017). However, historical and ongoing colonization and globalization have drastically altered the agricultural landscapes of Hawaiʻi (Hutchins & Feldman, 2021). For example, in the Kona Field System (KFS), an agricultural belt built on the leeward side of Hawaiʻi Island, the proliferation of coffee caused the contraction of land dedicated to agroforestry practices and the introduction (both intentionally and unintentionally) of a myriad of invasive arthropods (Allen, 2001; N. Lincoln et al., 2018). Some introduced arthropods have even been linked to the decline of native and endemic arthropods (King et al., 2010) and flora (Roy et al., 2019), along with crop production (Messing, 2012).

More recently, a growing food sovereignty movement across Hawaiʻi has revitalized agroforestry practices and the subsequent return of ʻōiwi community members and culturally significant species (N. Lincoln et al., 2018). In the KFS, after being abandoned for many years, agroforestry sites are being cultivated again by the ʻōiwi community, where they are growing crops with known associations with native arthropod diversity (Swezey, O.H., 1954). Today, these traditional agroforestry sites are nested within a complex landscape mosaic dominated by conventional coffee monocultures. Yet, whether greater agricultural diversification can provide suitable habitat to sustain native biodiversity rather than serve as an avenue for the proliferation and spread of non-native species remains unresolved. Therefore, our ongoing research in the Kona Field System asks: *to what extent can diversified agricultural landscapes support native arthropod diversity? How does arthropod community composition shift in response to crop diversification?*

3. Methods

Here, we present a simplified version of our methods. Please see our supplementary information for more details on our methods.

3.1 Site selection and arthropod sampling

We selected six farm sites along a diversification gradient, which was based on the presence of on-farm crop diversity, size (area in production), elevation, and similar utilization of inputs such as pesticides and fertilizer. Due to our interest in comparing farm arthropod community composition and structure to that in forested areas, two forest sites were sampled. Forest sites were selected based on the degree of disturbance and elevation: primary forests facing degradation from invasive plants and arthropods located between 792 to 914 meters in elevation. Therefore, forest sites had a mix of native and introduced vegetation. We also ensured that all sites were at least 800 meters apart.

3.2 Sample collection

We collected arthropods using vegetation beating (40 seconds) at five points (2m radius) along a 25-meter transect. Before beat sampling, we collected and sifted leaf litter from a 1x1m plot at each transect point. Then arthropods from litter samples were collected using a berlese funnel. All arthropod community samples were stored in 95% ethanol at -20 °C until DNA extractions.

3.3 DNA extraction

DNA extraction of size-sorted arthropod-plant community samples was performed using the Tissue protocol described in the Qiagen Puregene kit modified for automation (Lim et al., 2022).

3.4 Library preparation and sequence analysis

We used a primer combination (*ArF1 - Fol-degen*-rev) that targets a 418 bp fragment in the barcode region of the Cytochrome Oxidase I (COI) gene (Lim et al., 2022) in triplicate amplifications using the Qiagen Multiplex PCR kit (Qiagen). The three sample replicates were pooled, and the quality of all pooled PCR products was ensured through bead cleanup and fragment length analysis. Final amplicon libraries consisted of pooled equimolar samples and were sequenced on an Illumina® MiSeq (Illumina, San Diego, USA).

Sequences were demultiplexed on Illumina® BaseSpace. PCR primers were trimmed using Cutadapt (Martin, 2011). Sequences were merged, filtered, and denoised to amplicon sequence variants (ASVs) using DADA2 (version 1.14.1.; Callahan et al., 2016; Brandt et al., 2021). ASVs were then clustered to 3% radius (97%) OTUs using DECIPHER (2.14.0; Wright et al., 2012). A curated OTU table was created using LULU (version 0.1.0; Frøslev et al., 2017; Brandt et al., 2021). All remaining OTU sequences were compared to Genbank using ElasticBLAST on Amazon Web Services.

3.5 Native/Introduced Assignment

To assign a native or introduced status to all OTUs, we utilized NIClassify (https://github.com/tokebe/niclassify), a software tool that implements a machine-learning strategy based on the principles of Andersen et al. (2019). The tool has been used to accurately assign status to several arthropod datasets from Hawai'i (Graham et al., 2022; Kennedy et al., 2022).

3.6 Agricultural diversification index

To create the agricultural diversification index, we used the first principal component of a PCA matrix that included the scaled values of all management attribute variables (coffee cover, crop diversity, non-crop vegetation, canopy layers, litter depth, and distance to natural habitat) (Lu et al., 2022; Armengot et al., 2011). The index allowed us to explore the overall effect of agricultural diversification.

3.7 Statistical analysis

We assessed the alpha-diversity (observed "richness") and beta-diversity ("composition" based on Bray-Curtis dissimilarities of Hellinger-transformed community matrices) of native and introduced arthropods in two ways. First, we examined site-level differences between richness and composition to address farmer interests, including the individual environmental and management attributes that drive these differences and the individual arthropod taxa that contribute to site-level differences. Next, we tested the effect of agricultural diversification (combining all management attributes into a singular index) and distance to natural habitat (“close” and “far”) to examine the ecological mechanisms that drive the richness and composition of arthropods.

3.8 Site-level differences in arthropod communities

Alpha-diversity. We examined the differences in observed native and introduced arthropod richness (Poisson error) between sites using generalized linear mixed models with site as a random effect using the lme4 and lmertest packages in R (version 4.2.3) (Bates et al., 2015; Kuznetsova et al., 2017; R Core Team, 2020). Tukey HSD’s was also performed to observe pairwise comparisons between sites.

Beta-diversity. To determine the environmental and management attributes that significantly influenced introduced and native arthropod community composition, we used a distance-based redundancy analysis (dbRDA) using the vegan package (Oksanen et al., 2013). The dbRDA tests how much variation within a community (i.e., arthropod community composition) is explained by a group of explanatory variables (i.e., environmental and management variables) (Legendre & Anderson, 1999). Collinear variables were removed, and the significance of the coefficients was determined using a permutation-based ANOVA.

To understand the contribution of individual taxa to the dissimilarity between sites, we performed a similarity percentage (SIMPER) analysis on the introduced and native arthropod composition matrices.

3.9 Agricultural diversification and landscape effects on arthropod communities

Alpha-diversity. We tested the effect of agricultural diversification, distance to natural habitat (“close” vs. “far”), and their interaction on observed richness of introduced and native arthropods using generalized linear mixed models with site as a random effect using the lme4 and lmertest packages in R (version 4.2.3) (Bates et al., 2015; Kuznetsova et al., 2017; R Core Team, 2020).

Beta-diversity. To evaluate the effects of agricultural diversification, distance to natural habitat (“close” vs. “far”), and their interaction on introduced and native arthropod community composition, we used a permutational multivariate analysis of variance (PERMANOVA) using the package vegan (Oksanen et al., 2013). PERMANOVA tests compositional differences by examining whether the centroids of sample clusters differ. To illustrate arthropod community composition differences for the interaction between agricultural diversification and proximity to natural habitat, the composition matrices were ordinated by a principal coordinates analysis (PCoA) using the ‘pcoa’ command in the ape package (Fig. 2a) (Paradis et al., 2004).

4. Proactive Engagement in Research Development and Data Collection

4.1 Positionality and Motivation of Researchers during Engagement

Potential farmer participants in the project were engaged through the University of Hawaiʻi Cooperative Extension, pre-established relationships, and farm visits. Through discussions with the farmers, the project team gained a vital understanding of the history of the land, farmer interests, and pest issues. Importantly, these discussions also allowed farmers to ask questions about the project and its design. Although it is a best practice to co-develop the project goals with the community, the study design occurred before engagement. However, through initial engagements and conversations, the project team acknowledged their position as researchers and recognized the power, potential harm, and responsibility of conducting research on these lands. These relationships made engaging from that point onwards and guiding future research plans possible. For instance, during a discussion with one farmer, they expressed a passion for aligning academic research with on-farm applications. This led to a grant application for a co-developed project with a community partner, Kamehameha Schools, along with farmer input from within the KFS, which was successfully funded. Notably, this farmer is a paid consultant on the project with several others. This demonstrates that engagement at any point in the project lifecycle is highly beneficial.

Arthropod communities were also sampled from two forest sites using the abovementioned methods. To gain access to forest sites, as required by law, we submitted applications to obtain the appropriate permits to the Hawaiʻi State Department of Land and Natural Resources Office and the subsequent overseers that manage project-specific localities and taxa groups. This is a bureaucratic process with a clear application form and procedures for obtaining site access, unlike the site-by-site informal and formal conversations with farmers that are solely built on transparency, trust, and time. Therefore, in agroecosystems, engagement looks vastly different and requires more individualized relationship building.

The positionality of the research team during these engagements with the community and landscape is essential to identify and honor to understand the power imbalances and differing perspectives that occur. Regarding our research team, the lead author is part of the ʻōiwi community. A certain unmeasurable level of interpersonal communication comes with holding this identity, including how to approach and interact with community members and social normalities within local communities in Hawaiʻi. However, the lead author and the research team acknowledged their position as researchers from an institution such as UC Berkeley that creates a power imbalance (please see Baum et al. 2006 for further scholarship on the role of identity in participatory research).

The motivation behind the inception and planning of a research project with community partners is important to recognize and acknowledge. Motivation brought on by romanticsm, white savior complex, or a need to fulfill a grant requirement for broader impacts or a DEIJ (Diversity, Equity, Inclusion, and Justice) component can be common and do not create sustained and trustworthy relationships with communities. An example of romanticism is the desire to work in a location such as Hawaiʻi because of its beauty or historical public perception as a “paradise” or to engage with an Indigenous community based on notions of needing to “save” them from poverty or injustice. The motivation for our research comes from the lead author’s long-term, sustained interactions with both landscape and people over many years. This built relationship and the positionality outlined in the section above created a kuleana (responsibility) to continue building and bettering these project relationships.

4.2 Safeguarding metadata and ex-situ samples

While sampling arthropods at each site, we scored or measured various environmental and management attributes (Table 1). These attributes were selected based on their known ability to shape arthropod communities. Metadata collected through the project discloses in-depth information about each farm site and the arthropods on them. All metadata identified as culturally sensitive by the community, such as location and identity beyond the order level of species, was redacted from publicly available metadata according to Darwin Core standards (InformationWithheld; Table 2). This ensures that the most sensitive data revealing the location of arthropod and plant species, along with their identity, will not be available to those outside of the community, thus reducing the ability for unauthorized visits or access. Farmers and community members involved in the project will hve access to the complete, unredacted version of the metadata records about their site. Unredacted data sharing among farmers is facilitated through a case-by-case approval basis.

Once collected, the samples were transported to UC Berkeley for processing, where DNA extraction, library preparation, sequencing, and bioinformatics occurred. The gDNA from this project will be stored in a freezer on campus and not used for non-project purposes. The research team recognizes that the samples were processed far from their origin. All farmers were aware of the destination of the samples. In the future, there is tremendous potential for ʻōiwi geneticists and computer scientists to gather to create a lab and biobanking operation that is accountable to community standards, which could be modeled after the Native BioData Consortium, an Indigenous-led organization further discussed below (see section "Establishing Sustained and Culturally Appropriate Indigenous Resource Storage Solutions").

5. Data governance and storage

5.1 Contextualizing community data

Due to colonial practices and policies, the research enterprise has resulted in most Indigenous data being generated and analyzed away from the origin. Systemic inequities and power imbalances perpetuate unjust disconnections between Indigenous communities, their samples, and data. In Hawaiʻi, previous and ongoing biopiracy projects, plant patenting, and human genome projects have caused a rightful hesitancy amongst the ʻōiwi community concerning the genomic research enterprise (Goodyear-Kaʻōpua et al., 2014). In 2003, in response to the increasing commercialization, commodification, and exploitation of Indigenous resources, such as kalo (taro), ʻōiwi elders and cultural leaders crafted the Paoakalani Declaration (*Paoakalani Declaration*, 2003). This foundational document outlined ʻōiwi perceptions of traditional knowledge, genetic and biological material stewardship, and a governance framework (Figure 3).

In this project, the arthropods we collected are biological and genetic material from Hawaiʻi. Therefore, they are protected under the Paoakalani Doctrine. Moreover, culturally, arthropods are kin to ʻōiwi. Several species—both native and non-native— are mentioned in the Kumulipo (Figure 2B), the Hawaiian life origin story. The presence of arthropods in the Kumulipo ties them genealogically to the ʻōiwi community, as the creation of all life (from plants to insects to human beings) is recounted in the epic story and weaved together in succession– just like a phylogeny in the field of genetics. Arthropods are also discussed in moʻolelo and kaʻao (two types of storytelling) (Richard Paglinagwan, 2022). How these arthropods are described varies from revered cultural beings, such as having the designation of ʻaumakua (guardian), to agricultural pests. Therefore, there are many layers of traditional knowledge associated with arthropods, thus imbuing them with kinship.

Many of the arthropods in the Kumulipo were present in our data set. Therefore, sensitivity around the data from these Orders is elevated. However, since these orders represent dozens of families and species of arthropods, further discussion is required to untangle if each species is treated in the same way. Consequently, in the instance of the ant, it is a known introduced arthropod with significant negative impacts on ecosystems. How do you reconcile its presence in the Kumulipo with taxonomic origin and impact? These questions must be addressed by relevant cultural leaders, which we describe further in the "Recognizing Biocultural Significance and Considerations for Indigenous Data Futures" section below.

5.2 Operationalizing and Embedding Indigenous Data Sovereignty

As with the CARE principles, Paoakalani offers generalized, theoretical models for research governance and conduct in partnership with Indigenous communities. However, the research team is responsible for appropriately operationalizing these guidelines, specifically in the context of their research project. To operationalize the wishes of Paoakalani, our research team sought innovative modalities to safeguard IDS across all samples collected and data generated. For this, we utilized The Biocultural (BC) and Traditional Knowledge (TK) Notices developed by Local Contexts, an Indigenous-led organization, that are designed to provide Indigenous context and agency over Indigenous resources (Anderson, 2012; Jane Anderson & Kimberly Ann Christen, 2019). These Labels and Notices provide an extra-legal system of interest disclosure that creates space for community voices to be heard and address a pitfall in current Intellectual Property regimes that only recognize individual rights. To utilize the Label and Notices disclosure system, the project team created a researcher account through an online hub managed by Local Contexts. The application of these notices can be both visible as an icon in this publication (Figure 4) and as added fields in metadata tables with a specific project identifier (Liggins et al., 2021). However, commonly utilized genomic metadata standards still needed to be developed to include the disclosure of Indigenous rights, interests, and provenance information. Therefore, we added our own fields to the iBOL metadata manifest and filled them according to Mc Cartney et al. (2022) using language from the Local Contexts Hub (Table 2).

5.3 Recognizing Biocultural Significance and Considerations for Indigenous Data Futures

A limitation for our research team in using the BC and TK Notice is the lack of an account for the ʻōiwi community on the Local Context Hub. The usual streamlined process of using BC and TK notices is such that a community must have an account to be notified. From there, they decide how to address the research team and the data generated. In other Indigenous communities, community accounts are usually overseen by entities such as Tribal research review boards or designated oversight leaders. However, there is no centralized governance structure like this in Hawaiʻi for the ʻōiwi community. A typical path forward with this lack of governance structure is the formation of a hui (group) around central topics, which could be operationalized for managing genomic data among the ʻōiwi community. Previously, in the biological context, a hui comprised of ʻōiwi community members has been formed to discuss the cultural protocols, importance, and management of limu (seaweed; Kua ʻĀina Ulu ʻAuamo, n.d.), manu (birds; Paxton et al., 2022), and iʻa (fish; Vaughan & Caldwell, 2015).

We propose establishing a hui of cultural, arthropod, and farming leaders in Hawaiʻi to begin engaging in discussions on arthropods. This group could apply cultural, ecological, and on-farm knowledge (e.g., pest species) to different represented species and communities of arthropods. A hui such as these can provide expertise on the cultural knowledge aspect of species and engage in some forms of governance. For example, members of the Limu Hui decide who and when to share the location of gathering spots so as not to reveal a treasured gathering ground to a broader public not trained in proper gathering techniques or companies engaging in biopiracy. Nonetheless, there is a need for cultural taxon groups to engage in more structured governance. This could be achieved by looking at co-management structures currently in place in Hawaiʻi, such as those formed between the Office of Hawaiian Affairs, a cultural working group, and state and federal agencies to manage the Papahānaumokuākea Marine National Monument (Kikiloi et al., 2017). By including better governance structures, data access considerations and questions such as the following can be addressed:

1) How did kūpuna (elders, ancestors) manage access to knowledge and resources?
2) Who should have access to project-generated arthropod data?
    a) Lineal descendants of the different ahupuaʻa (land division on a local scale) or moku (land division on a regional scale) sampled in Kona?
    b) Those who are kamaʻāina (familiar) and have pilina (connection) with the different arthropods?
    c) Other farmers and researchers looking to do work that continues to support an agricultural future in Kona?

The result of this would be a comprehensive and streamlined access approach that can be applied at varying scales, including on the Local Context Hub.

5.4 Establishing Sustained and Culturally Appropriate Indigenous Resource Storage Solutions

The process of forming a hui and engaging in needed conversations and decision-making takes a considerable amount of time. Although our project integrated a mechanism to support the disclosure of the Indigenous rights and interests associated with the species samples and sequencing information generated, to fully realize IDS, a solution was needed for where genetic resources and sequencing data would be stored. Here, in this project, long-term access to the community participants and long-term storage capacity was prioritized. Similar to many Indigenous communities worldwide, Hawaiʻi does not have an Indigenous-led or driven biobank or storage facility to store Indigenous samples obtained, so an external repository for both the physical and digital Indigenous resources was required. When selecting an appropriate external repository, it was important that the entity could act as a safe harbor for the resources collected until the community could establish a local repository. The selection strategy considered whether the entity had cultural awareness and training in Indigenous resource management and had the necessary infrastructure to support community accessibility and governance over the resources.

Therefore, for this project, we chose the Native BioData Consortium (NBDC) as an external repository for storing genomic data. NBDC is a not-for-profit, Indigenous-driven organization situated on the lands of the Cheyenne River Sioux Tribe in South Dakota. NBDC acts as a "safe harbor" for Indigenous genetics resources and the associated sequencing data until a community has its own infrastructure to provide expertise, physical data storage, and legal services. It is also the only Indigenous-led bio-consortium in the United States. Both the raw and processed data, including the metadata, for this project will be hosted and stored on the NBDC server, with sequencing data access granted upon request to the community advisory board. Data decisions will be made on a case-by-case basis.

6. Research Communication and Dissemination

Although project questions were not co-created with farmers, we evaluated whether project-generated data could address farmer interests and provide information on potential benefits to the farmers. We also considered how farmer interests align with our main research question and in the communication of our results. Importantly, in interpreting the results of our analysis, we show that data can serve many purposes and be communicated in different ways depending on the audience. In addressing these questions, we place a particular emphasis on the taxonomic origin of species, whether they are native or introduced, for a few key reasons: first, native taxa are often indicators of environmental change (Medeiros et al., 2013; Gillespie et al., 2008); second, native taxa are culturally significant; and lastly, a whole suite of introduced taxa has caused considerable harm to ecological communities (Howarth, 1985) with significant consequences to Indigenous communities, such as the loss of culturally significant staple crops.

6.1 Overview of the data

In total, 222 OTUs were collected amongst all sites, of which 183 OTUs had introduced taxonomic status while 39 had native status. The orders Araneae, Coleoptera, and Lepidoptera represented many native OTUs (Figure S1). Conversely, most introduced OTUs held an equal proportion with some increase in Araneae and Coleoptera.

6.2 Exploring farmer interests

During conversations with farmers, we encountered two main interests regarding arthropods on their farms. Farmers asked: first, what arthropods are present on my farm? Second, how does this compare to other farms in the region? Some farmers also had specific questions about the Coffee Borer Beetle ("CBB"; *Hypothenemus hampei*), which is plaguing their farms (Aristizábal et al., 2016). We could address the first and second questions with the data we generated from this project (Figure 4A-E). However, we did not detect any CBB despite the presence of beetles from the same family (Curculionidae) as CBB in our samples. The lack of CBB is potentially due to seasonality and sampling methodology. CBB tend to be more abundant with the development of cherries and collected through extracting them from cherries or beetle-specific traps (Follett et al., 2016). Therefore, the data could not address any CBB-related questions.

To address the farmer's questions, we analyzed the observed richness of both introduced and native arthropods at the site level (1-8), with forest sites included as a reference baseline. We examined environmental and management attributes known in other studies to alter the composition of arthropods across individual sites (Table 1). All sites varied in environmental and management attributes, which included measurements on on-farm vegetation (e.g., coffee cover, crop diversity, and non-crops), canopy structure, the amount of leaf litter on the ground, and the distance to natural habitat (Figure 4A). The variation among sites captures that agricultural land use is heterogenous, and seemingly similar sites (e.g., a few numbers of crops) can still have different habitat/structural properties (Benton et al., 2003).

A Tukey HSD showed introduced arthropod richness did vary among some sites, with some farm sites significantly more (e.g., site 6 vs sites 1-4 and 7) or less (e.g., site 4 vs sites 5, 6, and 8) than other sites (Figure 4B). In contrast, native arthropod richness appears to be more variable between sites. The forest sites had the highest number of native arthropods. However, diversified farm sites 6 and 7 were similar to the forest sites in richness. Curiously, simplified farm site 5 appears to have a subset of native arthropods on all sites. Diversified farm site 8 had lower observed richness than other diversified sites, with richness on par with simplified sites 3 and 4. This could be described by the landscape surrounding site 8 being dominated by monocultures, while the other sites had a more complex landscape mosaic. An additional factor could be the time in management, which we attempted to control by ensuring each farm had been using simplified or diversified management for at least five years. However, site 8 had not been in diversified management for as long as the other diversified sites.

Changes in arthropod richness can be attributed to some on-farm environmental and management properties. Coffee cover ($P = 0.013$) and distance to natural habitat ($P < 0.001$) significantly altered the richness (SI Table 1) and composition of introduced arthropods (Figure 4D). Site 3, a simplified farm with the highest proportion of on-farm coffee cover, had an observed introduced arthropod richness comparable to several other sites (Figure 4B). However, the arthropod community sampled from site 3 differed from other sites (Figure 4C). For native arthropods, richness was impacted by several site features, negatively by greater crop diversity and positively with more canopy layers, but proximity to natural habitat had no effect. Interestingly, diversified farm site 8, which had the highest crop diversity, had one of the lowest numbers of native arthropods (Figure 4D); yet, the composition of this arthropod community was distinct from other farm sites due to its high level of crop diversity, especially Polynesian crops (see below in the “Addressing our ecological question” section for further discussion; Figure 4E). Therefore, there’s a potential for farms, even those located within an area with little natural habitat, to support a unique composition of arthropods through on-farm management practices such as increasing crop diversification and including more Polynesian crops.

A SIMPER analysis identified the native and introduced OTUs contributing the most to the differences between sites (Figure 5A-B). For introduced arthropods, some of the most important OTUs driving community variation included OTU9 (Entomobryidae, 10.2% variation), OTU3 (Amphipoda, 6.89% variation), OTU15 (*Brachymyrmex cordmoyi*, 4.52% variation) and OTU7 (Entomobryidae, 4.37% variation) (Figure 5A). OTU9 and OTU7 belong to the springtail family, which are detritivores that thrive in soil, and are some of the most abundant introduced OTUs across all sites. Springtails may be particularly abundant in diversified farm sites due to management strategies that promote the build-up of leaf litter and the use of mulch. Curiously, OTU15, an ant known to thrive in the Neotropics, is mainly abundant in simplified farm sites.

In terms of native arthropods, some of the most important OTUs driving community variation include OTU134 (Polydesmida, 11.69%) OTU187 (Tetragnatha, 10.79%), OTU257 (Psocoptera, 8.73%) OTU165 (Psocoptera, 7.95%), and OTU11 (Tetragnathidae, 6.61%) (Figure 5B). A commonality amongst all of these OTUs is that they have generalist feeding habits. OTU34 is a detritivore in the millipede family and is abundant at diversified farm sites. Again, this may be explained by the soil and leaf litter enhancement strategies on these diversified farms compared to simplified ones. OTU11 and 187 belong to Tetragnathidae, a well-studied family of spiders in Hawaiʻi that feed on various prey. These OTUs are well represented in farm and forest sites. Pscoptera (OTU257 and OTU165) were abundant across all sites and feed on lichen, fungi, and plant materials on various plant species. We further explore hypotheses on what mechanisms may be behind the retention of certain native taxa in farm sites below (see "Addressing our ecological question").

Drivers of site-by-site differences in arthropod richness and composition appear ambiguous, which could be aided by including more farmer participants/sites in future sampling and, thus, increasing statistical power. Yet, the data we collected could be more meaningful to individual farmers if it is not just aggregated to examine patterns that drive the number or composition of arthropods. Therefore, our farmer communication plan involves sharing a flier with individualized information for each farmer, including comprehensive information on the arthropod community detected on their farm. For example, by providing the trophic assignments for nearly all taxa observed on their farm, farmers can use this information to match what they see on the farm with the species list and hone in on pest species they may be encountering. Then, farmers can decide if they wish to engage in forms of Integrative Pest Management or work with the University of Hawaiʻi Extension or Natural Resource Defense Council to further inquire about the benefits of the species present (i.e., conservation payment programs). After receiving the flier, if a farmer wishes to engage further and learn more, we invite them to attend online or in-person one-on-one or group meetings. A communication plan ensures that project data will make it back to the community meaningfully, which is sometimes in contrast to project goals. This dualpproach allows farmers to engage based on their comfort and interest.

6.3 Addressing our ecological question

After addressing farmer interests, the research team sought to understand our main research question to understand how the degree of agricultural diversification alters the diversity and composition of arthropod communities across sites with distinct distances to natural habitats. There is an increasing understanding that the diversification practices within agroecosystems, rather than just the presence of agriculture, play an instrumental role in local and landscape biodiversity patterns (Esquivel et al., 2021). Yet, diversification practices are heterogeneous — as demonstrated in the above-mentioned site-by-site variation in agricultural practices (Figure 4B). Therefore, we created an agricultural diversification index to assess how the culmination of practices (rather than a singular feature) impacts the diversity and composition of arthropods.

We expected a general positive effect of agricultural diversification on both introduced and native arthropods that would be magnified when sites were closer in distance to natural habitat. Yet, we only partially observed these trends. The observed richness of introduced and native arthropods increased with agricultural diversification (Figure 6A, C). Surprisingly, however, when sites were further from natural habitat, native arthropod richness decreased on more diversified sites (Figure 6C). A possible explanation could be that the native species are predated on or in competition with the high amount of introduced species in these systems. This high amount of introduced species is spread across a diversity of orders (SI Figure 1A) representing various trophic positions, of which orders such as Coleoptera and Araneae, which commonly hold predator trophic positions, are especially abundant.

We expected a combination of diversification practices, such as the number of different crops and non-crops, could create habitat/opportunities for native arthropods (Figure 6E). With the shorter distance between farm sites and natural habitat, there is potential for repeated colonization from the natural habitat to the farm (i.e., a spillover effect), especially on farm sites with high agricultural diversification. As a result, the combination of agricultural diversification and proximity habitat may reduce competition between native and introduced arthropods. Further, more simplified farm sites also had a greater richness of native arthropods than diversified sites at similar distances. One possible explanation is that the more diversified farm sites were dominated by introduced arthropods (Figure 6A; SI Figure 1A). This suggests agricultural diversification, especially on sites further from natural habitat, may present opportunities for new, introduced species to establish and, consequently, may increase competition with native arthropods. In contrast, more simplified farms may generally have less habitat for introduced arthropods, thus presenting a less competitive environment for native species.

Despite the reduction in native arthropod richness, the further diversified farm sites harbored a unique composition of introduced and native species (Figure 6B, D). The composition of the native species present was heavily represented by mobile arthropods that feed on plant material or detritus (in the orders Lepidoptera, Diptera, and Psocoptera; SI Figure 1B; Figure 6B). In addition, one particular group of arthropods in the families Crambidae and Chloropidae, known to feed on Polynesian crops, was highly abundant on the furthest site dominated by Polynesian crops (e,g. Mai‘a (banana; *Musa acuminata*) and kō (sugarcane; *Saccharum officinarum*) (Swezey, O.H., 1954).

Unsurprisingly, the forest sites had the highest native richness (Figure 6C, 4D). However, few species were exclusively found in these sites, as there was much taxonomic overlap with farm sites (Figure 6E). The subset of arthropod species only present on these forest sites belongs to orders with narrower ranges because they co-evolved with specific plant taxa such as Hemiptera (Roderick & Metz, 1997; SI Figure 1B; Figure 5B). The general lack of unique taxa is likely attributed to lower-elevation forest sites being inundated with introduced flora and fauna. Both forest sites had invasive flora that spread fast, including Yellow Ginger (*Hedychium flavescens*) and Mickey Mouse plant (*Ochna serrulata*). Taken together with the Polynesian crop results above, there is room for new management paradigms.

Preserving and restoring native flora in these lowland forests is often labor-intensive and expensive due to the invasive traits of many introduced flora, often leading to forest systems in remain degraded. To combat this trend, hybrid approaches of restoration utilizing Polynesian and non-invasive crops alongside native plants as tools have been proposed (Burnett et al., 2006; Ostertag et al., 2020; Winter et al., 2020), especially as a means to connect and prompt the access of ʻōiwi community members to their lands (Hutchins & Feldman, 2021; N. Lincoln et al., 2018). Still, many in the conservation field believe native arthropods cannot be found on agricultural sites. However, our findings support the potential of hybrid systems utilizing Polynesian and other crop species to support native arthropod biodiversity.

7. Conclusion

This paper described the tangible steps we took to operationalize Indigenous Data Sovereignty to use genomic data in the Kona Field System on Hawaiʻi Island. We recognize there is continued room for improvement and engagement at each step of our workflow. Future work should include more co-designing with community members from the outset. In terms of the ecological portion of this paper, since the study utilized limited pilot data, future sample collection should be more robust to adequately address ecological questions, such as measuring landscape heterogeneity and explicitly conducting a study to look at a farm management chronosequence.

Lastly, we offer suggestions to those questioning how to utilize an Indigenous Data Sovereignty framework in their work.

- **Take some time to reflect on your motivation to study a particular system or work with a community.** Will your work detract from others in the community already conducting similar work? Is there a way to empower or build a partnership alongside that work? Engage in critical conversations with the project team on intention before and during the project. Understand your positionality to the land and community you seek to work with matters.
- **Seek the resources to understand the history of the communities you seek to work with and how to appropriately engage (or not).** Native-land.ca is a tremendous web resource for determining the native lands on which your research takes place. In the case of the United States, Tribes often have a website with the appropriate contact information for a research board or Tribal council. In addition, several universities have a tribal liaison who works to bridge the university with local Indigenous communities. In terms of communities with no centralized governance structure, as was the case in this paper, there are often local non-profit and government organizations that can offer guidance, such as a natural resources department or community health organization.
- **Be open to having critical conversations and receiving feedback from community members and partners.** You may be unable to conduct the specific project components you intended. Again, your positionality matters.
- **Allocate an adequate amount of time to establish a connection with a community.** The timeline to achieve all components varies widely. It depends on the context of your positionality, the community you seek to engage with, and the nature of your research. The first step in establishing a connection with a community should be done respectfully and provided a sufficient amount of time. Establishing a meaningful

relationship with a community can take years in it itself. Beginning engagement means you are open to sustaining a long-term relationship.

8. Acknowledgments

We thank the farmers and community members that welcomed us onto their lands and shared space with us. We thank Isabel Lee-Park, Juliet Capriola, and Victoria Chen for their help in processing arthropod samples for DNA extraction. We would like to thank Kevin Chang, Natalie Kurashima, and members of the Local Contexts hub for insightful conversations that helped to shape our data sovereignty workflow. We thank Cynthia King (Department of Land and Natural Resources) and Leah Laramee (Natural Area Reserve System) for access to state forest lands. LH was supported by a Berkeley Food Institute seed grant and a National Science Foundation INFEWS fellowship.

9. Data Accessibility and Benefit-Sharing Section

9.1 Data Accessibility Statement

All sequencing data generated by the project have been/will be archived in the Native Biodata Consortium repository that will act as a safe-harbor of the data until local capacity can be built. To obtain access, please send your requests to gutherie@nbdc.org. Requests should include name, affiliation and funders of the research team, as well as a one-page outline of how the data will be utilized if access is granted and how this use will benefit the community and society at large. Appropriate metadata associated with the sequencing data is available through BOLD (Code: DS-HULI), noting that all culturally salient metadata has been redacted consistent with Darwin Core.

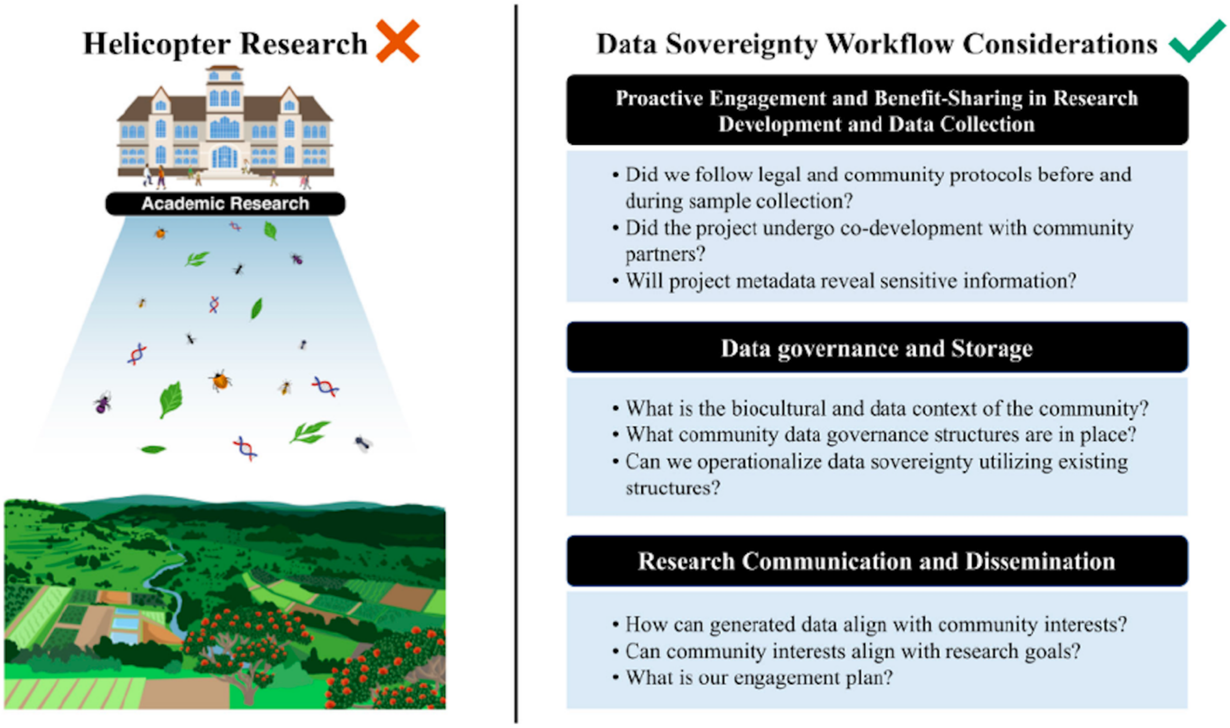
9.2 Benefit-Sharing Statement

This article has benefitted from the input of several Indigenous communities and is intended to support greater benefit-sharing consistent with the FAIR and CARE data principles. Use of the Local Contexts Notices ensures appropriate acknowledgement and recognition of the communities that have contributed to the project. The Biocultural Notice for this project (UPID: https://localcontextshub.org/researchers/projects/33) discloses cultural rights and responsibilities that need further attention for any future sharing and use of this material or data. This Notice recognizes the rights of Indigenous peoples to permission the use of information, collections, data and digital sequence information (DSI) generated from the biodiversity or genetic resources associated with traditional lands, waters, and territories.

10. Author contributions

LH and RG conceptualized the arthropod study. LH and AG collected the arthropod samples. LH and NG performed molecular processing of the samples. AG, NG, and LH conducted data analysis. AM and LH conceptualized the data sovereignty framework. LH and AM wrote the manuscript with input and comments from all co-authors.

11. Figures



Data Sovereignty Workflow Considerations ✓

Proactive Engagement and Benefit-Sharing in Research Development and Data Collection

- Did we follow legal and community protocols before and during sample collection?
- Did the project undergo co-development with community partners?
- Will project metadata reveal sensitive information?

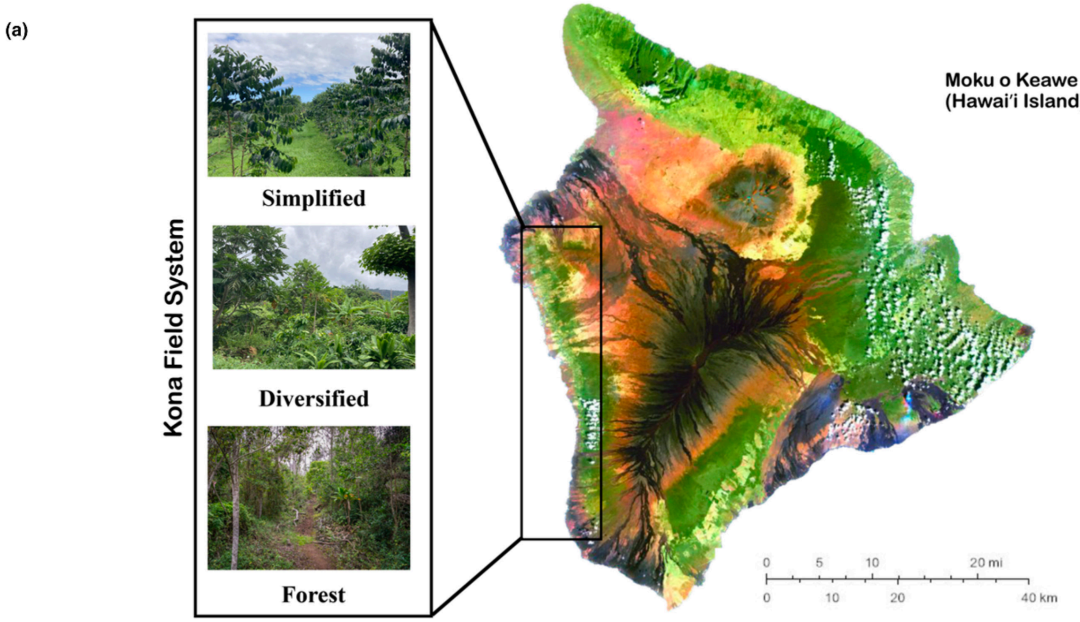
Data governance and Storage

- What is the biocultural and data context of the community?
- What community data governance structures are in place?
- Can we operationalize data sovereignty utilizing existing structures?

Research Communication and Dissemination

- How can generated data align with community interests?
- Can community interests align with research goals?
- What is our engagement plan?

Figure 1. Academic researchers commonly extract data from Indigenous lands and do little to engage in data benefit sharing and governance (helicopter science). We present data sovereignty workflow considerations to combat this that follows three main stages: collection, governance, and communication.



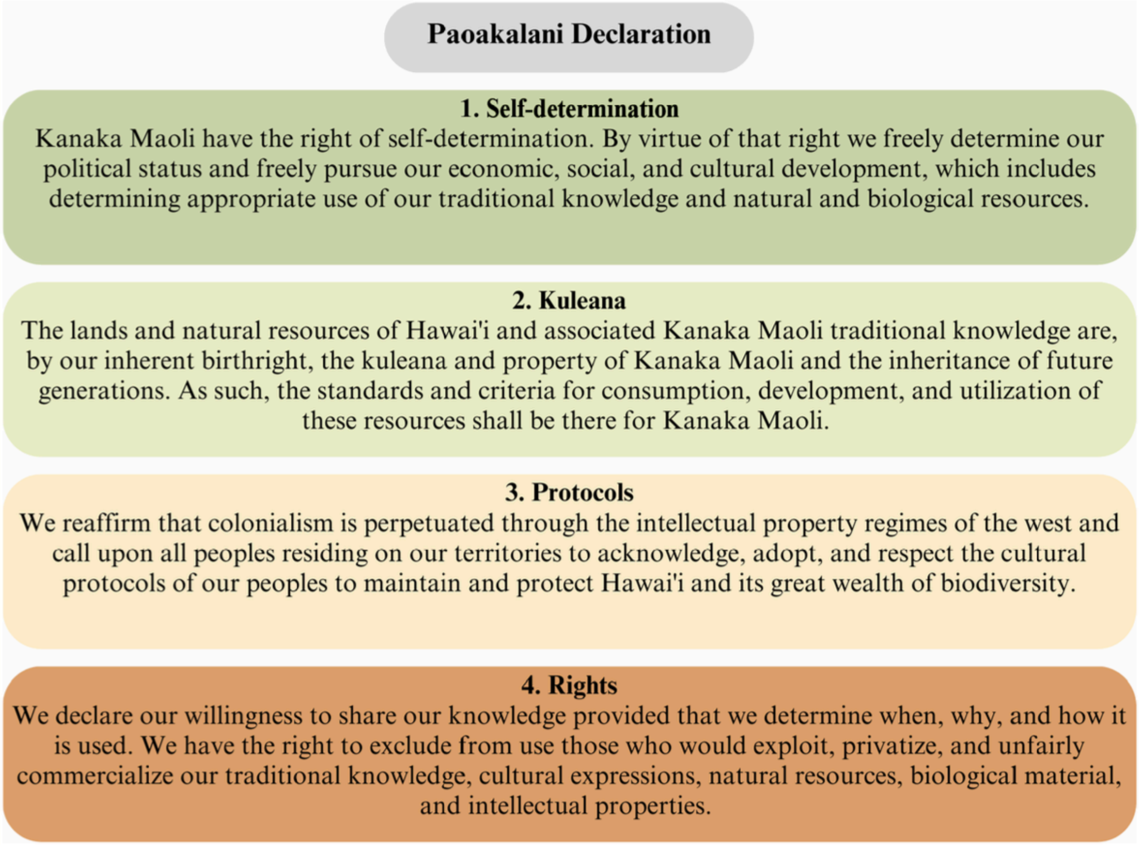
(b)

Hanau ka Huhu he makua
Born was the Wood border, a parent
Puka kana keiki he Huhulele, lele
Out came its child a flying thing, and flew
Hanau ka Pe'elua ka makua
Born was the Caterpillar, the parent

Hanau ka Naonao ka makua
Born was the Ant, the parent
Puka kana keiki he Pinao, lele
Out came its child a Dragonfly, and flew
Hanau ka Unia ka makua
Born was the Grub, the parent

Puka kana keiki he Uhini, lele
Out came its child the Grasshopper, and flew
Hanau ka Naio ka makua
Born was the Pinworm, the parent
Puka kana keiki he Nalo, lele
Out came its child a Fly, and flew

Figure 2. Arthropod samples were collected from forest sites as well as farms along a diversification gradient from simplified (monoculture) to diversified (agroforestry) on Hawaiʻi Island (A). Arthropods are culturally important to ʻōiwi, which can be exemplified by their inclusion in the Kumulipo, a creation chant (B).



Paoakalani Declaration

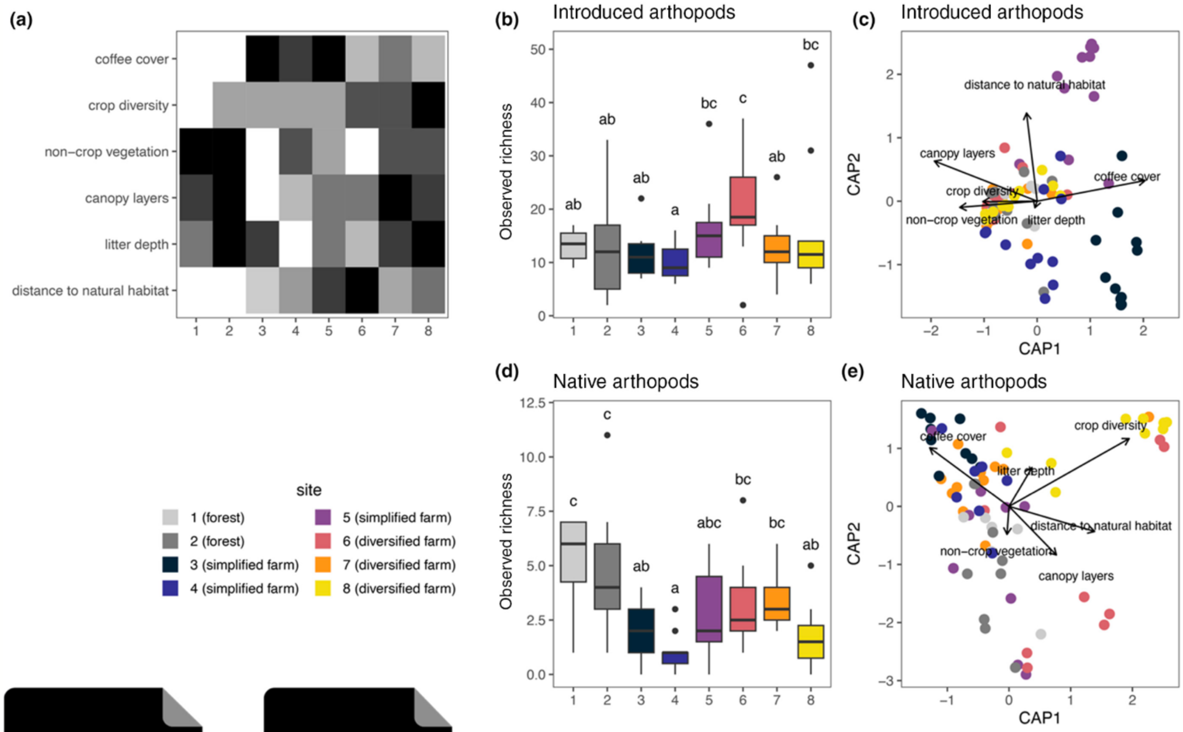
1. Self-determination
Kanaka Maoli have the right of self-determination. By virtue of that right we freely determine our political status and freely pursue our economic, social, and cultural development, which includes determining appropriate use of our traditional knowledge and natural and biological resources.

2. Kuleana
The lands and natural resources of Hawai'i and associated Kanaka Maoli traditional knowledge are, by our inherent birthright, the kuleana and property of Kanaka Maoli and the inheritance of future generations. As such, the standards and criteria for consumption, development, and utilization of these resources shall be there for Kanaka Maoli.

3. Protocols
We reaffirm that colonialism is perpetuated through the intellectual property regimes of the west and call upon all peoples residing on our territories to acknowledge, adopt, and respect the cultural protocols of our peoples to maintain and protect Hawai'i and its great wealth of biodiversity.

4. Rights
We declare our willingness to share our knowledge provided that we determine when, why, and how it is used. We have the right to exclude from use those who would exploit, privatize, and unfairly commercialize our traditional knowledge, cultural expressions, natural resources, biological material, and intellectual properties.

Figure 3. The Paoakalani Declaration was published by Kanaka Maoli (Indigenous Hawaiian; referred to as Kānaka ʻōiwi throughout the text of the paper) leaders to assert the governance their community has over their lands and resources. There are four main declarations put forth as part of a larger document



BC TK

Figure 4. To address farmer interests, we analyzed data at the site level. The heat map shows environmental and management attributes at each site (A). Darker colors represent higher values on a 0-1 scale. See Table 1 for description and scoring details. Boxplots show observed richness of introduced (B) and native (D) arthropods from each site. Significant differences (Tukey HSD) are indicated by different letters (a, b, c) above the boxplots. A distance-based Redundancy Analysis (dbRDA) of introduced (C) and native (E) arthropods is constrained by measured or scored environmental and management attributes. Biocultural (BC) and Traditional Knowledge (TK) notices created by Local Contexts are placed at the bottom of the figure to signify these samples were collected from Indigenous ʻōiwi lands.

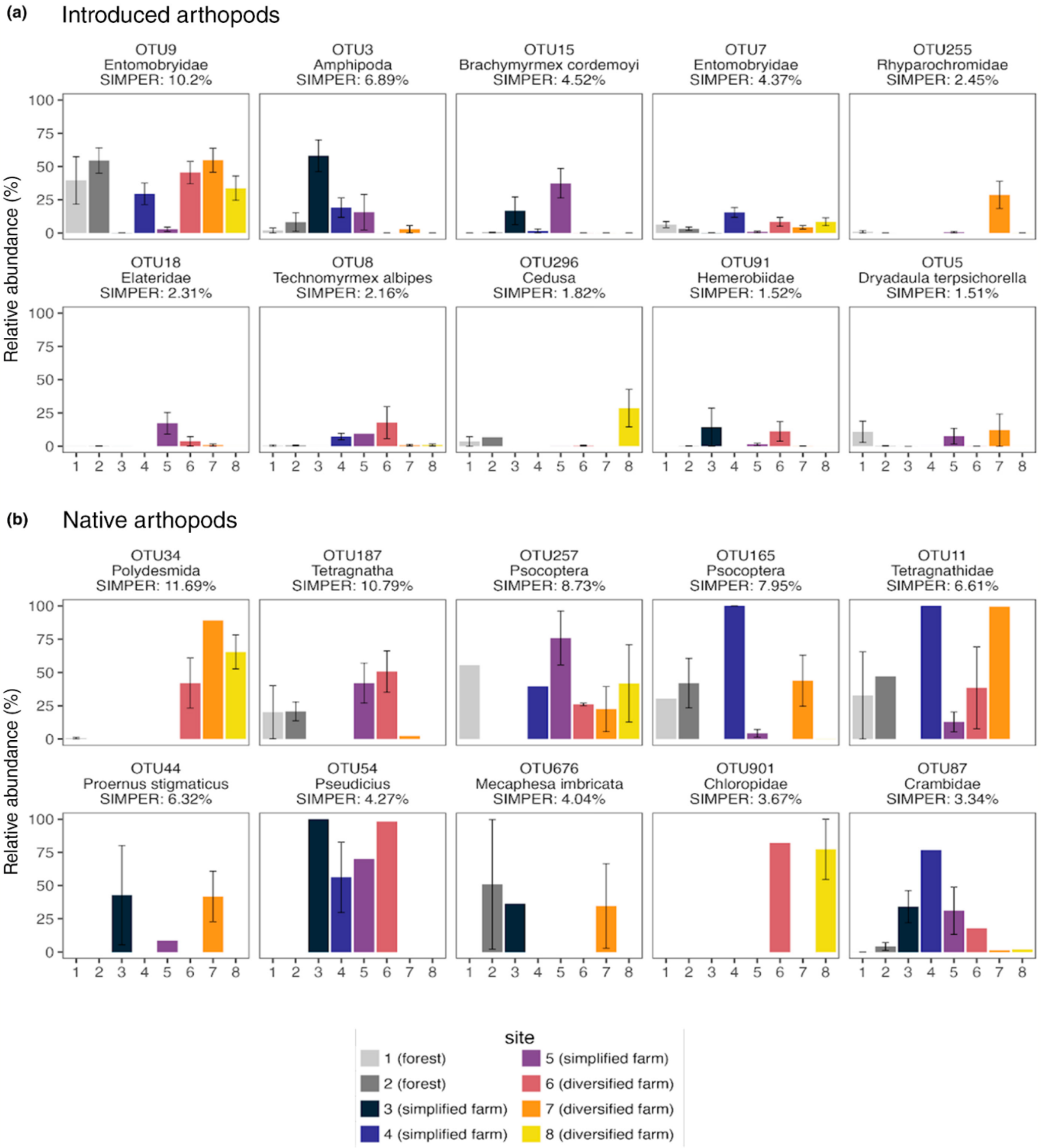


Figure 5. Ten OTUs that contributed the most to the community variations between sampled forest and farm sites according to a SIMPER analysis. The percentage of variation to which each OTU contributes is indicated. Error bars represent standard deviations

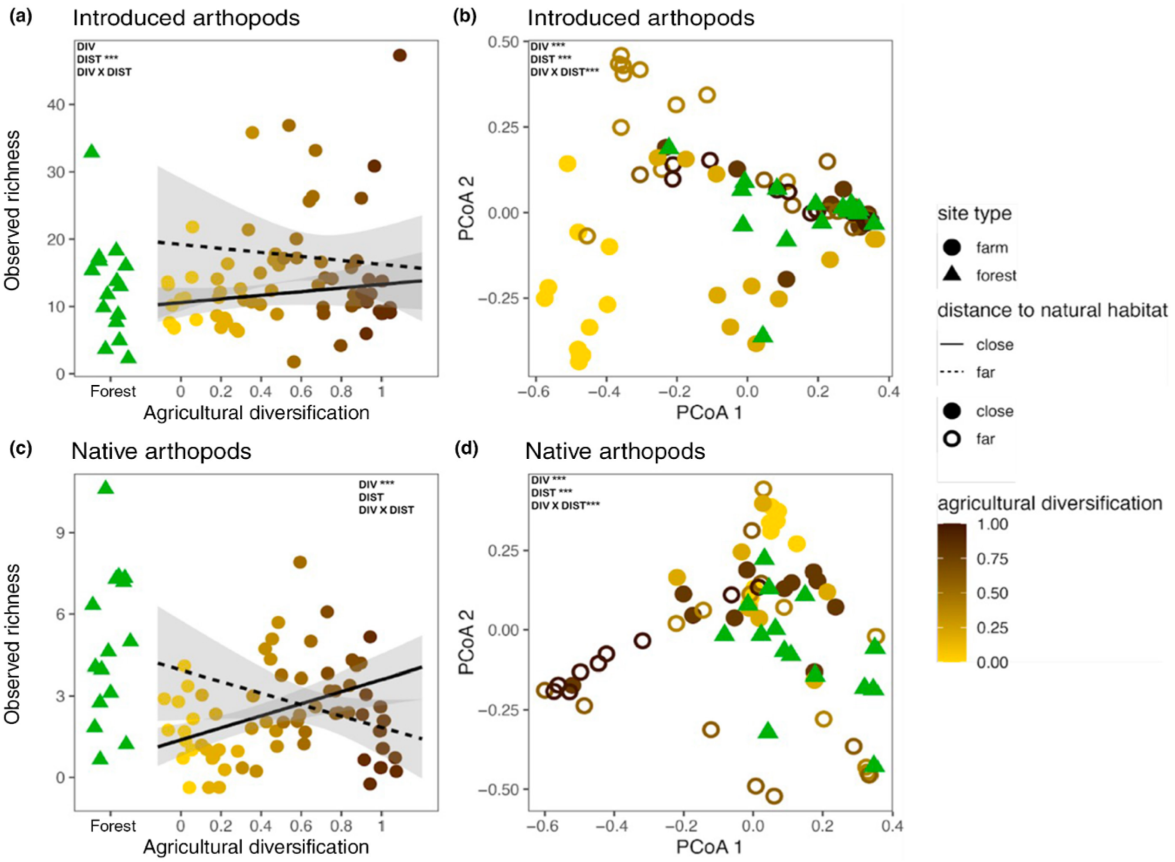


Figure 6. The estimated effect of agricultural diversification on introduced (A) and native (C) arthropod observed richness both close and far in distance from natural habitat. The Y-axis is derived from an agricultural diversification index based on measured and scored environmental and on-farm management factors. Forest sites have been seperated and are represented by the green arrow. PcoA plots (B, D) show samples in terms of the agricultural diversification scale, site, and distance to natural habitat (close and far). The symbols on the top of each panel indicate the following: DIV = Crop diversity, DIST = distance to natural habitat, and DIV X DIST = the interaction between diversity and distance. Statistical significance of the model: *** <0.001.

12. Tables

Table 1. Several environmental and management attributes were measured or scored at each site. These attributes were selected based on their known ability to shape arthropod communities.

Metric	Description
Coffee cover	The percentage of coffee cover at a site: no coffee (0), 25% cover (0.33), 75% cover (0.66), 100% cover (1).
Crop diversity	A score based on the number of different crops grown on a site: 0 crops (0), 1-2 crops (0.33), 3-8 crops (0.66), and 8+ crops (1).
Non-crop vegetation	A score based on the presence and taxonomic origin of non-crop vegetation: no non-crop vegetation (0), only non-native (0.33), both non-native and native (0.66), and only native (1).
Canopy layers	The sum of the presence (1) or absence (0) of different canopy layers on a site: herbaceous, shrub understory, lower canopy, upper canopy, and emergent
Litter depth	The average measurement of leaf litter depth at each sample collection point (inches).
Distance to natural habitat	The distance to the edge of the closest forest habitat measured on ArcGIS (meters). The range is distance for farm sites varied from 390 to 2188 meters.

Table 2. An example of the addition of metadata fields to reflect our Local Contexts Hub project-specific URL and the application of a Biocultural Notice (BC-Notice). Many metadata standards, including the iBOL manifest we utilized, do not have fields to recognize the rights of Indigenous peoples. We also redacted sensitive fields according to Darwin Core standards.

Sample ID	Order	Genus and Species	Location	rightsURL	rightsIdentifer
1	Diptera	InformationWitheld	InformationWithheld	**https://localcontextshub.org/researchers/projects/33**	**BC-Notice**

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CHAPTER 4

LANDSCAPE VERSUS LOCAL PROCESSES SHAPE ANTAGONISTIC NETWORK STRUCTURE AND ROBUSTNESS IN DISTINCT WAYS

Abstract

Biodiversity conservation must embrace the whole landscape, rather than just reserves, in the quest to maintain biodiversity in an era of increased species loss, climate change, and food injustice. Agricultural landscapes, particularly diversified ones, are especially promising habitat for biodiversity. While much focus on understanding biodiversity responses has looked at species composition only, we untangle the antagonistic interaction networks between spiders (predators) and their prey utilizing advances in DNA metabarcoding to analyze the gut content of spiders. These predator – prey interactions have ramifications throughout whole ecosystems and can dictate the long-term maintenance of biodiversity. We examine the response of established metrics that measure the structure and robustness of these networks to species loss at the local management and landscape level. At the landscape level, increased agricultural land cover increases generality, linkage density, connectance, interaction evenness and nestedness, which shapes networks to be filled with generalist and specialist taxa that interact heavily with one another, which increases the robustness of a network to species loss. At the local management level, we show an increase in plant diversity, average canopy cover, and average tree diameter, leads to a decrease increase in modularity and a decrease in generality and linkage density, which shapes networks filled with more specialist taxa that have compartmentalized interactions with few taxa, which can decrease the robustness of a network to species loss. These results highlight the complicated nature of maintaining specialized taxa needed to carry out essential interactions while maintaining a robust network overall. Therefore, conservation efforts need to be reconciled at both local and landscape levels to achieve biodiversity goals.

1. Introduction

The maintenance of biodiversity is dependent not only on nature reserves but whole landscapes (Perfecto and Vandermeer 2010). Agricultural landscapes can act as habitat for many species (Perfecto et al. 1996; Karp et al. 2013; Mendenhall et al. 2014; C. Kremen and Merenlender 2018). However, agriculture is not a monolith. Instead, there is wide variation in how farms are managed, and as such, their ability to have habitat quality depends on the extent and severity of their heterogeneity over space and time (Hutchins, Guzman, and Ponisio 2024). While numerous studies have analyzed how species richness and composition is shaped by the environmental conditions of different agricultural systems (see Hua, et al. 2024), the persistence and resilience of whole ecological communities to perturbations often requires an understanding of biotic interactions. In particular, antagonistic interactions, such as predator-prey interactions, can often act to stabilize networks (Allesina, et al. 2008), as predator-prey abundances are coupled together in a cycle that goes on to have ramifications for the state of a landscape and the organisms inhabiting that landscape (Abrams 2000).

Antagonistic interactions behave differently from mutualistic networks, such as plant-pollinator interactions, where most network research has been focused (Dunne, Williams, and Martinez 2002). The relationship between network structure and robustness has been extensively discussed (Thébault and Fontaine 2010), especially given the importance species interactions have in carrying out key ecosystem processes and services (Thébault and Fontaine 2010). Quantitative metrics have been established to characterize ecological network structures and their robustness to species loss. In essence, metric calculations are primarily based on the number of nodes (species), links (interactions), and their position (predator vs prey) (see Table 1 and *methods*). Certain metrics characterize the structure of a network, including interaction evenness, generality, vulnerability, and linkage density (Vieira and Almeida-Neto 2015; Olesen and Jordano 2002). Other metrics such as connectance, nestedness, and modularity elucidate robustness and the resistance of a community to change following species loss and species invasions (Olesen et al. 2007; Bascompte and Jordano 2014; Krause et al. 2003; Colwell, Dunn, and Harris 2012). Therefore, to understand the overall response of a network to a given management regime, we need a suite of network metrics along with applicable environmental variables.

Studies of organismal responses to agricultural modification have shown that patterns can differ at the landscape and local management levels (Tscharntke et al. 2005). When landscape composition, the relative proportion of different land cover types, increases in complexity and heterogeneity, species richness and abundance commonly increase (Marja, Tscharntke, and Batáry 2022). An increase in heterogeneity (i.e., crop diversity) and structural diversity (i.e., the number of canopy layers) at the local level also exhibits similar positive trends on richness and abundance. Therefore, even if a site is locally heterogenous, a homogenous surrounding landscape can lead to reduced richness and abundance beyond expectation. However, richness and abundance need not translate into resilience. This is particularly true in environments in which invasive pest and other non-native species tend to dominate foodwebs and can transform the environment. In such situations, the network structure can provide more useful information.

The current study is based in the Hawaiian Islands where modified systems tend to be invaded by non-natives (Johnson et al. 2005). Our particular focus was within a complex landscape matrix filled with coffee, agroforestry, and forests in the Kona area of the Big Island of Hawaii known as the Kona Field System (KFS; Figure 1). Previous work at this site has shown significant landscape level effects in determining whether diversified farm sites could retain native or non-native arthropod diversity (Hutchins et al. 2023), though specific taxonomic orders respond in different ways. Therefore, the current study sets out to look specifically at predator-prey (antagonistic) interactions in this system and their ability to capture the resilience of the ecosystem as a whole.

Our ability to construct whole community networks depends on a robust dataset. The emerging field of DNA metabarcoding allows us to taxonomically identify thousands of taxa rapidly (Kennedy et al. 2020; Krehenwinkel et al. 2019). In addition, the development of primers to selectively amplify the DNA of prey taxa within an abdomen (known as gut content analysis) of a predator can now unveil the diet of even the smallest predators, such as spiders that measure a few millimeters in the case of this study (Krehenwinkel et al. 2017). Besides the feeding interactions occurring between species, gut content analysis provides information on the range of prey on which predators are feeding, and hence can provide insights into interaction networks. Coupling such DNA metabarcoding approaches with network theory allows us to examine community patterns and signatures of resilience and change to disturbance on a whole new scale (Graham et al. 2023).

In this study, we draw on the fields of conservation biology, landscape ecology, network theory, and DNA metabarcoding, along with a spider gut content dataset comprised of 1685 spiders from 21 sites in the Kona Field System (KFS) (Figure 1), to address the following questions and hypotheses:

1) How does richness of both the spider predators and their prey (gut content) shift in relation to landscape composition and local management measurements?
   Diversity metrics provide information on change in the composition of arthropods at the local management and landscape levels. In addition, the diversity of predators and prey make up the architecture of the predator-prey bipartite networks we are examining.
      H1: Because the landscape in the KFS is dominated by simplified farms (Hutchins et al. 2023), and predator versus prey responses differ based on habitat utilization (Karp, Chaplin-Kramer, et al. 2018), we predict that as agriculture land cover increases, predator alpha and beta diversity will decrease while prey alpha diversity will increase. We predict the opposite to be true as vegetation land cover increases due to the heterogenous nature of vegetation in the landscape.
      H2: Local management factors such as plant diversity, canopy cover, and tree diamer that increase crop diversity and structure will increase alpha and beta diversity.

2) How representative is the gut content of a spider of the whole present arthropod community?

To test the ability of gut content to capture overall community composition, we compare the overall arthropod order composition represented in gut content to that of several common arthropod sampling methods, including beating, leaf litter, malaise traps, and pan traps.

H3: Since we sampled a wide variety of spider families, we predict there will be a shared number of taxa between gut content and each sampling method. However, since the spiders were collected from on top of vegetation, we predict there will be considerable overlap between gut content and beating. Moreover, because we observed an abundance of Lepidoptera larvae on plants, we predict there will be a considerable overlap between gut content and malaise traps, from which Lepidoptera are heavily captured.

3) What is the nature and extent of network structure and robustness change in relation to landscape composition and local management measurements?

To understand how network structure is affected by landscape composition, we estimate how networks change in relation to land cover composition classified as agriculture and vegetation measured by ArcGIS proportions up to 500 meters from each site (Figure 2 and 3) utilizing derived network metrics for structure and robustness (Table 1). We similarly estimate how networks change depending local management practices by using ecological measurements collected at each site including canopy cover, plant diversity, and average tree diameter (Figure 3 and Table 2).

H4: Because new species arrive to agricultural landscapes at higher rates (Püttker et al. 2011), and since generalists tend to dominate the species pool in modified and homogenous sites (Gardiner et al. 2014), we predict that increased agriculture land cover will increase network metrics of generality, connectance, interaction evenness, and linkage density metrics. For local management, we predict an increase in measurements to decrease all structural metrics.

H5: As local management measurements and vegetation land cover increase, networks will become more modular due to increased opportunity for specialization and the ability of these heterogeneous systems to host species with older co-evolutionary histories. Conversely, as local management measurements and vegetation land cover decrease, networks will become more nested with wider interaction niches. Previous studies of networks in agricultural systems have found similar modularity and nestedness trends (Morrison, Brosi, and Dirzo 2020; Tylianakis, Tscharntke, and Lewis 2007).

2. Methods

2.1 Study site

This study is based on the Leeward side of the island of Hawaiʻi (Big Island) in the Kona Field System (KFS) (Figure 1). The KFS was established by Kānaka ʻŌiwi (Indigenous Hawaiians) around 1400 AD. It was once primarily an agroforestry and forest belt (Lincoln and Ladefoged 2014). However, through colonization and the rise of coffee as a cash crop, it has transformed into a complex landscape matric comprised of farms of various diversification levels and forests (Hutchins et al. 2023). Hawaiʻi is a great model system for understanding resilience of biological communities in the face of perturbation as it experiences and grapples with struggles present globally: biodiversity decline, a need to increase local production, and a rising recognition of Indigenous knowledge systems and agriculture (Kurashima, Fortini, and Ticktin 2019; Vitousek 2002).

We selected 21 sites along the KFS and in Kaʻū. The 21 sites were comprised of 7 of each of simplified farms, diversified farms, and forests. Every simplified and diversified farm had coffee as a shared crop. Simplified sites had 1-3 crops while diversified sites had 8+ crops. Forest sites ranged from invaded secondary forest to primary forest. The matrix surrounding many of these sites is made up of rangeland, farms of varying diversification, housing and commerical development, and forest tracts. Average yearly rainfall amongst sampled sites ranged from 21 mm to 30 mm, with a mean of 23. The elevation profile amongst sampled sites ranged from 835 to 975, with a mean of 895. Sites were at least 500 meters a part.

2.2 Arthropod Sampling and processing

We utilized an established arthropod beat sampling protocol in which two 25 meter plots were established at each site. We collected arthropods using four different methods to capture the whole community: beating, leaf litter – berlese funnel, malaise traps, and pan traps (Figure 1). A plant survey was conducted to determine plant cover proportion. A total of 2 minutes for beating sampling was split based on plant cover proportion. Arthropods from all collection methods were stored at -20ºC in a falcon tube filled with ethanol.

We seperated all spiders from each beating sample and individually washed them following the protocol in Weber et al. 2024 (Figure 1). Washed spider speciemens were transfered to 96-well 2 ml block plates. For other sampling methods, the ethanol was poured off from falcon tubes (Figure 1). Specimens were washed two times with DI water and then submerged in 600 – 20,000 ul of lysis buffer based on volume. After incubation, 600 ul of lysate from each falcon tube was transfered to a block plate. Further steps of DNA extraction for spiders and other community samples was performed using the Tissue protocol described in the Qiagen Puregene kit modified for automation (Lim et al. 2022). DNA was eluted in 40 ml TE buffer.

2.3 Library preparation

For each spider sample, we used two different primer combinations to amplify prey versus predator DNA. First, to identify the spiders, along with all other sampling methods, we used a combination (*ArF1 - Fol-degen*-rev) that targets a 418 bp fragment in the barcode region of the Cytochrome Oxidase I (COI) gene (Lim et al., 2022). This combination has been tested to reliably amplify arthropod taxa in Hawaiʻi (De Kerdrel et al. 2020). To amplify the prey taxa within the abdomen of the spiders, we used a combination (*NoSpid_F1 - Laurelin_R1*) that targets a 70 bp fragment in the barcode region of the COI gene (Krehenwinkel et al. 2017). This combination has been specifically designed to minimize the amplification of the known COI barcode region all spiders share.

Each 96-well plate was amplified in triplicate with inline barcodes using the Qiagen Multiplex PCR kit according to the manufacturer's protocol (Qiagen), with 30 cycles and an annealing temperature of 46°C. A negative control containing no DNA template was prepared and sequenced regardless of a detectable PCR product on a gel. Amplicon libraries were prepared using a dual indexing strategy described in Lange et al., 2014, where a second round of PCR with six cycles is used to attach i5 i7 indexing primers. The three replicates per plate were pooled together. These pooled libraries were cleaned of residual primer using a 1x ratio of SPRI beads (Sera-Mag™). The four resulting library pools were visualized using fragment length analysis to ensure adapter ligation, quantified with qPCR (Applied Biosystems), and pooled together based on molarity. The samples were then sequenced on an Illumina® NovoSeq 6000 according to the manufacturer's protocol (Illumina, San Diego, USA) at The California Institute for Quantitative Biosciences at UC Berkeley. We aimed for a total of 68,000 reads per plate well.

2.4 Sequence analysis

We generated zero-radius operational taxonomic units (zOTUs) from raw reads with the unoise3 command (Edgar, 2016) following the recommended protocols in the usearch version 11 pipeline (Edgar, 2010). Specifically, the quality trimmed reads were dereplicated and clustered into zOTUs using the unoise3 command in usearch. Chimeras were removed de novo in usearch. zOTUs were then clustered into 97% OTUs using the clusters command in usearch. However, since amplicons for prey taxa were only 70 bp, we chose not to cluster them since it would lead to an over reduction of diversity. Curated zOTU and OTU tables were created using LULU (version 0.1.0) (Frøslev et al. 2017). OTU sequences were aligned and translated in Geneious Prime (version 2022.2.2; Biomatters Ltd.). OTU sequences containing stop codons in the correct reading frame were removed to reduce the influence of nuclear mitochondrial pseudogenes (numts) on downstream analyses. Numts have been shown to inflate diversity estimates in metabarcoding data (Graham, Gillespie, and Krehenwinkel 2021; Andújar et al. 2021). The resulting 97% OTUs and zOTUs were compared against the NCBI GenBank database and our custom-made DNA reference library for Hawaiian taxa using blastn with a maximum of 10 target sequences. All non-arthropod zOTUs and OTUs were removed from the dataset. Taxonomic assignment was considered trustworthy if the percent similarity of the metabarcoding sequence to the NCBI GenBank or DNA reference voucher was between 88-94% for family, at least 94% for genus, and equal to or greater than 97% percent similarity for species, while matches below 88% similarity were made only to order. To validate the taxonomic identification of each OTU at higher levels (e.g., order and family), a neighbor-joining tree was created in Clustal Omegas using default parameters. Raw reads were filtered based on an abundance distribution and then rarified using the command "rarefy" in the R package vegan (version 4.2.3).

2.5 Quantifying landscape metrics

Using USGS NAIP imagery compiled by Esri in 2021, the center points of each site were identified and a buffer of 500 meters around the center point was created. Landscape effects have been shown to be significant up to 500 meters. Next, sites were classified based on four categories: development, agriculture, vegetation, and open (Figure 2). Development includes parts of sites that have housing structures, roads, and construction areas. Vegetation refers to forested or vegetated areas not being managed/cultivated for agricultural purposes. Open is considered land that is not covered by agriculture, vegetation, or development (i.e., grass or dirt). The total area at each site 785,398 square meters ($\boxed{\pm}$ 0.2 square meters). To distinguish between agriculture and vegetation, which can be especially difficult in landscapes dominated by agroforestry, we classified agriculture based on the following considerations: 1) What is the arrangement of vegetation like? (i.e., are there distinct rows, pathways, etc.); 2) Because agricultural sites tend to be managed, is there some form of development nearby? 3) Does our designation align with past classifications of the area? 4) What specific property information can be gained from different Tax Map Keys (TMK)? 5) Ground truthing of portions of the site to gain final validation.

2.6 Local management and environmental measurements

To test hypothesis 2, we measured several local management and environmental factors at each site. We define local management as plant-based measurements such as diversity, canopy cover, and diameter. On the other hand, environmental factors include elevation, rainfall, and other related variables. At each plot, we measured plant diversity (i.e., the number of unique plants) and the origin identification of each plant as native, introduced, or Polynesian. Hired field technicians with extensive experience working with local conservation organizations identified the plants using their plant knowledge along with a key. Canopy cover was measured in 5 directions at 3 points using a densitometer. At each sampled plot we measured the diameter of each present tree using a calibrated tape measure. We obtained the elevation and measured the distance of each site to the closest forest reserve using ArcGIS Pro 3.3. Lastly, we used the Rainfall Atlas of Hawai‘i curated by the University of Hawai‘i at Mānoa (McLean et al. 2021) to obtain average rainfall, temperature, and evapotranspiration. We tested the correlation and importance of these variables in shaping diversity between sites by conducting a Distance Based Redundancy Analysis (dbRDA, please see Table 4 and statistical analyses below). Overly correlated variables (Spearsons R > 0.6) were removed and variables of significance identified by the dbRDA were explored.

2.7 Network and Statistical analyses

2.7.1 Richness

2.7.1.1. Alpha-diversity. We examined the effect of landscape and management on richness using generalized linear mixed models with the ‘lme4’ and ‘lmertest’ packages in R (version 4.2.3) (Bates et al., 2015; Kuznetsova et al., 2017; R Core Team, 2020). Arthropod richness was calculated as the number of unique OTUs per site. In addition, we calculated the Shannon Diversity Index for each site with the ‘vegan’ package (Oksanen et al., 2013) in R. All models for arthropod richness used Poisson error and included a random effect of site to account for multiple sampling units per site.

2.7.1.2 Beta-diversity. To determine the environmental and management attributes that significantly influenced community composition, we used a distance-based redundancy analysis (dbRDA; based on the Bray-Curtis dissimilarity metric on Hellinger transformed community matrices) using the ‘capscale’ function in the ‘vegan’ package in R (Oksanen et al., 2013). The dbRDA tests how much variation within a community (i.e., arthropod community composition) is explained by a group of explanatory variables (i.e., environmental and management variables) (Legendre & Anderson, 1999). The number of variables in the dbRDA model was minimized via automatic stepwise model selection using the function ‘ordistep’ in R, and collinear variables were removed based on variance inflation factors calculated using the function ‘vif.cca’. Then a permutation-based ANOVA, using 999 permutations, was performed on the dbRDA model to determine the significance of the coefficients.

2.7.2 Bipartite networks, network metrics, and significance and correlation

We joined our predator (spider) OTU table with our prey (gut content) OTU table by shared sample number and block plate well number. In doing so, each unique predator OTU and relative abundance was matched with the unique prey zOTUs and relative abundance amplified in its gut. We used the resulting dataset to construct bipartite networks using the function "plotweb" command in the 'Bipartite' package (Dormann et al., 2014) (Figure 2). To plot the networks, we first created 35 matrices, one for each site, with predators as columns and prey as rows. We measured the strength of interaction based on the relative prey read abundance associated with a predator. Further insights into matrix curation can be found in Graham et al. 2023.

Network metrics can be qualitative (binary) or quantitative (Beckett 2016). Qualitative metrics treat interactions equally no matter their magnitude or frequency making them sensitive to variation in sampling effort. In contrast, quantitative metrics account for the flow of biomass between species by considering the prey read abundance associated with each predator, and are less sensitive to sampling effort. We used the "networklevel" command in 'Bipartite' to calculate seven quantitative metrics, including connectance, linkage density, generality, interaction evenness, modularity, nestedness, and vulnerability (Table 1). Lastly, we calculated the ratio of resource species to consumers for the qualitative matrices, which is the ratio of prey genera to predator OTUs.

We generated 1,000 synthetic networks and used null models to test the statistical significance of our empirical weighted network metric values (Vasquez & Aizen, 2006). The null model assumes the identities of any two species involved in a forbidden interaction are unimportant. Therefore, the model only conserves the interaction weights between predator – prey and not their identities. To test how likely the null model is derived from our empirical networks and metrics, we compared synthetic and empirical networks and matrices through p-values and z-scores.

To compare the effect of landscape composition and local management measurements on network size, diversity and network metrics, we regressed the dependent variables against agriculture and vegetation (landscape composition), as well as canopy cover, plant richness, and average tree diameter (local management) for each collection site (Figure 3 and Table 2). We tested the significance of the correlation between network size and landscape composition and management measurements, each network metric and landscape composition and management measurements, and each network metric and network size, using Spearman's correlation tests.

3. Results

3.1 Summary

Our sequence run yielded 386 spider libraries and 288 prey libraries. After running these libraries through sequence analysis and cleaning, our dataset contained 187 unique predator OTUs spanning 14 families, while prey had 801 unique OTUs spanning 104 families.

3.2 Richness and network architecture

3.2.1. Hypothesis 1: Landscape composition x alpha diversity

Prey zOTU richness (measured as the number of unique OTUs per site) decreased and abundance increased with increasing agriculture land cover (Figure 4). The opposite is true for predator OTU richness, with richness and abundance decreasing with increasing agriculture land cover (Figure 3, see supplement 1 for bar plot predator families). As vegetation land cover increased, both predator richness and abundance increased, while only prey richness increased. The Shannon Diversity Index (Table 3) results mirror the results above with stronger trends ($p<0.001$). For network architecture, the number of links and nodes decreased with increased vegetation land cover and increased with agriculture land cover, though these trends are not statistically significant (Table 3). These links and nodes makeup the architecture of networks and correspond to the metrics that dictate structure and robustness (Figure 2).

3.2.2. Hypothesis 2: Local Management measurements x alpha and beta diversity

In terms of beta diversity, a Distance based Redundancy Analysis on predator OTUs showed that local management factors such as canopy cover average ($p < 0.001$), average tree diameter ($p = 0.003$), and plant richness ($p = 0.011$) especially drove community dissimilarity (Table 4). For alpha diversity, predator OTU richness and abundance decreased with canopy cover average and increased with plant richness and average tree diameter. Following similar trends to predator OTUs, prey zOTU richness decreased with canopy cover average.

In addition, prey zOTU richness and abundance increased with plant richness and average tree diameter. A Shannon Diversity Index again mirrored the results above with strong trends (Table 3). For network architecture, links and nodes decreased with average canopy ($p = 0.0431$ and $p = 0.00069$) (Table 3).

3.3 Hypothesis 3: Gut content overlap with other sampling methods

Gut content contained far more unique families (42) and orders (4) than other sampling methods (Figure 5). It shared the most families with beating out of other sampling methods. Gut content shares Lepidoptera relative abundance on par with leaf litter and malaise sampling methods. However, there is a noticeable lack of Hemiptera, Orthoptera, and Malacostraca (Figure 7). Lastly, there is an overrepresentation of Neuroptera in gut content.

3.4 Network metrics

3.4.1 Hypothesis 4: Landscape composition x network metrics

In terms of agriculture land cover, we observed a moderate positive effect of structural network metrics increasing as agriculture land cover increased (Figure 5). However, for robustness metrics, nestedness increased with agriculture while modularity decreased. A Spearman's correlation test found the relationship between agriculture land cover and linkage density, vulnerability, and nestedness to be statistically significant (Table 5). Conversely, for vegetation, we observed a negative effect of structural and robustness network metrics decreasing as vegetation land cover increased (Figure 5). A Spearman's correlation test found the relationship between vegetation and linkage density, generality, interaction evenness, and nestedness to be statistically significant (Table 5).

3.4.2 Hypothesis 5: Local Management measurements x network metrics

Canopy cover had a mixed effect on structure and robustness metrics. Linkage density, generality, interaction evenness, and modularity decreased as canopy cover, increased while connectance, vulnerability, and nestedness increased (Table 6). All metrics decreased with an increase in plant richness. For average tree diameter, we observed an increase in vulnerability and a decrease in generality, modularity, and nestedness. A Spearman's correlation test found relationship between nestedness and average tree diameter and number of plants to be statistically significant, while weighted connectance and modularity had a significant relationship with average canopy cover (Table 6).

3.5 Null models and zscores

To test how likely the null model is derived from our empirical networks and metrics, we compared synthetic and empirical networks and matrices through p-values and z-scores. We rejected the null hypothesis for 19 out of 21 sites (Table 7). For the remaining sites, there were some metric values not significantly ($p < .05$) different from values produced from synthetic matrices (Table 6). We calculated zscores by subtracting the mean of synthetic values from our empirical values and dividing the product by the standard deviation of synthetic values. The plotted zscores generated similar trends observed by our empirical values for each landscape and management variable, with a few points of variation (Figure 7).

4, Discussion

Our analysis of taxa richness and antagonistic networks yielded interesting trends. Predator and prey richness and abundance responded in similar ways to landscape composition. Both decreased with agriculture land cover and increased with vegetation land cover. At the landscape level, we observed opposite trends for agriculture land cover and vegetation land cover, with network metrics of generality, linkage density, connectance, vulnerability, interaction evenness and nestedness showing an increase with agriculture land cover and decrease with vegetation land cover. This opposite trend suggested that agriculture land cover is shaping generalist networks that might be more robust to species loss, while vegetation land cover is shaping specialist networks less robust to species loss. Our local management results aligned with vegetation land cover showing that increasing heterogeneity decreases network metrics and makes them modular. We further contextualize these results below.

1) How do predator and prey taxa richness shift in relation to landscape composition and local management measurements?

4.1 Hypothesis 1 & 2: Richness and abundance patterns, prey identity, and non-crop habitat

In hypothesis 1, we expected opposite trends for predator and prey richness and abundance patterns with agriculture land cover and vegetation land cover. However, our results were mixed. Predator richness and abundance decreased with an increase in agriculture land cover and increased as vegetation land cover increased. Conversely, while abundance increased with agriculture land cover, richness decreased. Moreover, like predators, vegetation land cover had a positive effect on prey richness as well.

Our predator trends are in line with empirical and meta-analyses studies that have been done with predator dynamics in agroecosystems (Bianchi, Booij, and Tscharntke 2006; Rusch et al. 2016). Predators prefer non-crop habitat for supplemental food resources, nesting, preferable environmental conditions (e.g., more shaded cooler areas), and to avoid harsh disturbance events (e.g. harvest or pesticide application). For example, studies of spiders from different guilds benefit from particularly woody non-crop habitat (Michalko and Birkhofer 2021). Ecologists tend to leave prey (or "pests" as they are commonly framed by farming practitioners) out of the non-crop conversation and focus on the conservation win-win that is increasing predator diversity while reducing prey populations that may feed on crops and impact farmers. However, in our study, prey patterns with vegetation benefitted from non-crop habitat as well, echoing results of Chaplin-Kramer et al. 2011). In addition, our local management results enumerated that plant richness and average tree diameter had a positive effect on both predator and prey richness and abundance, thus confirming hypothesis 2. These mixed results are similar to the findings of Karp et al. (2018) where landscape context is deemed as important and produces inconsistent results between agroecosystems globally.

Considering prey in the context of the whole community and the balance between native and non-native taxa, as Joern (2005) and Hutchins et al. (2023) found, native arthropods and beneficial arthropods can be present within and benefit from agricultural landscapes. In this study, we did find arthropod orders in the gut content of the predators that are known to primarily have native families present in Hawaiʻi (Figure 7). This highlights the importance of diving deeper into understanding the composition of a prey community and not just applying broad classifications to anything present, though we do not want to discount the impact that pests (mostly non-native prey) can have on farmer livelihoods.

We can partially accept hypothesis 2. All local management variables including plant diversity, canopy cover, and tree diameter had a significant effect on predator richness. Richness decreased with canopy cover but increased with average tree diameter and plant richness. Abundance decreased with average canopy cover and increased for average tree diameter and plant richness. These trends were mirrored for prey though results were not significant. As we have just highlighted, there are positive effects to increasing local plant diversity and structure (agroforestry). In most studies, "non-crop" habitat is non-food or material producing plants incorporated onto or within the margins of a farm either intentionally or non-intentionally. In some studies, an assemblage of non-crop habitat is referred to as an island in a sea of disturbance. This seemingly mirrors debates in the biodiversity conservation field on land sparing and land sharing: Whether biodiversity can be better conserved by increasing agricultural production in certain areas and leaving space for biodiversity to persist in reserves (i.e., land sparing) versus shifting management practices in working landscapes so that landscapes become multifunctional and preserve biodiversity in all habitats (Kremen and Merenlender 2018).

2) How representative is a spider gut content of the whole present arthropod community?

4.2 Gut content as a rapid way to get the pulse of a system

Because spiders are generalist predators, we expected considerable overlap between the arthropod orders found in gut content and beating and malaise samples (hypothesis 3). However, the overlap between gut content and different sampling methods was not conclusive. Order composition did not have much overlap with one specific method, but instead included most orders from all methods, with a few key missing and additional orders. This highlights that gut content can be a good beginning indication of the composition of a community. However, since several orders are missing from gut content, especially Diptera, and because the length of no-spider sequences is too short to do in depth composition metric, traditional whole community sampling is still the best way to gain a comprehensive understanding of community dynamics within a system.

3) What is the severity of network structure and robustness change in relation to landscape composition and management measurements?

4.3 Landscape composition and species feeding preferences

We expected the predator-prey bipartite network structure to become more nested with increased agriculture land cover and more modular with increased vegetation land cover (Hypothesis 5). We partially observed these trends (Figure 5; Table 5). Our robustness metric results align with other network analyses done in agricultural systems (Morrison, Brosi, and Dirzo 2020; Grass et al. 2018). Nestedness increased with agriculture land cover and decreased with vegetation land cover. However, unlike other studies (Morrison, Brosi, and Dirzo 2020; Tylianakis, Tscharntke, and Lewis 2007; Olesen et al. 2007), we found no significant negative relationship between modularity and agriculture land cover but did see it increase with vegetation land cover. Environmental fluctuations, such as what occurs in agroecosystems, can promote nestedness (Karp, Frishkoff, et al. 2018). High nestedness has been attributed to increased connectance and species abundance because empirical networks have found that super generalized species with flexibility in their diet can become the core of a nested network (Baselga 2010). Our network structure results showed a significant effect of agriculture land cover on increased linkage density and vulnerability, thus highlighting that these networks are indeed connected and filled with generalist species, thus confirming hypothesis 4 for these aforementioned metrics.

Whether a species has broad (generalist) or narrow (specialist) feeding preferences impacts their ability to withstand changing environmental conditions. For example, in a highly nested system, if multiple predators are feeding on one pest species, even if one predator is lost, the other predators will continue to carry out that interaction (Baselga 2010; Hui 2021). This can be particularly important in maintaining a balanced prey population that do not become pests. All of this is highlighting that agricultural landscapes are adaptive to new species entering a network and can conserve specialized ones. However, the persistence of the new species within the network will depend on how much resource redundancy is occurring and if the generalist species at the core of the network start to dominate. It is important to also consider the type of species benefiting from a highly connected and nested system. For example, native species have been found to be impacted by interactions with introduced species in networks with high connectance and nestnedness (Hui 2021). Moreover, the specialized species that are able to persist in these networks may not carry out essential feeding interactions that may benefit ecosystem processing, instead they could feed on critical taxa for ecosystem functioning or endangered taxa.

4.4 The relationship between agroforestry management practices, vegetation land cover, and networks

Though we have been discussing agricultural landscape composition broadly, these landscapes are heterogenous, and unlike other studies, we looked at the relationship between network metrics and specific management practices. We expected an increase in local management measurements to make the networks more modular (hypothesis 5). The presence of trees within a site had an effect on network structure and robustness. Forests are not the only systems that contain large trees equating to high tree diameter and canopy cover measurements. Many of the diversified farm sites we sampled from were agroforests with large fruiting trees such as avocado, ʻulu (breadfruit), and mango. Tree diameter had a negative effect on nestedness while canopy cover had a positive effect on connectance and a negative effect on modularity. Moreover, canopy cover was the only variable to have a significant (negative) relationship with the number of links and nodes in a network.

Diversified farm sites have higher plant richness than simplified ones. Plant richness had a negative effect on nestedness. Many of these results mirror that of our landscape composition results with vegetation land cover, thus confirming hypothesis 5. Landscape composition with increased vegetation has opposite trends when compared to agriculture. In particular, vegetation land cover had a significant negative effect on nestedness, linkage density, generality, and evenness (hypothesis 4). Therefore, in contrast to agriculture land cover, networks based on landscapes with more vegetation and in more diversified farm sites have less generalists and more compartmentalized interactions (i.e., more weighted interactions between just two species). In trophic networks, compartmentalized networks tend to increase robustness to environmental distance by offsetting the spread of network disturbance by having one compartment impacted at a time (Thébault & Fontaine 2010). These networks have been found to support native species (Olesen et al. 2007), though they are not robust to species loss and invasion.

4.4 Caveats of Network Metrics

When looking at landscape composition, we have shown that agriculture land cover and vegetation land cover have very different structured networks with consequences on robustness to species loss. In addition, network metric trends for local management practices align with vegetation land cover. However, even with a bevy of metrics and a growing body of research on networks, there are still differing interpretations of metrics and what constitutes a "good" network? Some studies, including this one, have classified a good network as one that is more robust (Morrison, Brosi, and Dirzo 2020), while others state it is one that can support more native species (Giannini et al. 2015) or can carry out essential ecosystem services (Tylianakis, Tscharntke, and Lewis 2007). In the case of this study, we found agriculture land cover to increase generality and nestedness, which can indicate a robust network. However, it could be a network producing little ecosystem services that contains introduced species and is in a positive reinforcement loop that is hard to disrupt. On the other hand, vegetation land cover and local management measurements are supporting more compartmentalized networks that can support native species but can be vulnerable to invasion and disruption. More empirical robust studies of networks with a close examination at specific interactions if needed to further elucidate insights into the benefits of certain networks over others.

5. Conclusion

Biodiversity maintenance in the Anthropocene and under climate change must rely on whole landscapes to be achieved. Community composition is one way to understand biodiversity patterns and maintenance. However, to grasp long-term persistence, an understanding of network structure and robustness is needed. Here, we presented findings that alpha and beta diversity as well as network metrics that measure structure and robustness respond in drastically different ways between agriculture landscape composition or vegetation landscape composition and local management level. Agriculture land cover shaped networks filled with generalists that are nested. Vegetation land cover and local management that increased plant diversity and structure shaped modular networks filled with higher predator and prey diversity comprised of specialist species with co-evolved histories. In essence, vegetation land cover is supporting greater arthropod diversity and specialists but is less robust than networks set in agriculturally dominated landscapes. How farmers and resource managers manage their individual sites matters locally while contributing to the greater effects of the landscape. Moreover, it takes a community and cooperation amongst neighbors to increase heterogeneity at the landscape level to maximize benefits for biodiversity.

6. Figures

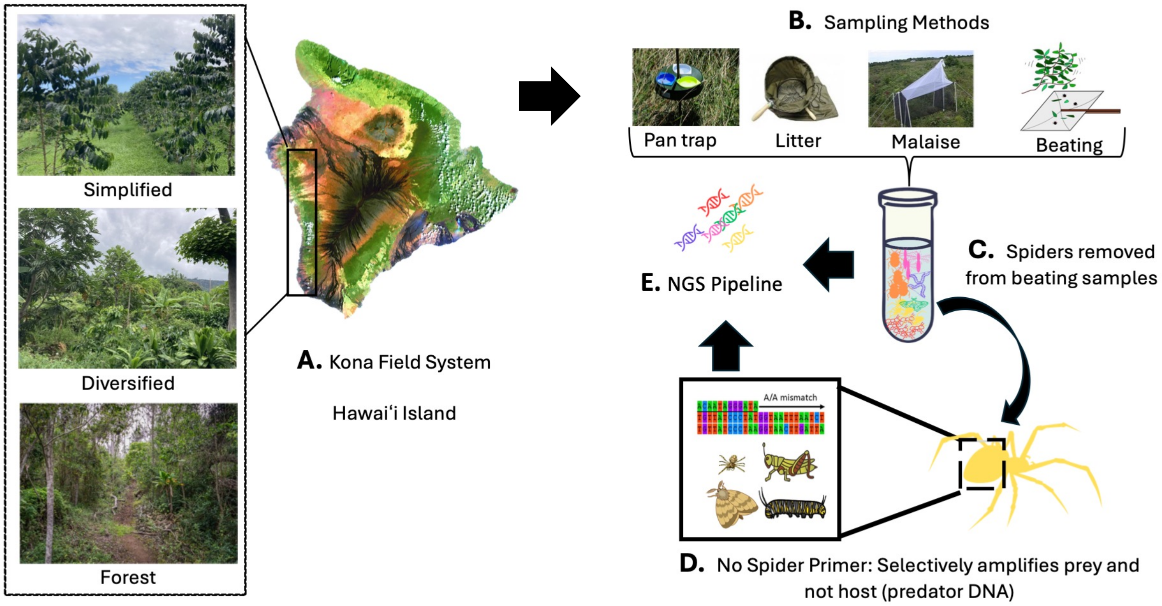


Figure 1. Methods used in this study to sample arthropods and sequence their DNA in the Leeward side of Hawaiʻi island within the Kona Field System. Arthropods were collected from forest sites as well as simplified and diversified farm sites (A). We utilized four types of

sampling methods to capture whole communities of arthropods. These included pan traps (white, blue and yellow), leaf litter – Berlese funnels, malaise traps, and vegetation beating (B). In the lab, spiders were removed and processed from beating samples (C) and the prey within their abdomens were selectively amplified during the Polymerase Chain Reaction process utilizing a developed no-spider primer (D). Lastly, the spiders, prey, and all other community samples went through metabarcoding library preparation and a Next Generation Sequencing pipeline (E).

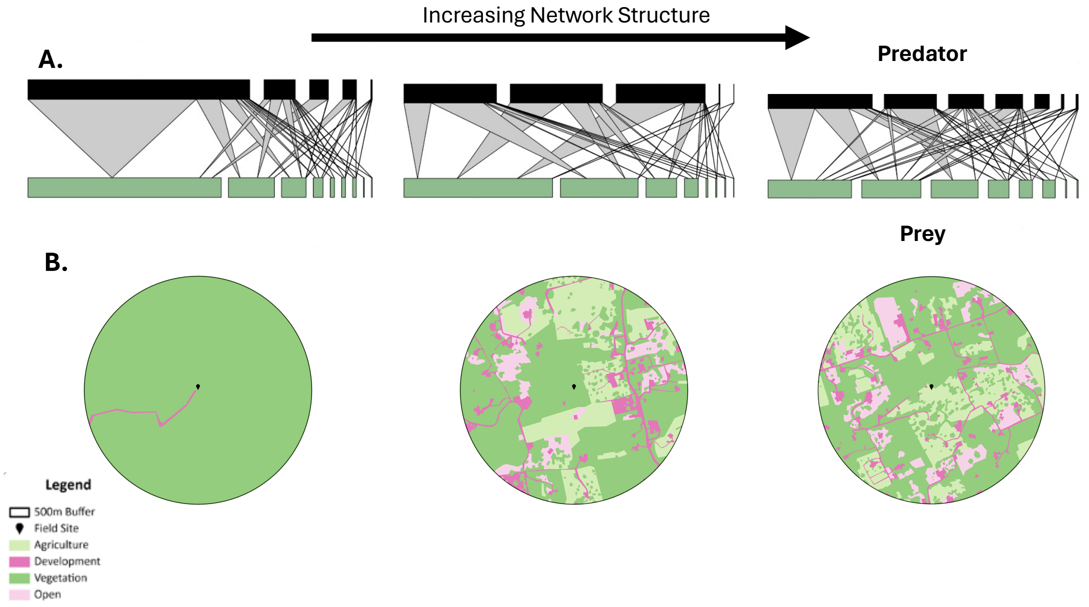


Figure 2. More complex landscapes lead to more complex ecological networks. Quantitative bipartite networks were created for each site to visualize the feeding interactions between predators (spiders) and their prey (arthropods found within the gut of the predators and amplified through a Polymerase Chain Reaction). Here we present three networks that illustrate the range of our sites (A). Each black bar represents a unique predator family (top) and each green bar represents a unique prey family (bottom). The thickness of the gray links between them

represents the read abundance of the prey found within the gut of each predator. Each bipartite plot is paired with a landscape composition plot (B) that denotes the site that network was sampled from (black dot) and the classification of the area within 500 meters into four categories: agriculture, development, vegetation, and open (see methods for additional details). We used these landscape composition calculations in our richness and network metric analyses.

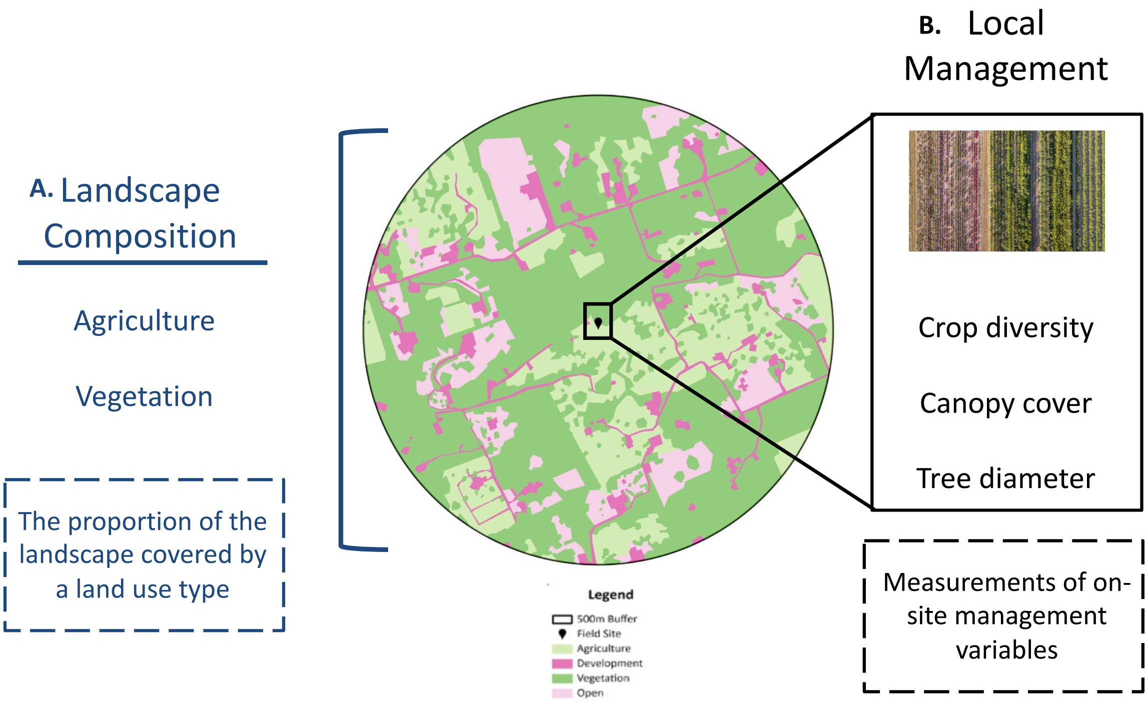


Figure 3. We analyzed diversity and network metric trends at the landscape level (A) and local management level (B). At the landscape level, we utilized measurements of landscape cover as either agriculture or vegetation (see x). At the local management level, we utilized measurements of crop diversity, canopy cover, and tree diameter taken from sampled plots at each sampling site.

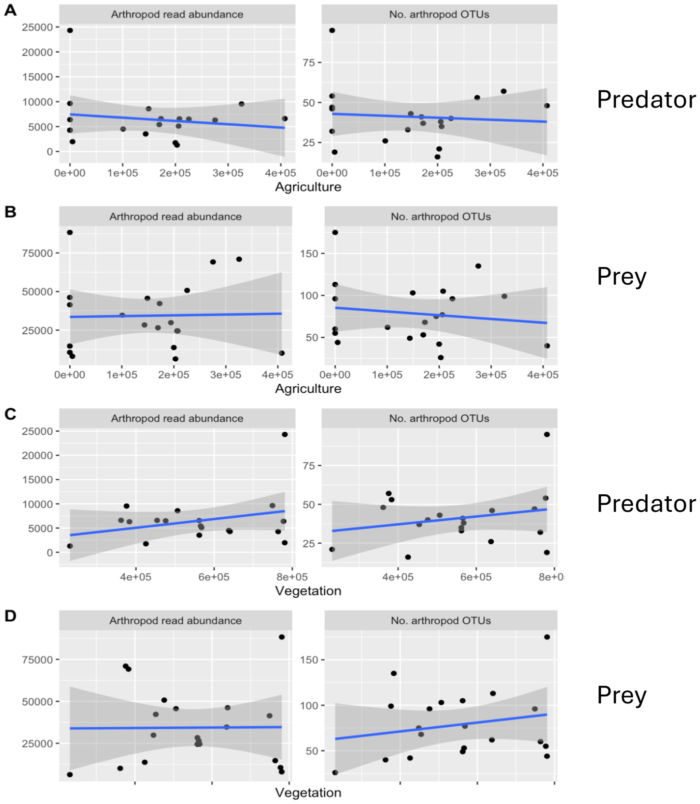
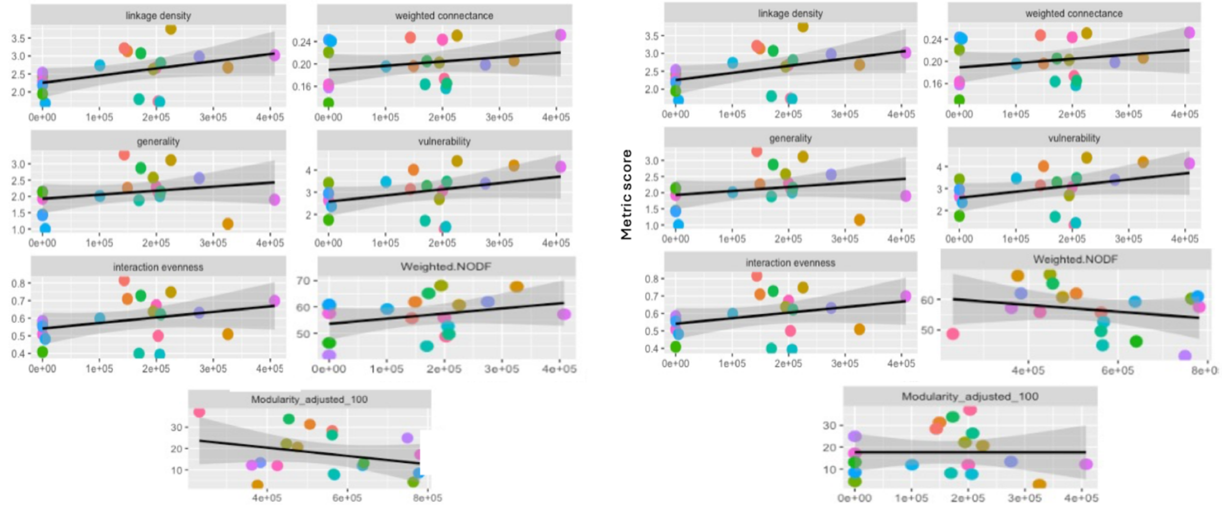


Figure 4. Effect of landscape composition on predator and prey richness and read abundance. For richness, each point represents the number of distinct OTUs for either predator or prey at each site. In terms of read abundance, each point represents the sum of reads at each site. On the Y-axis, is the proportion of land cover in agricultural production (agriculture) or covered in vegetation as measured by ArcGIS using NAIP imagery up to 500 meters from each sampled site. Linear model regression results are given in Table 2. Note: our plots are presented in the standard for the network field. However, Table 2 provides the Shannon Richness Index, a more appropriate measure in the field of ecology when doing linear regression.



A. Agriculture **B.** Vegetation

Figure 6. Effect of landscape composition on quantitative ecological network metrics. Each point represents a site from each of 21 sampled sites (each colored uniquely). Each network was weighted with the read abundance of the arthropod OTUs associated with the predator (spider) it was collected from at each site. We measured four landscape composition metrics: agriculture, vegetation, development, and open. Here we present agriculture (A) and vegetation (B) land cover size in hectares on the x-axis. For agriculture, three metrics were statically significant: linkage density, vulnerability, nestedness. For vegetation, four metrics were statically significant: linkage density, generality, interaction evenness and nestedness. Spearman's correlation test values are given in Table 4. Results of the null model analysis for quantitative network metrics are presented in table 6.

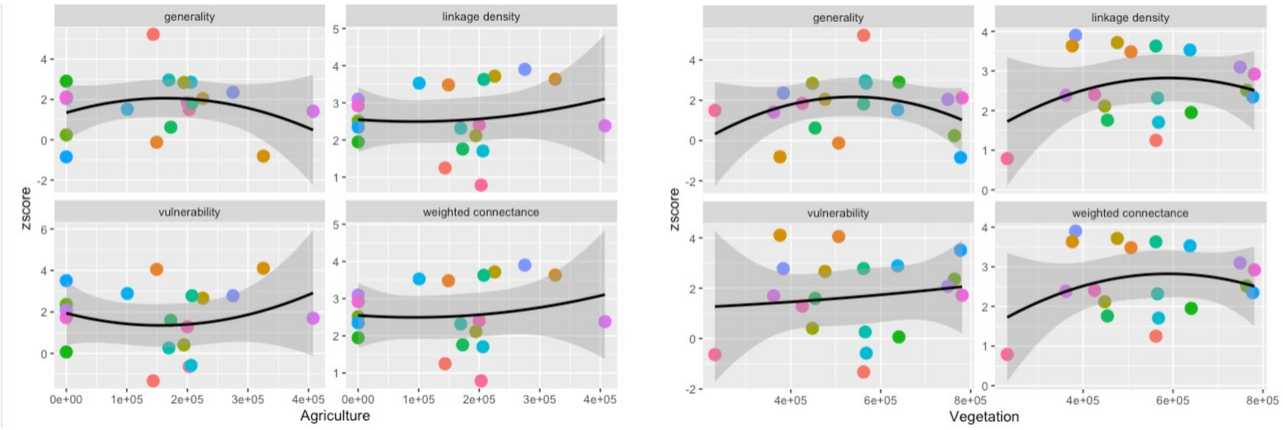


Figure 7. *Z*-scores from null model analysis of weighted metrics are plotted by landscape composition. Each point represents a network from each of 21 sampled sites (each colored uniquely).There are no null values or z-score for interaction evenness because the null model we used was not appropriate given that interaction evenness is based on the empirical distribution of weights, regardless of which species those weights are between.

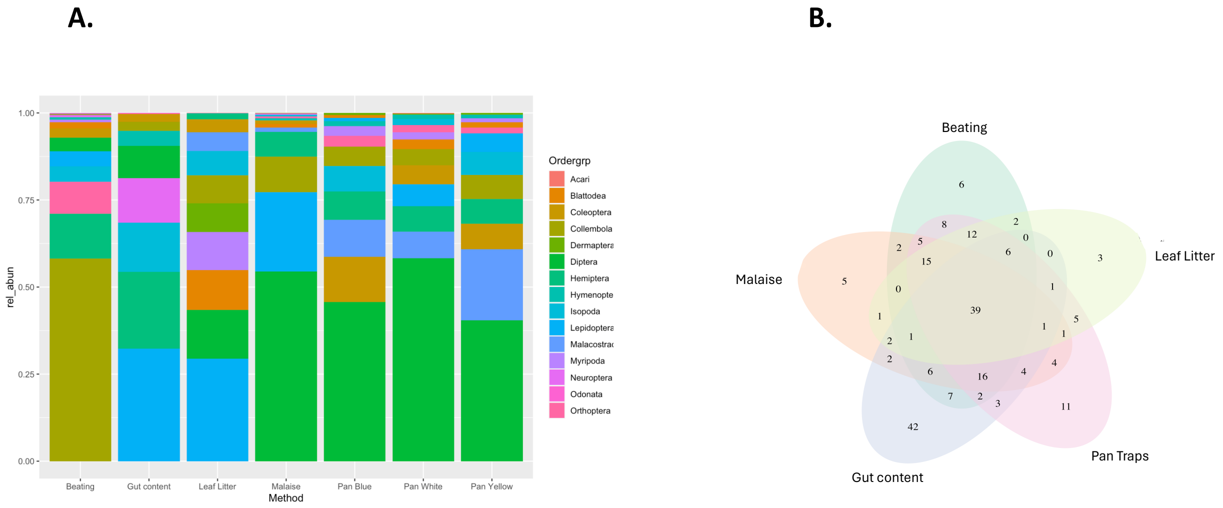
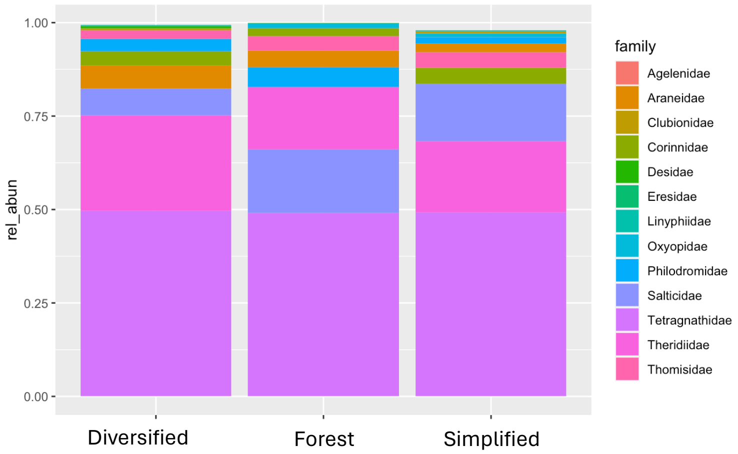


Figure 5. Stacked bar plot with relative read abundance on the y-axis and sampling method on the x-axis (A). The bar plot is filled with the arthropod orders collected through one of four direct sampling methods—vegetation beating, leaf litter – Berlese funnels, malaise traps, and pan traps— along with spider gut content, the arthropods amplified in the abdomen of spiders through a Polymerase Chain Reaction that utilized a developed no-spider primer. We collapsed smaller related orders together to simplify visualization. (B) Venn diagram of unique and shared arthropod families shared between sampling methods. Pan traps were collapsed together for visualization.



Supplement 1. Stacked bar plot with site type on the x-axis and relative abundance on the Y-axis. The barplot is filled with predator families.

7. Tables

Table 1. Quantitative metrics utilized in our analyses, how they are calculated, and the ecological context of each.

Metric	Calculation	Ecological meaning
Connectance	L/(R × C) LDq/S Proportion of realized links	Increased connectance enhances the robustness of network to change through an increased redundancy of interaction partners. Connectance is coupled with richness. Each new species added to a network significantly increases the number of potential links (Olesen and Jordano 2002).
Interaction evenness	$E_2 = H_2/\ln L$ Shannon entropy of interaction weights	Are there few species with many links or many species with few links? An indication that a site is dominated by a handful of species with heavily weighted interactions (based on read abundance). If a heavily weighted species is removed, it may cause instability (Bufford et al. 2020) (P. Vázquez et al. 2007).
Generality	L/C Gq, (25) Average number of resource species per consumer species	High generality indicates a site with an abundant prey base but limited predators (Peralta et al. 2014).
Vulnerability	L/R Vq, (27) Average number of consumer sp. per resource sp	High vulnerability indicates a site with many predators feeding on a small prey base (Tylianakis, Tscharntke, and Lewis 2007).
Linkage density	L/S LDq, (14) Average number of interactions per species	High linkage density is associated with a greater number of generalists with many interactions (Bufford et al. 2020).
Nestedness	Weighted NODF Pairwise overlap between adjacent rows and columns in a network matrix (Almeida-Neto et al. 2008).	A nested system will have a greater number of spiders with specialized feeding preferences interacting with the prey that generalists feed on as well. Nestedness increases network robustness against the loss of specialist species, as long as the generalist core of the network is maintained (Bascompte and Jordano 2014).

Modularity	Evaluation of which nodes form into separate subsets from the rest of the network (Beckett 2016).	High modularity indicates a site that is dominated by specialized, perhaps co-evolved species, interactions between two species. These two species form a "module" that is isolated from the other interactions in the network. Modularity promotes short term network stability but reduces its robustness to the loss of specialized species. Modularity is common in predator-prey networks (Pocock, Evans, and Memmott 2012).

Table 2. The different analysis variables we utilized in this study along with their diversity (see Table 3 and results) and network metric correlation significance (see Table 4 and results).

Variable	Type	Meaning	Diversity	Network Metrics
Agriculture land cover (Continuous)	Landscape composition	A measurement of land cover dedicated to vegetation managed for agricultural production up to 500 meters from the center point of a site	$P < 0.001$***	Linkage density P = 0.02243 Vulnerability P = 0.0493 Nestedness P = 0.03282
Vegetation land cover (Continuous)	Landscape composition	A measurement of land cover dedicated to non-agricultural vegetation from up to 500 meters from the center point of a site	$P < 0.001$***	Linkage density P= 0.04508 (-) Generality P=0.04739 (-) Interaction evenness P = 0.03005 (-) Nestedness P = 0.04496 (-)
Canopy cover (Continuous)	Local management	Average of 25 canopy densitometer measurements from a site	$P < 0.001$***	Modularity P = 0.0299 (-) Connectance P = 0.0281
Plant richness (Continuous)	Local management	Number of unique plants within a plot	$P < 0.001$***	Nestedness P= 0.0336 (-)
Average tree diameter (Continuous)	Local management	Average measured diameter of plants within a plot	$P = 0.00358$**	Nestedness P = 0.0330 (-)

Table 3. Linear regression model output for Shannon Diversity Index and landscape composition and management measurements. Linear regression model output for number of links (num.links) and number of nodes (num.nodes) and landscape composition and management measurements. Stastically significant p-values are highlighted in gray.

Metric	Variable	Estimate ± Standard error	*p*
Shannon	Agriculture land cover	-4.191e-06 ± 1.778e-07	<0.001***
Shannon	Vegetation land cover	2.820e-06 ± 1.122e-07	<0.001***
Shannon	average canopy cover	-0.0033764 ± 0.0002563	<0.001***
Shannon	average tree diameter	0.006340 ± 0.002173	0.00358**
Shannon	number of plants	0.133885 ± 0.006379	<0.001***
num.links	Agriculture land cover	9.914e-06 ± 7.353e-06	0.181
num.links	Vegetation land cover	-9.112e-06 ± 5.379e-06	0.0934
num.links	average canopy cover	0.04970 ± 0.02423	0.0431*
num.links	average tree diameter	0.02666 ±0.08750	0.761
num.links	number of plants	-0.3094 ± 0.3056	0.314
num.nodes	Agriculture land cover	3.075e-06 ± 2.196e-06	0.165
num.nodes	Vegetation land cover	-2.107e-06 ± 1.617e-06	0.196
num.nodes	average canopy cover	-0.02427 ± 0.00692	0.00069***
num.nodes	average tree diameter	0.01607 ± 0.02596	0.537
num.nodes	Number of plants	-0.05609 ± 0.09114	0.54

Table 4. Model output of a distance based redundancy analysis with predator OTUs and management measurements, including the average of 20 canopy cover measurements, number of plants sampled, number of plants identified as introduced, number of plants identified as Polynesian crops, and the average diameter of a all trees in a sampled plot.

Variable	***F***	***P***
Canopy cover average	3.152513	0.001
Number of plants	1.26914	0.012
Number introduced	1.3323	0.089
Number Polynesian	1.418108	0.054
Average tree diameter	2.128178	0.003

Table 5. Spearmans correlation test for network metrics and landscape composition. Spearmans correaltions tests were used to determine the significance of the relationship between each quantitative network value and agriculture and vegetation. Significant correlations are highlighted in gray.

metric	variable	S	*p*	rho
Linkage density	Agriculture land cover	816.12	0.02243	0.3863747
Weighted connectance	Agriculture land cover	949.13	0.2209	0.2863719
Generality	Agriculture land cover	1037	0.352	0.2197033
Vulnerability	Agriculture land cover	795.97	0.0493	0.4015267
Interaction evenness	Agriculture land cover	957.19	0.2313	0.2803111
nestedness	Agriculture land cover	869.62	0.03282	0.2371774
modularity	Agriculture land cover	1148.1	0.9971	-0.0070799
Linkage density	Vegetation land cover	912	0.04508	-0.437594
Weighted connectance	Vegetation land cover	1732	0.1948	-0.3022556
Generality	Vegetation land cover	838	0.04739	-0.3819549
Vulnerability	Vegetation land cover	1758	0.1163	-0.3218045
Interaction evenness	Vegetation land cover	982	0.03005	-0.4150376
nestedness	Vegetation land cover	856	0.04496	-0.277193

Table 6. Spearmans correlation test for network metrics and management measurements. Spearmans correaltions tests were used to determine the significance of the relationship between each quantitative network value and average tree diameter, number of plants sampled, and the average of 20 canopy cover measurements. Significant correlations are highlighted in gray.

metric	variable	S	*p*	rho
Linkage density	average tree diameter	1070	0.8027	0.06143046
Weighted connectance	average tree diameter	1168	0.9205	-0.0245722
Generality	average tree diameter	1219	0.7779	-0.0693287
Vulnerability	average tree diameter	1123	0.9517	0.01491883
Interaction evenness	average tree diameter	1126	0.9602	0.01228609
Nestedness	average tree diameter	809	0.0330	-0.3360685
Modularity	average tree diameter	1324	0.509	-0.1614743
Linkage density	number of plants	1070	0.8027	0.06143046
Weighted connectance	number of plants	1168	0.9205	-0.0245722
Generality	number of plants	1219	0.7779	-0.0693287
Vulnerability	number of plants	1123	0.9517	0.01491883
Interaction evenness	number of plants	1126	0.9602	0.01228609
Nestedness	number of plants	904	0.0336	-0.3360685
Modularity	number of plants	1324	0.509	-0.1614743
Linkage density	average canopy cover	1150	0.9741	-0.0087719
Weighted connectance	average canopy cover	844	0.0281	0.4596491
Generality	average canopy cover	1278	0.6207	-0.1210526
Vulnerability	average canopy cover	1056	0.7647	0.07368421
Interaction evenness	average canopy cover	1202	0.8259	-0.054286
Nestedness	average canopy cover	1081	0.8358	0.05096669
Modularity	average canopy cover	902	0.0299	-0.3513185

Table 7. The network metrics of 1000 null matrices were compared to the network metrics of the empirical matrix. The null hypothesis is said to be true if the empirical values are within the null model distribution. This is a two tailed distribution. A "1" indicates that every null model value that we compared to our observed was greater than or equal to the observed value. A "0" indicates that no null model value that we compared to our observed was greater than or equal to the observed value. A value of greater than 0 and less than 1 is simply the number values that the null metric was greater than the empirical metric. Non-correlated values are highlighted in gray.

site	pval.Connectance	pval.LD	pval.Gen	pval.Vul	pval.Nodes
1	0.007	0.007	0.024	0.019	1
2	0.005	0.005	0.034	0.027	1
3	0.007	0.007	0.034	0.005	1
4	0.241	0.241	0.091	0.718	1
5	0.002	0.002	0.475	0.002	1
6	0	0	0.025	0.013	1
7	0.003	0.003	0.039	0.003	1
8	0.017	0.017	0.015	0.11	1
9	0.113	0.113	0	0.949	1
10	0	0	0.038	0.011	1
11	0.05	0.05	0.034	0.226	1
12	0.032	0.032	0.008	0.025	1
13	0.013	0.013	0.048	0.048	1
14	0.032	0.032	0.014	0.029	1
15	0.018	0.018	0.012	0.136	1
16	0	0	0.039	0	1
17	0.002	0.002	0.038	0.018	1
18	0.042	0.042	0.038	0.06	1
19	0.003	0.003	0.048	0.014	1
20	0.023	0.023	0.047	0.049	1
21	0.045	0.045	0.04	0.021	1

8. References

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