Conservation Biology

Contributed Paper

Linkages between measures of biodiversity and community resilience in Pacific Island agroforests

Tamara Ticktin,[1]* Shimona Quazi,[1] Rachel Dacks,[2] Mesulame Tora,[1,3] Ashley McGuigan,[1,3] Zoe Hastings,[1] and Alivereti Naikatini[3]

[1]Botany Department, University of Hawaiʿi at Mānoa, 3190 Maile Way, Honolulu, HI, 96822, U.S.A.
[2]Biology Department, University of Hawaiʿi at Mānoa, 2538 McCarthy Mall, Honolulu, HI, 96822, U.S.A.
[3]South Pacific Regional Herbarium and Biodiversity Center, Institute of Applied Sciences, University of the South Pacific, Private Bag, Laucala, Campus, Suva, Fiji

Abstract: *Designing agroecosystems that are compatible with the conservation of biodiversity is a top conservation priority. However, the social variables that drive native biodiversity conservation in these systems are poorly understood. We devised a new approach to identify social–ecological linkages that affect conservation outcomes in agroecosystems and in social-ecological systems more broadly. We focused on coastal agroforests in Fiji, which, like agroforests across other small Pacific Islands, are critical to food security, contain much of the country's remaining lowland forests, and have rapidly declining levels of native biodiversity. We tested the relationships among social variables and native tree species richness in agroforests with structural equation models. The models were built with data from ecological and social surveys in 100 agroforests and associated households. The agroforests hosted 95 native tree species of which almost one-third were endemic. Fifty-eight percent of farms had at least one species considered threatened at the national or international level. The best-fit structural equation model (R^2 = 47.8%) showed that social variables important for community resilience—local ecological knowledge, social network connectivity, and livelihood diversity—had direct and indirect positive effects on native tree species richness. Cash-crop intensification, a driver of biodiversity loss elsewhere, did not negatively affect native tree richness within parcels. Joining efforts to build community resilience, specifically by increasing livelihood diversity, local ecological knowledge, and social network connectivity, may help conservation agencies conserve the rapidly declining biodiversity in the region.*

Keywords: adaptive capacity, agroforestry, Fiji, livelihood diversity, local ecological knowledge, social ecological systems, social networks, structural equation models

Conexiones entre las Medidas de la Biodiversidad y la Resiliencia Comunitaria en los Agro-Bosques de las Islas del Pacífico

Resumen: *El diseño de agro-ecosistemas que sean compatibles con la conservación de la biodiversidad es una prioridad de suma importancia para la conservación. Sin embargo, se entiende muy poco sobre las variables sociales que conducen a la conservación de la biodiversidad nativa en estos sistemas. Diseñamos una nueva estrategia para identificar las conexiones socio-ecológicas que afectan los resultados de conservación en los agro-ecosistemas y de manera más general en los sistemas socio-ecológicos. Nos enfocamos en agro-bosques costeros en las islas de Fiyi, los cuales, similares a los agro-bosques de otras pequeñas islas del Pacífico, son de mucha importancia para la seguridad alimentaria, contienen la mayoría de los bosques de tierras bajas que aún permanecen en el país, y tienen niveles de declinación rápida de la biodiversidad nativa. Evaluamos las relaciones entre las variables sociales y la riqueza de especies nativas de árboles en los agro-bosques con modelos de ecuaciones estructurales. Los modelos se construyeron con datos de censos ecológicos y sociales en 100 agro-bosques y hogares asociados. Los agro-bosques incluyeron a 95 especies nativas de árboles, de las cuales casi un tercio son endémicas. El 58% de las granjas tuvieron al menos una especie considerada como amenazada a nivel nacional o internacional. El modelo de ecuación estructural mejor*

*email ticktin@hawaii.edu
Article impact statement: *Identifying social–ecological linkages shows how strengthening aspects of community resilience directly and indirectly enhances conservation.*
Paper submitted September 9, 2017; revised manuscript accepted March 3, 2018.

Conservation Biology, Volume 32, No. 5, 1085–1095

DOI: 10.1111/cobi.13152

adecuado (R^2 = 47.8%) mostró que las variables sociales que son importantes para la resiliencia comunitaria – el conocimiento ecológico local, la conectividad en redes sociales, y la diversidad de sustentos – tuvieron efectos positivos directos e indirectos sobre la riqueza de especies nativas de árboles. La intensificación del cultivo comercial, un conductor de la pérdida de la biodiversidad en otras partes, no afectó negativamente a la riqueza de especies nativas de árboles dentro de las parcelas. La unión de esfuerzos para construir una resiliencia comunitaria, específicamente al incrementar la diversidad de sustentos, el conocimiento ecológico local, y la conectividad en redes sociales, puede ayudar a las agencias de conservación a conservar la biodiversidad que declina rápidamente en la región.

Palabras Clave: agro-silvicultura, capacidad adaptativa, conocimiento ecológico, Fiyi, diversidad de sustentos, modelos de ecuaciones estructurales, redes sociales, sistemas socio-ecológicos

摘要: *设计出可以与生物多样性保护相适应的农业生态系统是保护的首要任务。然而, 这些系统中驱动原生生物多样性保护的社会因素尚不为人所知。我们设计了一个新方法来确定在农业生态系统及更广泛的社会——生态系统中影响保护成效的社会——生态联系。我们的研究关注斐济 (Fiji) 的沿海农林, 它们和其它太平洋小岛的农林一样, 对粮食安全十分重要。它包含了该国大部分剩余的低地森林, 且原生生物多样性水平已快速下降。我们用结构方程模型检验了农林生态系统的社会变量和原生树种丰富度的关系, 模型的数据来自 100个农林和相应家庭的生态学及社会学调查。农林生态系统中有 95种原生树种, 其中近三分之一是特有种。百分之五十八的农场有至少一种在国家或全球水平上被认为是受威胁的物种。拟合最好的结构方程模型 (R^2 = 47.8%) 显示, 影响群落恢复力的重要社会变量 (当地生态学知识、社会网络连通性和生计多样性) 对原生树种丰富度有直接和间接的积极作用。在其它地方导致生物多样性丧失的经济作物集约化, 而在我们研究的地块中对原生树种丰富度却没有负面影响。通过增加生计多样性、当地生态学知识和社会网络连通性, 共同努力建立群落恢复力, 可能有助于保护机构保护该地区快速下降的生物多样性。*【**翻译: 胡怡思; 审校: 魏辅文**】

关键词: 适应能力, 农林业, 斐济, 当地生态学知识, 生计多样性, 社会生态系统, 社会网络, 结构方程模型

Introduction

Designing and promoting agricultural practices compatible with the conservation of biodiversity is widely recognized as a top priority for conservation (Chazdon et al. 2009; Perfecto & Vandermeer 2010; Tscharntke et al. 2012). Growing human populations are expected to increase forest clearance for agriculture, especially in the tropics (Tilman et al. 2001). Protected areas play a critical role but will not be sufficient to stem this tide (Pimm & Raven 2000; Kremen 2015). Traditional agroforestry systems, where crops are grown within shifting mosaics of forests and fallows, are widespread globally, have been practiced for millennia, and are capable of producing food while maintaining high levels of native biodiversity and ecosystem function (Bhagwat et al. 2008; Clough et al. 2011; Quazi & Ticktin 2016). Because they tend to focus on locally adapted crops, can be biodiverse at multiple ecological scales, and require low inputs, agroforests are also thought to be more resilient to climate change than other agricultural systems (Mijatović et al. 2013; Nguyen et al. 2013). As such, there are growing calls from governmental and nongovernmental agencies worldwide to promote these systems (e.g., FAO 2010; Bell & Taylor 2015).

However, traditional agroforests do not all conserve biodiversity equally. Factors such as proximity to surrounding forests, soil type, and slope can affect species richness (Scales & Marsden 2008; Anand et al. 2010; Quazi & Ticktin 2016). As farmers intensify their cash crops, species richness often decreases (Philpott et al. 2008; Scales & Marsden 2008; Hariyadi & Ticktin 2012). However, there is little information on other social variables that may influence differences in biodiversity outcomes (Valencia et al. 2016). This is surprising because agroforests are social-ecological systems (SES), where social systems pertaining particularly to governance and knowledge shape and are shaped by ecological structure and dynamics (Berkes et al. 2008). For example, local worldviews and values influence formal and informal social institutions and the latter guide decisions on resource management, which in turn have ecological outcomes. Similarly, the structure and dynamics of local ecosystems can influence social systems through feedbacks from communal learning and adaptation (Berkes 2012). In SES that are adaptive, such as traditional resource management systems that have persisted over millennia, linked social and ecological components foster social-ecological resilience (i.e., the ability of the SES to buffer or absorb disturbance while maintaining essentially the same function (Berkes et al. 2008). For example, social characteristics that strengthen adaptive capacity such as social learning, social networks, and diversification of livelihood strategies both lead to, and are linked reciprocally to, resource management practices that can foster ecological resilience—such as maintaining or increasing ecological diversity at multiple scales (e.g., genes, species, functional traits, and landscapes) (Berkes et al. 2008; Berkes 2012; Bergamini et al. 2014). Despite the need to understand social–ecological linkages for designing conservation strategies (Rissman & Gillon 2017) and the existing information on social characteristics that are hypothesized to lead to resilient social-ecological agroecosystems (Cabell & Oelofse 2012; Bergamini et al. 2014), there are few empirical tests of whether and how they link to biodiversity outcomes, especially in the context of global change. In a review of social-ecological studies, Rissman and Gillon (2017) found that <1% of social–ecological connections assessed had a biodiversity variable as the independent variable.

We devised an approach to identify and quantify social–ecological linkages important to biodiversity outcomes. We focused on coastal agroforests in Fiji, which, like small Pacific Island lowland forests more broadly, represent priority systems for identifying social drivers of biodiversity conservation. Natural lowland forests in Fiji are rare, vascular plant endemism is high (about 50%; Department of Forests 2010), and there are few terrestrial formally protected areas (Keppel et al. 2012). Instead, lowland agroforests, which include patchworks of managed areas with crops and forests in different stages of succession, have effectively protected much of the region's remaining diversity (Thaman & Clarke 1993). However, this diversity has declined rapidly with global and local socioeconomic changes, which have led to an increased emphasis on monoculture cash crops and introduced timber species (Thaman 2014). Pacific Island agroforests also make critical contributions to the food security of local communities (Thaman & Clarke 1993; Thaman 2014), and these contributions are expected to increase with climate change as food resources from coral reefs decrease (Keener et al. 2012).

We tested the relationships among 3 indicators of adaptive capacity, local ecological knowledge (LEK), social network connectivity, and livelihood diversity, and an indicator of ecological resilience in agroforest systems and biodiversity, native tree species richness. The latter has been declining rapidly (Thaman 2014). Richness of native canopy trees is also an important predictor of avian species richness (Harvey & Gonzalez Villalobos 2007; Quazi & Ticktin 2016) and of some insect groups (Bos et al. 2007; Philpott et al. 2008; Tscharntke et al. 2008) in multiple types of agroforest systems. Fiji's terrestrial birds, half of which are endemic, are a conservation concern because they are increasingly threatened by destruction of native forests, and many play important roles as seed dispersers (Watling 2013). Because increasing native tree species richness can increase the potential for ecological self-regulation and for diversity of responses to disturbance, such as cyclones, it is also an indicator of resilience in agroecosystems (Cabell & Oelofse 2012). We also examined the effects of cash-crop intensification on these relationships.

We used structural equation modeling (SEM) to test our hypotheses. Structural equation models allow for correlations among predictor variables and for testing both direct and indirect effects (Grace 2006). As such, SEM is increasingly used to model ecological systems and provides an approach to quantitatively model SES.

We tested the following hypotheses (Table 1, Fig. 1a). First, LEK is positively correlated with native tree species richness. Local ecological knowledge encompasses knowledge-practice-belief systems about

Table 1. Hypothesized linkages between indicators of adaptive capacity and biodiversity conservation.

Variable	*Contribution to adaptive capacity*	*Hypothesized link to biodiversity conservation outcome*	*Studies showing social–ecological linkages**
Local ecological knowledge (LEK)	strengthens cultural identity and collective long-term memory needed to understand, learn from, and adapt to change	Use of culturally important plants and associated knowledge of ecological processes can motivate conservation of culturally and ecologically important species and landscapes.	1–3
Social network connectivity	provides support network across time and space	Increased access to planting resources for and knowledge of species can increase species richness. Species that provide resources for exchange may be maintained to support social networks.	4–5
Livelihood diversity	spreads risk to hedge bets against climatic and economic uncertainty	A greater diversity of agricultural landscapes can provide more ecological niches for native species and lead to more associated LEK.	2
Cash-crop intensification	NA	As cash-crop intensification increases, there may be less interest and space for noneconomic plants and therefore decreased species richness.	6–8

**References: 1, Ticktin et al. 2002; 2, Berkes 2012; 3, Reyes-García et al. 2016; 4, Ban & Coomes 2004; 5, Díaz-Reviriego et al. 2016; 6, Philpott et al. 2008; 7, Scales & Marsden 2008; 8, Hariyadi & Ticktin 2012.*

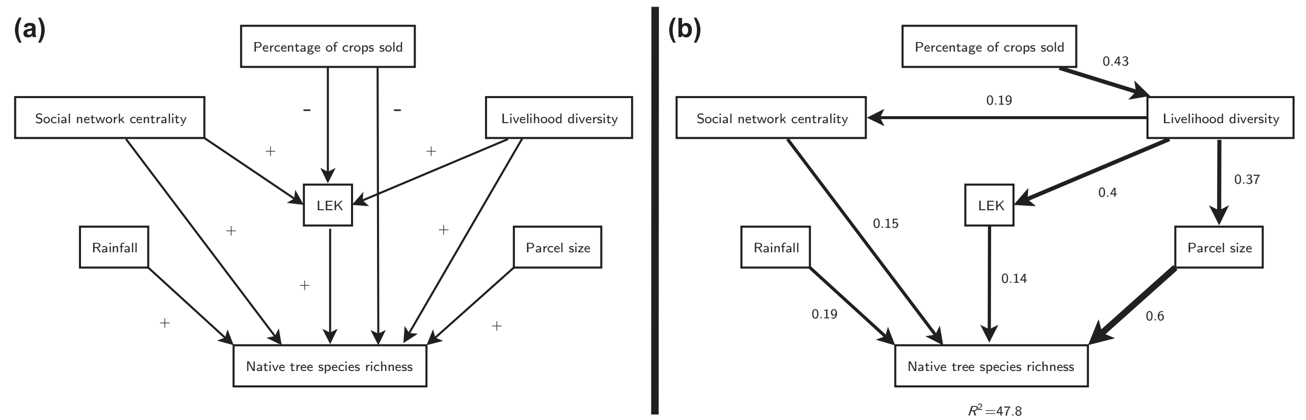

Figure 1. (a) Hypothesized social correlates of native tree species richness in Fijian agroforests (plus and minus signs, hypothesized positive or negative correlations, respectively) and (b) best-fit structural equation model (values, standardized path coefficients representing expected change in one variable as a function of change in another in SD units; arrow thickness proportional to strength of path coefficients).

relationships between people and their natural environment and is adaptive (Berkes 2012). Farmers who use culturally important native plants and have more associated knowledge of their ecology may be more likely to plant or maintain them than farmers with less knowledge. Second, social network connectivity, measured as network centrality, is positively correlated with native tree species richness and with LEK. Individuals who exchange more resources (food, propagules, and information) may have more species-rich agroforests and more associated LEK. Measures of social network connectivity for medicinal plant knowledge and materials can be correlated with medicinal plant species richness in home gardens (Díaz-Reviriego et al. 2016). Third, livelihood diversity is positively correlated with native tree species richness and with LEK. Farmers with multiple livelihoods may work with more agroecosystem types, which may support a wider range of species; therefore, farmers may also have greater knowledge of more species. Fourth, the proportion of crops sold is negatively correlated with native tree species richness and LEK. As farmers sell more cash crops, this may leave less time and space to plant or maintain native trees and lead to less LEK.

Methods

We surveyed 100 coastal agroforests in 20 villages across 5 districts of the Fiji Islands (Fig. 2). These locations represented a range of socioeconomic conditions and, except for the 2 villages in Malolo, were sites where we had carried out preliminary research and developed rapport with communities. The agroforests ranged from dry to wet, with mean annual precipitation ranging from 1536 to 3554 mm (Barker et al. 2006). Like many traditional agroforests across the Pacific Islands (Thaman 2014), these agroforests consisted of mixed species plantings of understory root crops such as taro, cassava, yams, or sweet potatoes, interspersed with other crops and trees, including native trees and introduced fruit trees. Parcels are established from forests and fallows by clearing vegetation, sometimes with fire. In the process of establishing a parcel, farmers may decide to spare or to plant individuals or patches of native or aboriginally introduced tree species, especially those perceived to provide ecosystem goods (e.g., foods, medicines, and timber) and services (e.g., shade, nitrogen fixation, and erosion control). As such, the presence of native trees is directly linked to the decision-making process of the farmer.

Like most coastal villages in Fiji's larger islands, the 20 villages are mixed subsistence economies, where agroforests and fishing provide food for both subsistence and sale. Although there is variation within and across villages, agroforest products are frequently among the top 3 sources of household income. Generalized reciprocity, in which there is not necessarily an expectation for an exchange in return, is culturally important across the Pacific Islands (McMillen et al. 2014), and a substantial portion of resources from agroforests is often shared with family and friends.

We obtained permission from Fiji national and district governments, village headmen and the University of Hawaii Institutional Review Board (CHS-20991) to conduct surveys and interviews. We then interviewed the head of each village and obtained a list of all households in the village. We randomly selected 5 households per village for agroforest surveys to obtain a total sample size of 100. Villages ranged from 12 to 115 households (mean = 34). With each farmer, we carried out a participatory mapping exercise to understand the number, size, and location of agroforest parcels and other resources. Then, we surveyed the main agroforest parcel of each farmer such that they represented the parcel where the farmer grew most of his subsistence crops, included

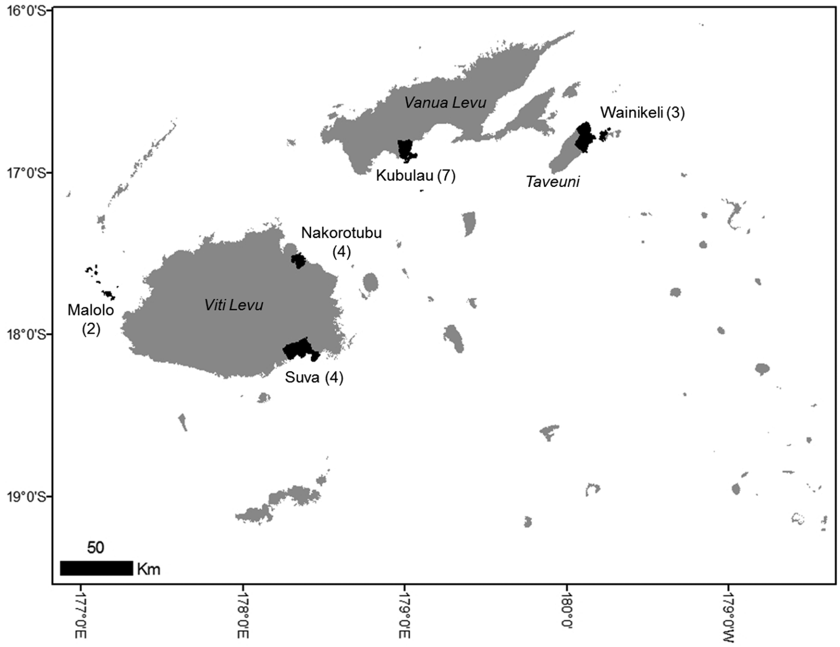

Figure 2. Study sites in the Fiji Islands (black, 5 study districts; numbers, number of villages surveyed). Villages ranged from 12 to 115 households (mean = 34).

active cropping areas, and were within an hour's walk of the village. Parcels ranged from 0.25 to 5.00 ha and were located under 100 m elevation, except for 1 parcel with an elevation of 196 m.

With each farmer, we recorded all tree species observed in the parcel (including in crop, forest, and fallow areas) and understory crops. Because some resource areas are shared within family groups and clans, we included all adjacent areas where farmers had access to resources. Species unidentified in the field were identified at the South Pacific Regional Herbarium. During each agroforest survey, we carried out semistructured interviews with each farmer on management practices.

We also carried out household semistructured interviews with all but 2 of the farmers whose agroforests we surveyed. These lasted 45 min to 1 h. We asked questions on socioeconomics, LEK, livelihoods, and resource sharing (Table 2 & Supporting Information). For livelihoods, participants were asked to name all the on-farm and off-farm livelihoods, including nonincome-generating livelihoods that their household participated in (subsistence use or sale of taro, kava, handicrafts, livestock, vegetables, fishing, remittances, etc.). To conduct the social network analysis, we asked at least 80% of households in each village to identify the other households from which they received or gave resources (e.g., fish, crops, and prepared food) within the previous 2 weeks.

Focus group discussions and village-level participatory mapping exercises were conducted to triangulate information. All interviews were conducted in Fijian language. Field surveys and interviews took place from August to December 2014, and follow-up interviews were carried out in September 2015 and January to April 2017.

We calculated native tree species richness directly from the parcel counts. Based on a pilot survey in 2013, we developed 10 questions on Fijian cultural-ecological knowledge and practice relevant today to create an index of LEK (Table 2 & Supporting Information). All questions were asked as part of the larger, semistructured interview and concerned generalist as opposed to specialist knowledge, and practice (e.g., known only by specialists such as healers). We used responses to questions about knowledge of crop varieties, medicinal plants, and famine foods as indicators of knowledge. We used responses to questions about preparing for cyclones, responding to disturbance events (cyclones, fire, drought, etc.), adapting new crop species or varieties, and the presence or absence of weaving practices (from *Pandanus* leaves) in the household as indicators of practice. Practice is of course directly linked to associated knowledge. We considered whether respondents reported that they formally or informally pass on LEK to the young as an indicator of knowledge transmission (Table 2).

Responses to the 10 questions were scored and then standardized (Supporting Information). We weighted scores as follows to create the index: responses to questions about plant knowledge (40%), practice (40%), and transmission (20%). These scores provide an index of LEK but not a comprehensive measure (Zent & Maffi 2009). Because small differences in the index are not meaningful, we grouped the scores from low to high based on 3 broader groupings.

To measure social network connectivity, social network maps were created in Visone software (Brandes & Wagner 2004). We used degree centrality (sum of the number of households the respondent's household

Table 2. Description of and methods used to quantify 3 indicators of adaptive capacity and cash-crop intensification.

Variable	Description	Survey method
Local ecological knowledge (LEK)	index of local cultural-ecological knowledge, practice, and innovation (Supporting Information)	household, semistructured interviews; score created by weighing standardized scores from responses to questions about plant knowledge (40%), practice (40%), and transmission of LEK (20%); LEK grouped into 3 levels based on scores
Social network connectivity	social network centrality: sum of the number of households the respondent's household shares with or receives shared resources from	survey of structure of household social network; ≥80% of households in community interviewed
Livelihood diversity	number of livelihood sources in the household, including sources of income and livelihoods that procure food or handicrafts for cultural offerings	household, semistructured interviews
Cash-crop intensification	proportion of cash crops sold	household interviews: proportion of taro and kava sold

gave or received resources from) to indicate the household's connectedness (Table 1) (Borgatti et al. 2013). We calculated degree from an undirected graph because we did not need to distinguish between giving and receiving resources. Livelihood diversity was calculated as the number of different livelihoods mentioned during the household interview (Table 2). Our analyses were therefore all carried out at the household level. The exception was LEK, information on which was obtained from individuals responsible for managing the household agroforest. To control for potential variation in self-reporting among participants, social network centrality and livelihood diversity values were grouped into 4 and 5 broader categories, respectively. However, results of all our analyses remained consistent with or without these groupings.

We used general linear mixed models (Zuur et al. 2009) to regress indicators of adaptive capacity against native tree species richness per farm. Models included village nested within district as a random effect to account for potential spatial autocorrelation. Model residuals were examined for normality and homogeneity of variance, and variables were examined for multicollinearity. We used single-variable regressions because our predictors were not independent. Then, we used SEM (Grace 2006) to identify how social variables correlate directly and indirectly with native tree species richness. To account for spatial autocorrelation, we used a nested structure of parcels within village within district. Starting with a model of hypothesized links (Fig. 1a), we used modification indices to identify missing paths grounded in theory or existing knowledge (Grace 2006). Nonsignificant correlations were sequentially eliminated, and the best-fit model was determined by comparing all models with Akaike's information criterion. We carried out the SEM in the lavaan package (Rosseel 2012). All analyses were done in R version 1.0.136.

Results

The 100 coastal Fijian agroforests hosted a total of 149 tree species, including 95 native species (Supporting Information). Nearly, one-third (29) of the native species were endemic and 15 were threatened, either nationally (11 species [Department of Forests 2010]) or internationally (5 species [IUCN 2017]). Fifty-eight percent of farms had at least 1 species considered threatened at the national or international level. The number of native tree species per farm ranged from 0 to 26 (Supporting Information). Most species were recorded from a small number of farms (Fig. 3).

Parcel size, LEK, social network centrality, and livelihood diversity (Supporting Information) were all significantly positively correlated with species richness ($p < 0.01$) (Fig. 4). The number of livelihood sources, which included income and nonincome-generating resources, ranged from 6 to 19. Income-generating livelihoods included both agricultural (sale of taro, kava, livestock, and vegetables) and marine (fish and invertebrates) resources and handicrafts, remittances, and, for those villages close to town, salaries from jobs in town. The proportion of cash crops sold ranged from 0% to 75% and was not correlated with native tree species richness (Fig. 4).

The best-fit structural equation model ($\chi^2 = 0.782$) explained 47.8% of the variation in native tree species richness (Fig. 1b). The path coefficients represent the expected change in one variable as a result of change in another while holding all other variables constant (Supporting Information). The standardized path coefficients (Fig. 1b) represent predicted change in SD units and allow comparisons among variables. Bigger parcels and those with higher rainfall had higher native tree species richness. Holding those variables constant, LEK and social network centrality had direct positive effects on native tree species richness. Livelihood diversity had an indirect

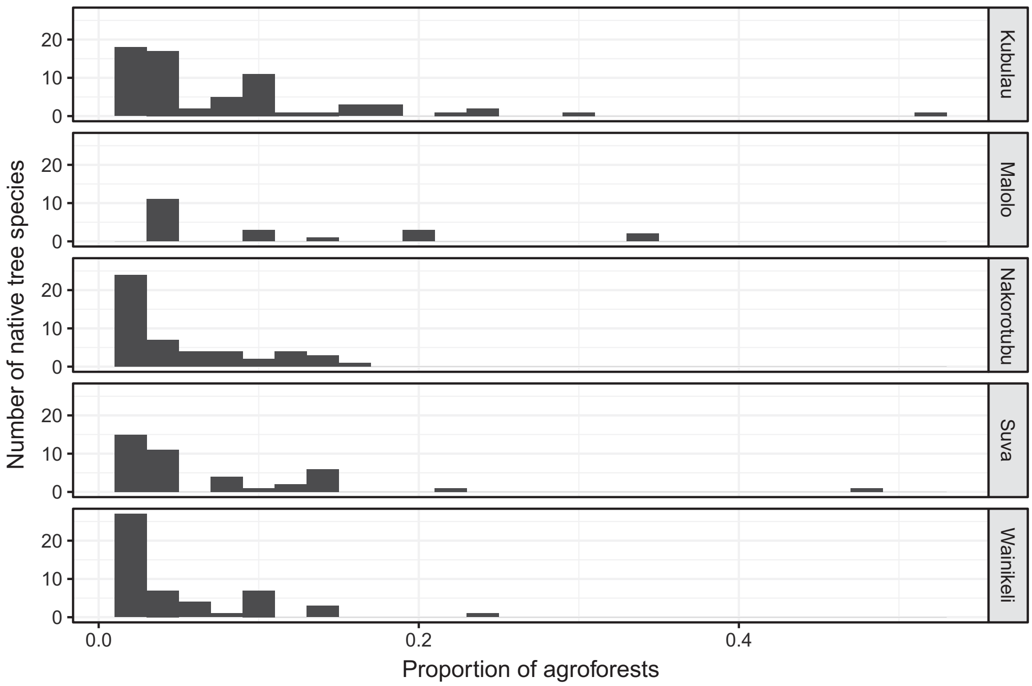

Figure 3. Distribution of native tree species across agroforests in 5 districts of Fiji (proportion is of agroforests containing those species found in that district).

positive effect on species richness and was positively correlated with LEK and social network centrality and farm size. The proportion of crops sold had indirect positive effects on native tree richness through increased livelihood diversity.

Discussion

In Fiji and across many small Pacific Islands, conservation of lowland forest biodiversity, especially coastal forest diversity, has depended on agroforests that have dominated the landscape for over a millennium (Thaman 2014). However, biodiversity in these systems has rapidly declined due to socioeconomic and other changes (Thaman 2014). Although there are no similar unmanaged coastal lowland forests with which to compare our findings, our results suggest that agroforests still contain substantial levels of native tree biodiversity and clearly are not protecting only widespread, common species. Nonetheless, the low frequency of most native trees at both parcel and village levels suggests that further declines are likely.

Today, Pacific Island governmental and nongovernmental agencies are investing in strategies to enhance and maintain community resilience in the face of climate and socioeconomic changes. At the same time, there are increasing calls to develop more culturally appropriate and integrative approaches to conservation (Keppel et al. 2012; Jupiter et al. 2014), but there is little information on which kinds of integrated approaches may be most effective. By identifying significant linkages among social variables and levels of biodiversity, our SEM approach provides insight on the kinds of integrated conservation strategies that may be most effective. In the case of Fiji agroforests, our results indicated that strengthening specific components of Pacific Island community resilience may also foster positive outcomes for biodiversity conservation. Three indicators of adaptive capacity (part of community resilience)—social network centrality, LEK, and livelihood diversity—were positively correlated with the conservation metric native tree richness.

Although we are unaware of other research that has quantified these social–ecological linkages, our findings are consistent with theory and findings at the system (e.g., Berkes et al. 2008; López-Angarita et al. 2014) and individual variable levels (Table 1). Strengthening LEK increases adaptive capacity by strengthening both cultural identity and the collective long-term memory needed to understand, learn from, and adapt to change (Berkes et al. 2008; McMillen et al. 2014; McMillen et al. 2016). In Fiji, LEK is founded on native species and aboriginal introductions from about 3000 years ago. However, LEK is dynamic, and non-native species are highly culturally and economically important. The correlation between LEK and richness of all taxa recorded in the parcels (trees and understory crops) is likely stronger than that for native trees only.

Complex social networks have formed the backbone of Pacific Island resilience for millennia (Thaman 2008;

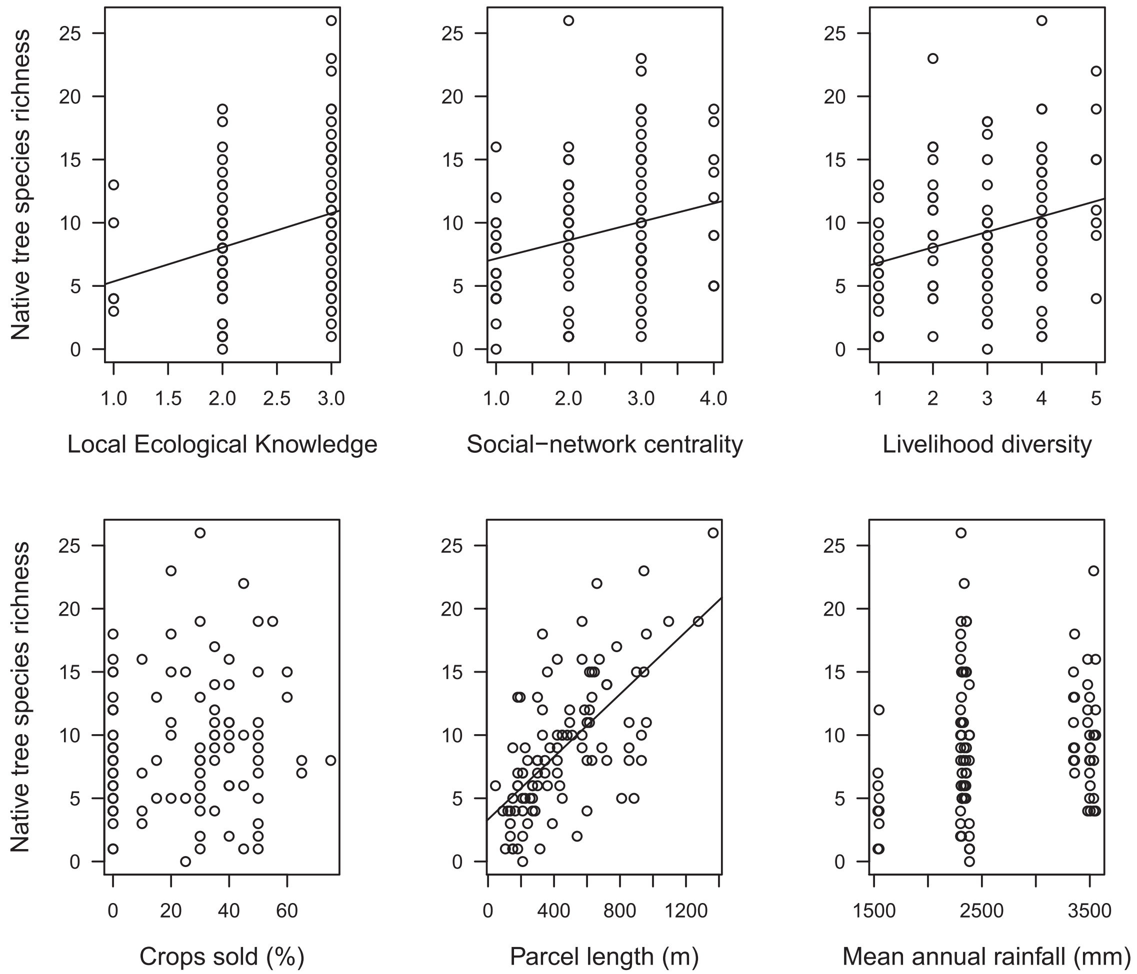

Figure 4. Correlations of social variables and native tree species richness in Fijian agroforests (plots with regression lines, significant correlations, $p < 0.01$; plots without lines, no significant correlation). All models include district or village as a random term.

McMillen et al. 2014). Measures of social network connectivity can be positively correlated with cultivated plant diversity in home gardens (Ban & Coomes 2004; Díaz-Reviriego et al. 2016), but to our knowledge this is the first test of the role of social networks in maintaining native forest biodiversity. Our social network questions focused on exchange of resources. Had they also included exchange of information, we would have expected a correlation between LEK and social network centrality.

Although livelihood-diversification programs have been promoted as conservation strategies for decades, many have been unsuccessful because they tend to be based on faulty assumptions (Wright et al. 2016). Our SEM showed that in the context of Fiji agroforests, livelihood diversity contributes to native tree species richness, but it does so indirectly by increasing LEK, social network centrality, and farm size. The correlations between livelihood diversity and LEK and social network centrality are likely due to farmers who use a relatively wider variety of production strategies and have more knowledge and more products to exchange with community members. Other research has demonstrated the role of off-farm livelihood activities and associated social networks in maintaining agrobiodiversity (Zimmerer 2014). Our results highlight the importance of approaches like SEM to understanding social–ecological linkages because effects may be both direct, such as the effect of LEK on native tree species richness, or indirect, such as the effect of livelihood diversity on native tree species richness.

Parcel size was the strongest predictor of native tree richness. Although we expected this because patch or fragment size is a strong ecological correlate of species richness (e.g., MacArthur & Wilson 1967; Laurance et al. 2011), here parcel size was in turn a function of social variables. In the villages where we worked, land is communally owned and abundant relative to population size. Therefore, parcel size does not reflect access to financial or other resources; rather, it reflects management decisions farmers make, such as the use of traditional long-rotation fallows, multiple crop species, and multiple habitat types (larger parcels) or of short or no fallows, few crop species, and more intensive plantings (smaller parcels). Farmers with more livelihood options, both agricultural and others, had larger, less-intensive plantings. Farmers whose primary income was salaried income such as tourism, tended to have fewer livelihoods and smaller parcels. Decreasing parcel size has had additional negative consequences for conservation as abandoned fallows provide prime habitat for invasive species, now one of the region's most important drivers of native species declines (Thaman 2014). In this context, maintaining diverse agroforests by increasing livelihood options, and supporting LEK and social networks, conserves biodiversity better than options that lead to abandoned fallows.

Although the contribution of parcel size to native tree richness was much stronger than that of LEK and social network connectivity, our findings are very likely underestimates of the latter 2. The variation we captured in LEK within villages was limited because our sampling did not capture the low and high ends of the spectrum. Although much LEK has been lost (Thaman 2014), each village or district still had keepers of LEK, but we often missed them in the random sampling of 5 households. Informal observations of the agroforests of some of the keepers of LEK revealed them to be invariably highly diverse. We also undersampled households with the lowest LEK levels because they tended to work exclusively outside the village. In terms of social networks, we captured most of the variation within villages because we sampled at least 80% of households in each. However, we expect much greater variation in both social network centrality and LEK in larger and more heterogeneous villages. We also expect that a higher sample size would yield more social–ecological linkages; our sample size of 100 was relatively small for SEM with multiple variables. These findings offer clear directions for future studies. Other nonsocial variables we did not measure may influence species richness, such as composition of the surrounding matrix (Anand et al. 2010) and soil type and fertility among others. However, the variables we examined explained nearly 50% of the variation in native species richness, highlighting their importance.

Linkages between social and ecological resilience may change over time because socioeconomic and environmental changes may decrease or uncouple linkages. Intensification of cash crops often decreases biodiversity (Philpott et al. 2008; Scales & Marsden 2008), and we expected it would decrease both LEK and its correlation to native tree richness because farmers would dedicate less time and space to native species. In other Pacific Islands, cash cropping of kava in upland forests has been a major contributor to forest destruction (Merlin & Raynor 2005). Some farmers in our study also grew commercial kava and taro monocultures in upland forests. Although we did not sample upland sites, we found that the proportion of crops sold by the household (from all parcels) did not negatively affect native tree conservation in agroforests that farmers used for both subsistence and sale. This is consistent with findings elsewhere that agricultural intensification can be compatible with agrobiodiversity conservation when cash crops are grown in separate fields (Zimmerer 2013).

We examined the effects of indicators of adaptive capacity on ecological outcomes because agroforests are dominated by human actors, but we emphasize that these variables are likely linked through feedback loops. For example, farmers with more LEK may conserve more trees because they have more knowledge of their cultural and ecological values. But having more trees may also allow farmers to better retain, learn, and pass down LEK. Understanding the nature and strength of these feedback loops is an important next step. An SEM approach with time series data makes this possible (Grace 2006).

Although native tree richness is an important indicator of richness of other taxa in multiple types of agroforestry systems (e.g., Bos et al. 2007; Philpott et al. 2008; Quazi & Ticktin 2016), testing these relationships in the context of other Pacific Islands is a next step. For example, bats play a critical role as pollinators in the Pacific Islands, and 5 out of Fiji's 6 bat species are threatened (Scanlon et al. 2014*a*). The large overlap (96%) between forest tree species valued by bats and people in Fiji (Scanlon et al. 2014*b*) suggests that increasing native tree richness may also benefit bats and their pollination services.

Our results suggest that increasing livelihood diversity can increase social network centrality, LEK, and parcel size, all of which can contribute to biodiversity conservation. Programs that expand livelihood options while integrating economically valuable native species and aboriginal introductions (e.g., sandalwood among others) should be prioritized. One challenge not unique to Fiji is that administration of agroforestry spans multiple government units, including agriculture, horticulture, forestry, and culture. Increased cooperation is essential. Initiatives to teach LEK in the modern context (e.g., through hands-on activities in schools) must also be strengthened. The cultural renaissance across the Pacific Islands provides a timely opportunity to do so. Important precedents have been set in Hawaii and New Zealand from which much can be learned (Sterling et al. 2017).

After over a millennium of management, most Fiji coastal forests, like many across the globe, are in effect SES. Identifying the nature of the social–ecological linkages in these systems can inform new strategies to improve conservation outcomes. By joining forces with efforts to build community resilience, conservation agencies can develop additional and effective ways to conserve biodiversity in the region.

Acknowledgments

We thank the members of the 20 villages in which we worked who generously offered their time, knowledge, and insight, as well as K. Rosi Batibasaga, U. Wasa Vuli, M. Tuiwawa, A. Whistler, S. Jupiter, and the Wildlife Conservation Society Fiji. We also thank M. Reed and 3 anonymous reviewers for comments on a previous version of this manuscript. This study was approved by the University of Hawaii IRB (CHS-20991) and funded by NSF CNIC Award #OISE-1160830 and NSF Coastal SEES Award #SES-1325874, as well as NSF GRFP #1329626 to R.D. and Fulbright U.S. Student Research Fellowship to A.M.

Supporting Information

Local ecological knowledge interview questions (Appendix S1), the list of native tree species found in agroforest parcels (Appendix S2), a description of social and ecological variables measured (Appendix S3), and results of the SEM (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Supporting Information

Literature Cited

Anand MO, Krishnaswamy J, Kumar A, Bali A. 2010. Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: remnant forests matter. Biological Conservation **143:**2363–2374.

Ban N, Coomes OT. 2004. Home gardens in Amazonian Peru: diversity and exchange of planting material. Geographical Review **94:**348–367.

Barker GM, Price RJ, McGree S. 2006. Climate surfaces for Fiji. LandCare Research, Hamilton, New Zealand.

Bell J, Taylor M. 2015. Building climate-resilient food systems for Pacific Islands. Program Report: 2015-15. WorldFish, Penang, Malaysia.

Bergamini N, et al. 2014. Toolkit for the indicators of resilience in socio-ecological production landscapes and seascapes. Policy report. UN University Institute for the Advanced Study of Sustainability, Tokyo, Biodiversity International, Rome, Institute for Global Environmental Strategies, Japan, and the UN Development Programme, New York.

Berkes F. 2012. Sacred ecology: traditional ecological knowledge and resource management. 3rd edition. Routledge, New York.

Berkes F, Colding J, Folke C. 2008. Navigating social-ecological systems: building resilience for complexity and change. Cambridge University Press, New York.

Bhagwat SA, Willis KJ, Birks HJB, Whittaker RJ. 2008. Agroforestry: A refuge for tropical biodiversity? Trends in Ecology & Evolution **23:**261–267.

Borgatti SP, Everett MG, Johnson JC. 2013. Analyzing social networks. Sage, Thousand Oaks, California.

Bos MM, Steffan-Dewenter I, Tscharntke T. 2007. The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. Biodiversity and Conservation **16:**2429–2444.

Brandes U, Wagner D. 2004. Analysis and visualization of social networks. Pages 321–340 in Jünger M, Mutzel P, editors. Graph drawing software. Mathematics and visualization. Springer, Berlin.

Cabell JF, Oelofse M. 2012. An indicator framework for assessing agroecosystem resilience. Ecology and Society **17:1** https://doi.org/10.5751/ES-04666-170118.

Chazdon RL, et al. 2009. Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. Biotropica **41:**142–153.

Clough Y, et al. 2011. Combining high biodiversity with high yields in tropical agroforests. Proceedings of the National Academy of Sciences of the United States of America **108:**8311–8316.

Department of Forests, The Ministry of Fisheries and Forests for The Republic of Fiji, The Secretariat of Pacific Communities. 2010. The state of the world's forest genetic resources country report: Republic of Fiji. UN Food and Agriculture Organization, Rome.

Díaz-Reviriego I, González-Segura L, Fernández-Llamazares Á, Howard PL, Molina JL, Reyes-García V. 2016. Social organization influences the exchange and species richness of medicinal plants in Amazonian homegardens. Ecology and Society **21** https://doi.org/10.5751/ES-07944-210101.

FAO (Food and Agriculture Organization). 2010. Building resilience to climate change: root crop and fishery production. Pacific Food Security Toolkit. Food and Agriculture Organization, Rome.

Grace JB. 2006. Structural equation modeling and natural systems. Cambridge University Press, New York.

Hariyadi B, Ticktin T. 2012. From shifting cultivation to cinnamon agroforestry: changing agricultural practices among the serampas in the Kerinci Seblat National Park, Indonesia. Human Ecology **40:**315–325.

Harvey CA, González Villalobos JA. 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodiversity and Conservation **16:**2257–2292.

IUCN (International Union for Conservation of Nature). 2017. The IUCN Red List of threatened species. Version 2017-1. IUCN, Gland, Switzerland. Available from http://www.iucnredlist.org (accessed May 2017).

Jupiter S, Mangubhai S, Kingsford RT. 2014. Conservation of biodiversity in the Pacific Islands of Oceania: challenges and opportunities. Pacific Conservation Biology **20:**206–220.

Keener VW, Marra JJ, Finucane ML, Spooner D, Smith MH. 2012. Climate change and Pacific Islands: indicators and impacts. Report for the 2012 Pacific Islands Regional Climate Assessment (PIRCA). Island Press, Washington, D.C.

Keppel G, Morrison C, Watling D, Tuiwawa MV, Rounds IA. 2012. Conservation in tropical Pacific Island countries: why most current approaches are failing. Conservation Letters **5:**256–265.

Kremen C. 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Annals of the New York Academy of Sciences **1355:**52–76.

Laurance WF, et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biological Conservation **144:**56–67.

López-Angarita J, Moreno-Sánchez R, Maldonado JH, Sánchez JA. 2014. Evaluating linked social-ecological systems in marine protected areas. Conservation Letters **7:**241–252.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

McMillen H, Ticktin T, Springer HK. 2016. The future is behind us: traditional ecological knowledge and resilience over time on Hawai'i Island. Regional Environmental Change **17:**579–592.

McMillen HL, et al. 2014. Small islands, valuable insights: systems of customary resource use and resilience to climate change in the Pacific. Ecology and Society **19:**44.

Merlin MD, Raynor W. 2005. Kava cultivation, native species conservation, and integrated watershed resource management on Pohnpei Island. Pacific Science **59:**241–260.

Mijatović D, Van Oudenhoven F, Eyzaguirre P, Hodgkin T. 2013. The role of agricultural biodiversity in strengthening resilience to climate change: towards an analytical framework. International Journal of Agricultural Sustainability **11:**95–107.

Nguyen Q, Hoang MH, Öborn I, van Noordwijk M. 2013. Multipurpose agroforestry as a climate change resiliency option for farmers: an example of local adaptation in Vietnam. Climatic Change **117:**241–257.

Perfecto I, Vandermeer J. 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. Proceedings of the National Academy of Sciences of the United States of America **107:**5786–5791.

Philpott SM, et al. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. Conservation Biology **22:**1093–1105.

Pimm SL, Raven P. 2000. Biodiversity: extinction by numbers. Nature **403:**843–845.

Quazi SA, Ticktin T. 2016. Understanding drivers of forest diversity and structure in managed landscapes: secondary forests, plantations, and agroforests in Bangladesh. Forest Ecology and Management **366:**118–134.

Reyes-García V, Guèze M, Díaz-Reviriego I, Duda R, Fernández-Llamazares Á, Gallois S, Napitupulu L, Orta-Martínez M, Pyhälä A. 2016. The adaptive nature of culture: a cross-cultural analysis of the returns of local environmental knowledge in three indigenous societies. Current Anthropology **57:**761–784.

Rissman AR, Gillon S. 2017. Where are ecology and biodiversity in social–ecological systems research? A review of research methods and applied recommendations. Conservation Letters **10:**86–93.

Rosseel Y. 2012. lavaan: an R package for structural equation modeling. Journal of Statistical Software **48:**1–36.

Scales BR, Marsden SJ. 2008. Biodiversity in small-scale tropical agroforests: a review of species richness and abundance shifts and the factors influencing them. Environmental Conservation **35:**160–172.

Scanlon AT, Petit S, Bottroff G. 2014*a*. The conservation status of bats in Fiji. Oryx **48:**451-459.

Scanlon AT, Petit S, Tuiwawa M, Naikatini A. 2014*b*. High similarity between a bat-serviced plant assemblage and that used by humans. Biological Conservation **174:**111-119.

Sterling E, et al. 2017. Culturally grounded indicators of resilience in social-ecological systems. Environment and Society: Advances in Research **8:**63–95.

Thaman R. 2014. Agrodeforestation and the loss of agrobiodiversity in the Pacific Islands: a call for conservation. Pacific Conservation Biology **20:**180–192.

Thaman RR. 2008. Pacific Island agrobiodiversity and ethnobiodiversity: a foundation for sustainable Pacific Island life. Biodiversity **9:**102–110.

Thaman RR, Clarke WC. 1993. Agroforestry in the Pacific Islands: systems for sustainability. Pages 191–215 in Clarke WC, Thaman RR, editors. Agroforestry in the Pacific Islands: systems for sustainability. UN University Press, Tokyo.

Ticktin T, Nantel P, Ramirez F, Johns T. 2002. Effects of variation on harvest limits for nontimber forest species in Mexico. Conservation Biology **16:**691–705.

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. Science **292:**281–284.

Tscharntke T, Clough Y, Wanger TC, Jackson L, Motzke I, Perfecto I, Vandermeer J, Whitbread A. 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation **151:**53–59.

Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi NS, Hoehn P, Tylianakis JM. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology **89:**944–951.

Valencia V, Naeem S, García-Barrios L, West P, Sterling EJ. 2016. Conservation of tree species of late succession and conservation concern in coffee agroforestry systems. Agriculture, Ecosystems and Environment **219:**32–41.

Watling D. 2013. Fiji: state of birds. Nature Fiji-MareqetiViti, Suva, Fiji.

Wright JH, Hill NAO, Roe D, Rowcliffe JM, Kümpel NF, Day M, Booker F, Milner-Gulland EJ. 2016. Reframing the concept of alternative livelihoods. Conservation Biology **30:**7–13.

Zent S, Maffi L. 2009. Final report on indicator no. 2: methodology for developing a vitality index of traditional environmental knowledge (VITEK) for the project "Global Indicators of the Status and Trends of Linguistic Diversity and Traditional Knowledge." Terralingua, Canada.

Zimmerer KS. 2013. The compatibility of agricultural intensification in a global hotspot of smallholder agrobiodiversity (Bolivia). Proceedings of the National Academy of Sciences of the United States of America **110:**2769–2774.

Zimmerer KS. 2014. Conserving agrobiodiversity amid global change, migration, and nontraditional livelihood networks: the dynamic uses of cultural landscape knowledge. Ecology and Society **19:** https://doi.org/10.5751/ES-06316-190201.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects modelling for nested data. Pages 101–142 in Mixed effects models and extensions in ecology with R. Springer, New York.