Farmer perception and utilization of leaf functional traits in managing agroecosystems

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Abstract

1. Using knowledge of leaf functional traits, such as those forming the Leaf Economics Spectrum (LES), to understand plant responses to environmental change is well established and now being more widely applied to agroecosystems. Yet, little is known about how farm managers invoke leaf functional traits to inform management decisions.

2. The objectives of this research were to i) evaluate if farmers use knowledge of intraspecific trait variation (ITV) in LES traits (or trait proxies) of target crops as response indicators of management conditions; ii) determine if LES trait values are ranked consistently among multiple farmers along a "Farmer Leaf Economics Spectrum" (FES); iii) evaluate how a FES corresponds to the LES; and iv) identify the farmer- and farm attributes that best predict the agreement between the FES and the LES.

3. We collaborated with coffee (*Coffea arabica*) farmers in the Turrialba Valley, Costa Rica. We used a visual elicitation tool of fresh leaves along an intraspecific spectrum of leaf size, leaf thickness, and leaf colour (as a proxy for leaf nutrients); respondents were asked to rank leaves in response to shade and nutrient scenarios as well as yield potential. On-farm biophysical data, management practices, and socio-economic attributes were also collected.

4. The majority of farmers demonstrated a developed system of utilizing coffee leaf- and whole-plant ITV as indicators of management practices. Farmers managing smaller farms tended to more commonly acknowledge ITV in LES chemical-morphological traits, as compared to those managing large farms. The agreement between a respondent-identified ranking of leaf thickness ITV as a function of light environment, and an empirically-defined thickness-to-light ranking, was partially explained by farmers' physical engagement with plants.

5. *Synthesis and implications*. In scientific literature, analyses of crop intraspecific trait variation have provided important insights into the mechanistic bases of multiple key

agroecological processes. We demonstrate that farmers use crop leaf variation as an indicator to both evaluate management prescriptions, and to initiate management actions including shade-tree species selection and abundance, crop- and shade-tree pruning regimes, and fertilization treatments. These findings signify that functional traits represent a key nexus between scientific and local knowledge.

Introduction

Plant functional traits in agroecosystems

Diversified agroecosystems are increasingly being recognized as an environmentally and economically sustainable alternative to biologically simplified conventional agricultural systems (Tscharntke *et al*. 2005; Tomich *et al*. 2011). Commonly, greater diversity in agroecosystems stimulates nutrient capture and cycling processes leading to a reduced reliance on fertilizers (Drinkwater & Snapp 2007; Isaac & Kimaro 2011), while simultaneously enhancing the provisioning of other ecosystem services such as carbon (C) sequestration, improved hydrological cycling, or enhanced maintenance of biodiversity across multiple trophic levels (Jose 2009). In agroecological research and management, on-farm diversity has traditionally been described based on taxonomy (i.e. number of crop species or varieties) or the range of plant functional types (e.g. number of annuals vs. perennials; herbaceous vs. woody crops; N_2-fixing legumes vs. non-N_2-fixing species). However, in diverse agroecosystems, theory and observations suggest that describing agricultural diversity based on plant functional trait variation is likely to offer mechanistic insights into agroecological processes, including (but not limited to) plant responses to environmental change, determinants of soil nutrient cycles, and rates of species interactions such as pollination (Garnier & Navas 2012; Martin & Isaac 2015; Wood *et al*. 2015).

There has been considerable work identifying the morphological, physiological, and phenological traits of plants (and crops) that drive differences in plant performance across environmental gradients (e.g. Violle *et al*. 2007). Leaf functional traits in particular have been shown to be critical predictors of aboveground biomass (e.g. Diaz *et al*. 2007), litter decomposition (e.g. Santiago 2007), and ultimately yield (Gagliardi *et al*. 2015); as a result, certain leaf traits are included, in some form, into most regional or global assessments of agroecosystem structure and function (e.g. Box 7-1 in Porter *et al*. 2014).

In the functional ecology literature, the concept of a global functional leaf trait spectrum – a continuum that describes universal patterns of leaf morphological, physiological, and chemical trait co-variation among all plants worldwide – was arguably most widely popularized by publication of the "Leaf Economics Spectrum" (LES)

(Wright *et al*. 2004). The LES describes co-variation between certain leaf functional traits (namely, leaf mass per area (LMA), leaf nitrogen (N) and phosphorus (P) concentrations, maximum photosynthetic capacity, leaf respiration, and leaf lifespan) that occurs along a single axis, or spectrum, which in turn describes trade-offs among resource acquiring traits and resource conservation traits (Westoby *et al*. 2002; Wright *et al*. 2004; Chave *et al*. 2009; Reich 2014; Diaz *et al*. 2016). While foundational papers on the LES and other trait spectra (e.g. stems, roots, and whole-plant functional traits) have been based on trait comparisons across hundreds of species (e.g. Wright *et al*. 2004), recent work has shown that certain spectra also describe patterns of intraspecific trait variation (ITV) among plants within a species (e.g. Hajek, Hertel & Leuschner 2013; Gagliardi *et al.*, 2015; Niinemets, 2015; Isaac *et al*. 2017). For example, recent studies on ITV in coffee (*Coffea arabica*) – the focus of our study here – suggest that the LES also describes functional variation in crops of the same variety (Martin *et al*. 2017).

Plant functional traits in action

Functional trait-based approaches have not been widely applied to crops and agroecosystems. This is despite the fact that trait-based research, particularly research that focuses on ITV in crops, could make significant contributions to understanding the effects of management and changes in the farm environment on productivity and general plant performance (Martin & Isaac, 2015). Certain traits do factor heavily into applied research on plant breeding, which largely focuses on how long-term trends in crop domestication are due to selection for suites of "domestication traits", including yield, nutritional quality, harvest factors (such as shattering in grains), or propagation (Doebley, Brandon & Smith 2006; Meyer, DuVal & Jensen 2012). However, farmers are also known to both evaluate the impacts of management and make management decisions based on other observable and tactile traits, such as leaf colour, size, and thickness, or phenology (Gibson *et al*. 2008; Mwanga *et al*. 2011) that are not necessarily part of a domestication syndrome. For example, in coffee agroforestry systems in Central America, farmers commonly select shade trees through an understanding of traits such as leaf texture and size, foliage density, and rooting patterns (Cerdán *et al*. 2012), while in cocoa agroforestry systems in West Africa, farmers select shade trees based on observable leaf traits that are critical for ecosystem processes including organic matter accumulation

(Isaac, Dawoe & Sieciechowicz 2009). Similarly, in rice production systems, studies have found that farmers select varieties based on traits associated with plant phenology, which has greater implications for the timing of harvests in response to market prices, as opposed to strictly yield maximization (Dalton 2004).

Research further suggests that the degree to which farmers make decisions based on functional traits that are not strictly related to yield, is contingent on management practices. For example, Isaacs *et al*. (2016) showed that farmers placed plant architectural traits as the second most important factor in breeding programs, just below yield potential; the authors also showed that the use of plant traits in crop selection other than yield alone, was of two-fold-greater importance for farmers managing diverse intercropping systems as compared to those managing monocultures. There is reason to expect farmers who manage for greater on-farm diversity, are also likely to manage for multiple simultaneous agroecosystem functions such as C storage and nutrient cycling; ecosystem functions that require the selection and management of plant characteristics beyond just yield.

Plant functional traits in perception

Despite a large and growing number of independent analyses on i) ITV in the ecological literature, and ii) local knowledge of functional traits for agricultural management and decision-making, there are few studies to date that have integrated these two fields (Martin & Isaac 2015, Wood *et al*. 2015). Applied understandings of functional traits may not be precisely analogous to the ecological literature, but farmers may employ knowledge of certain plant characteristics that approximate the traits commonly evaluated in ecological literature such as the LES. For example, from a strict empirical perspective, leaf N concentration determinations demand some type of elemental analysis (Pérez-Harguindeguy *et al*. 2013), but farmers may make decisions based on this trait as approximated by leaf colour (Friedman, Hunt Jr. & Mutters 2016). Similarly, there is evidence that farmers evaluate plant response based on leaf texture, or how “soft” or “hard” a leaf feels to the touch (Cerdán *et al*. 2012). While texture may not be a correlate of the LES *per se,* from a functional perspective it may approximate LMA or other ecologically important measures of leaf morphology such as thickness (Niinemets 2001) or toughness (Westbrook *et al*. 2011). There is therefore reason to expect that certain traits ecologists have focused on when exploring plant community structure and function – namely LES traits – also factor prominently into the development and deployment of local knowledge surrounding farm management decision making (Clinquart 2010; Humphries *et al*. 2015; Isaacs *et al*. 2016).

To address this expectation, we collaborated with coffee farmers in the Turrialba Valley, Costa Rica. Our research objectives were to i) evaluate if farmers use target crop intraspecific trait variation (ITV) in LES traits (or trait proxies) as response indicators of management conditions; ii) determine if LES traits are ranked consistently among multiple farmers along a "Farmer leaf Economics Spectrum" (FES); iii) evaluate how a FES corresponds to the LES; and iv) identify the farmer and farm attributes that best predict the agreement between the FES and the LES. We hypothesize that ITV in coffee leaf traits are perceived and utilized by farmers as response indicators of management decisions in coffee agroecosystems. We also expect that the agreement on leaf trait expression under various light and nutrient environments between a FES and LES, is explained by key management-related characteristics including the size of the farm, the level of on-farm biodiversity, the degree of input intensification, and the degree to which farmers report touching leaves of coffee plants.

We wish to emphasize that our study is not designed as a verification or test of the "accuracy" of local knowledge, but rather to investigate an interchange between i) established general ecological theory, and ii) the highly nuanced and lived local knowledge. While these two bodies of knowledge vary both spatially and temporally (Brook & McLachlan 2005), and impressing scientific boundaries on this exchange creates inherent power dynamics, we impose the leaf as the unit of analysis within this study, with the full recognition that we are confining our analysis based on the establish LES. In doing so, it is our explicit intention to locate complementarity among knowledge systems (Altieri 2004; Richards 1985) in order to inform our understanding of agroecosystem management and function.

Materials and Methods

Study region

This study was conducted in the Cantón Turrialba, Cartago Province of Costa Rica (9.7960° N, 83.5497° W). Within this region, coffee is produced at both low and high altitudes (range 690-1100 m a.s.l.) and across a range of management practices from monocultures, to highly diverse shade coffee agroforestry systems. Long-term consequences of on-farm nutrient depletion and unpredictable rainfall patterns are also prevalent in the region (Cerdán *et al*. 2012), and farmers in the region are currently contending with the devastating effects of coffee leaf rust caused by the fungus (*Hemileia vastatrix*): a widespread leaf fungal epidemic throughout Central and South America that has occurred within the last decade (Avelino *et al*. 2015). Amid low soil fertility and constraints to, or undesirability of, fertilizer use, farmers have developed techniques to promote soil and crop nutrition, primarily through the maintenance of shade tree intercropping and predominantly with the commonly occurring shade tree *Erythrina poeppigiana* (Fabaceae).

The effects of shade trees on coffee have been fairly well described with respect to bulk soil nutrient pools and aboveground coffee growth, yield, and physiology (Beer *et al*. 1998; DaMatta, 2004; Harmand *et al*. 2007; Frank & Vaast 2009; Munroe *et al*. 2015). In the region, shade trees moderate adverse microclimatic conditions, stabilize year-to-year coffee yields, boost yields under poor edaphic and climatic conditions, extend coffee plant longevity, and improve nutrient availability for coffee plants, particularly in low or moderate fertilizer systems (Beer *et al*.1998; Harmand *et al*. 2007; Haggar *et al*. 2011; Gagliardi *et al*. 2015). The incorporation of dinitrogen (N_2)- fixing shade trees in the region results in significant inputs of N (246-340 kg N ha^{-1} $year^{-1}$ (Haggar *et al*. 2011; Beer *et al*. 1998)) with additional contributions from pruned shade tree litter (Munroe & Isaac 2014). Ultimately though, coffee farms in the region are variable in shade tree density and composition.

Respondent and biophysical attributes

To identify farmer participants, we worked with the farmer network of the "Ecosystem-based Adaptation for Smallholder Subsistence and Coffee Farming Communities in Central America" (CASCADE) project, led by Conservation International and the Tropical Agricultural Research and Higher Education Center (CATIE) (Cerda *et al*. 2017). Specifically, our study identified 25 randomly selected participants from the broader CASCADE group of farmers. Potential respondents in this region were selected randomly at two levels, for the original CASCADE project, and from the CASCADE network for our case. The 25 respondents in this study received no substantial or exclusive training in comparison to other famers in the region of study, though the general proximity to CATIE may enhance the agricultural knowledge base of these farmers in comparison to other regions of Costa Rica. This research received ethics approval from the Social Sciences, Humanities and Education Research Ethics Board, University of Toronto for research involving human participants. Informed consent was secured in advance of every interview.

At each farm semi-structured interviews were conducted. We collected data from each respondent on the number of years farming (Y), the age of coffee (A), the number of coffee varieties planted (V), and level of inputs, which included both "fertilizers" (applications per year; F) and "total practices" (the sum of all practices including F, as well as pesticide inputs, herbicide inputs, weeding and pruning of coffee and shade trees; P). We also operationalized an "engagement with leaves" (E) variable, coded as a binary response to whether or not respondents reported touching coffee leaves on their farms, when inspecting the farm and making management decisions and prescriptions. Field surveys of each coffee farm were also conducted to collect data on farm size (L; ha), coffee planting density (D; plants ha^{-1}), and shade tree composition which were converted into two diversity indices; Shannon Index (H) and Simpson Index (D) as well as a categorical shade class (S) which entailed classes categorized into i) full sun (no shade trees) ii) coffee intercropped only with *Erythrina poeppigiana*, or iii) coffee intercropped with diverse shade trees (up to seven species per farm). Of these continuous variables H, D, P, A, and D met assumptions of normality (Shapiro-Wilk test p-value > 0.05), Y was marginally non-normal and not transformed prior to analysis (Shapiro-Wilk $p = 0.04$), F could not be transformed to meet normality but did visually approximate a normal distribution and was not transformed (Shapiro-Wilk test $p = 0.01$), while L and V were log-transformed prior to analysis to improve normality (Shapiro-Wilk test $p = 0.4$ and 0.02, respectively on log-transformed data).

Semi-structured interviews: setting the leaf spectra

Following completion of questions on farming characteristics and practices, we used a visual elicitation tool based on empirically framed researcher-created visual data (Prosser & Loxley 2008). The visual elicitation tool, or the "leaf book", was based on a collection of fresh *C. arabica* leaves displaying a range of ITV (Fig. 1). We used four leaf spectra that closely link with ecological studies on the importance of leaf traits, including: 1) coffee leaf size, 2) coffee leaf thickness, 3) a coffee leaf colour trait (as an approximation of leaf nutrition), and 4) multiple coffee leaf traits in relation to yield potential. We used *C. arabica* var. Caturra, as it is the most dominant variety of coffee in Central America (McCook & Vandermeer 2015). For each interview day, a new leaf book was made (based on data described below), to ensure that all respondents in the study were presented with directly comparable leaves. Leaves in the leaf book were not adjusted to individual farms, in order to maintain comparability of responses across all respondents.

In order to bound an appropriate coffee leaf size spectrum, our leaf size values were based on a collection of 216 fully expanded coffee leaves at the same location in the coffee canopy (i.e. two-thirds the height of the plant) under monoculture and shade treatments, in order to collect maximum ITV of leaf size within the study region. We measured leaf area (cm^2) using digital photos analyzed with Image J software (Abramoff, Magalhaes & Ram 2004). Our leaf area ranged 4-fold from 14.6 to 64.7 cm^2, with a mean of 39.0 cm^2. We selected six leaves covering this range (minimum and maximum values as well as the 20th, 40th, 60th and 80th percentiles) in leaf area, which were in turn associated with decreasing light availability from full sun monoculture to high shade agroforestry. This is supported by Gagliardi *et al.* (2015) in a study from the same species, where the authors report a ~4 fold increase in coffee leaf area under shade canopies versus leaf area under full sun monoculture.

The leaf thickness spectrum was based on the same 216 leaves. A low-force micrometer (No. 227-101, Mitutoyo Co., Japan) was used to measure leaf thickness across a given leaf while avoiding major veins. Leaf thickness ranged from 0.23-0.33 mm, which corresponded to light environments ranging from high shade agroforestry to full sun monoculture. We selected six leaves covering the minimum and maximum values as well as 20th, 40th, 60th and 80th percentiles in leaf thickness in order to capture the full potential range of leaf thickness associated with increasing light availability. Both Morais *et al.* (2004) and Fahl *et al.* (1994) report such an increase in coffee leaf thickness under sun versus under shade (due to increase size of palisade and spongy parenchyma tissue under sun conditions). Similarly, Martins *et al.* (2014) report an increase of 15% in thickness of coffee leaves under sun versus under shade.

Coffee leaf colour was not based on the collection of 216 leaves, but was rather determined by locally developed colour patterns which were based on an established coffee nutrient deficiency chart for N (published by the Instituto del Cafe de Costa Rica), as well as for P and zinc (Zn), two other common deficiencies in coffee plantations. We displayed a spectrum of leaves ranging from deficient to sufficient status. We selected five leaves ranging from green to yellowing veins (indicative of N deficiency), or exhibiting red coloration (indicative of P deficiency) or inter-vein fading (indicative of Zn deficiency).

The leaf-based yield potential spectrum was based on multiple studies. Gagliardi *et al.* (2015) showed that multivariate suites of leaf traits were significantly related to plant-level reproductive output, but in general along the LES, coffee plants associated with higher LMA were associated with greater reproductive output as compared to those with low LMA. Therefore, our high leaf-based yield potential end of the spectrum depicted mid-range to larger green leaves with average thickness. DaMatta (2004) showed that smaller leaf area, particularly under drought, corresponds to lower yield due to modified C partitioning to plant tissue in pot-grown *C. arabica*. Therefore, the lower end of the leaf spectrum associated with leaf-based yield potential was populated with smaller leaves exhibiting yellowing in their venation.

Semi-structured interviews: respondent rankings

We asked a set of questions with regards to ranking the importance of leaf and plant characteristics for farm decision-making. Specifically, respondents were asked to rank a suite of coffee leaf traits (i.e. leaf size, colour, and thickness) and a suite of whole-plant traits (i.e. coffee plant height, sprout diameter, and crown radius), in order of importance for making decision on plant and farm management.

Following a pre-tested semi-structured interview guide, respondents were also asked to rank leaves in relation to a specific environmental scenario. For leaf size, we described various light environments (a six-point qualitative gradient ranging from “high shade” to “no shade”) and respondents were asked to rank leaves in relation to shade growing conditions. Similarly for leaf thickness, we operationalized light environments (high shade to no shade gradient) and respondents were asked to rank the six leaves in the leaf thickness spectrum that correspond to high shade growing conditions to low shade growing conditions. For leaf nutrients, we operationalized soil fertility (a five-point qualitative gradient ranging from “high soil fertility” to “low soil fertility”) and respondents were asked to rank the five leaves in the leaf nutrient spectrum that correspond to sufficient to deficient conditions. For yield potential, respondents were asked to rank the six leaves in the leaf-based yield potential spectrum that correspond to a six-point qualitative gradient ranging from “high yielding” to “low yielding” plants. These scenarios were used to delimit the spectra in order to achieve a ranking from respondents and therefore, define a FES. Following this ranking, questions and prompts were used to gather information on reasons for the selection.

Statistical Analysis

We use the concept of “agreement” in order to evaluate the agreement between respondent-identified leaf rankings and empirical leaf rankings. For the size, thickness and nutrient leaf spectra, we used a cumulative proportion agreement where the proportion of agreement between i) the empirically-defined leaf trait values and ii) the respondent-identified leaf rank in response to described environmental scenarios per respondent, were recorded. For yield potential, we conducted a Spearman rank correlation between i) empirically-supported rankings of leaves to yield potential, and ii) respondent-identified ranking of leaves to yield potential. All response data was normally distributed.

We then used a backwards-stepwise linear modelling procedure to identify the strongest farmer- and farm-level variables predictors of the agreement between the respondent rank and the established rank. For this analysis, the full model was of the form:

$$\rho_{\mathrm{i}} = \beta_0 + \beta_1 \log \mathrm{L}_{\mathrm{i}} + \beta_2 \mathrm{A}_{\mathrm{i}} + \beta_3 \mathrm{D}_{\mathrm{i}} + \beta_4 \mathrm{Y}_{\mathrm{i}} + \beta_5 \log \mathrm{V}_{\mathrm{i}} + \beta_6 \mathrm{E}_{\mathrm{i}} + \beta_7 \mathrm{F}_{\mathrm{i}} + \beta_8 \mathrm{P}_{\mathrm{i}} + \beta_9 H_{\mathrm{i}} + \beta_{10} D_{\mathrm{i}} + \beta_{11} \mathrm{S}_{\mathrm{i}}$$

(Equation 1)

where ρ_{i} represents the agreement between how the i^{th} respondent ranked leaves, and the empirical rankings of leaf traits based on empirical analysis (quantified as either a Spearman rank correlation coefficient (for the yield potential spectrum) or a proportion of agreement (for size, thickness, and colour spectra)), β_0 represents an overall model intercept, and β_1 through β_{11} represent the parameter estimates for L, A, D, Y, V, E, F, P, H, D and S, respectively, all of which were measured on the i^{th} farm. Collinearity among all pair-wise sets of predictor variables was initially assessed with correlation analysis; of the 55 possible pairwise relationships only six were statistically significant (Spearman rank correlation $p \leq 0.05$; Table S1) so all variables were included in our full model. Models were then compared using Akaike's Information Criteria (AIC), with the lowest AIC score indicating the most parsimonious model fit. Significance of predictor variables in each AIC-selected model was then assessed using multiple regression.

We then used a principal component analysis (PCA) the 'vegan' R package (Oksanen *et al*., 2013), to evaluate responses in multivariate space. Specifically, for each respondent, there were four different values of agreement (i.e. ρ_i in Equation 1), which were evaluated in multivariate space. We then used a one-tailed *t*-test to determine if PCA axis one scores differed significantly across farms of different sizes (i.e. between small (< 1 ha) vs. large (≥ 1 ha) farms). All statistical analyses were performed using R v. 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Respondent attributes

The majority of respondents maintained on average 2.8 (± 2.1 s.d.) coffee varieties, on farms ranging in size from very small farms (0.1 ha) to moderate sized farms (4 ha) (Table 1). On-farm shade tree communities were composed primarily of *E. poeppigiana*, and tended toward higher diversity rather than monocultures (Table 1). Respondents experience with farming ranged from a low of 4 years, to a maximum of 86 years (Table 1). Over half of respondents (60%) reported evaluating leaf traits as a regular process during farm inspection (Table 1).

Important leaf- and plant traits

Respondents indicated that the most important leaf- and whole-plant traits when prescribing management practices were the leaf colour and the coffee canopy radius, respectively (Table 2). Surprisingly, plant height was less important than plant canopy radius in decision-making, and sprout diameter was considered the least important trait to farmers when making management decisions (Table 2).

Certain traits ranked consistently among multiple farmers along an FES (Table 3). Well over half of respondents (64%) ranked the largest leaf in the leaf size spectrum as corresponding to a low light/ high shade environment, while 56% of respondents agreed that the smallest leaf in the size spectrum corresponded to a high light/ no shade environment (Table 3). The thickest leaf was identified by 68% of respondents as associating with a low light/ high shade environment. In terms of leaf nutrition traits, 80% of respondents identified a large green leaf as an indication of sufficient nutrient supply, while 68% identified small yellow leaves as belonging to nutrient deficient conditions (Table 3). Over 60% of respondents agreed that the largest green leaf in the spectrum was associated with the highest yield potential (Table 3).

Selecting leaf traits based on management scenarios

Leaf size

The AIC-selected model that best predicted the agreement between i) the empirically-defined leaf trait values and ii) the respondent-identified leaf rank in response to described leaf size-light environment relationships, included only farm size (L) (r^2 = 0.146; Table 4). With a negative coefficient, this indicates that farmers managing larger farms tend to have a lower agreement between the ranks of leaf size-light environment relationships (Table 4).

Leaf thickness

The agreement between i) the empirically-defined leaf trait values and ii) the respondent-identified leaf rank in response to described leaf thickness-light environment relationships, was most parsimoniously predicted as a function of eight variables: the age of coffee plants (A), the coffee density (D), the number of coffee varieties (V), whether a respondent was physically engaged with the coffee leaves (E), the level of fertilizer use (F), both shade tree diversity indices (H and D) as well as shade tree class (r^2 = 0.213; Table 4). Whether or not a respondent physically touched leaves when inspecting plants had a significantly positive effect on the likelihood of agreement between the ranks of leaf thickness-light environment relationships (Table 4). Similarly, respondents with older coffee plants and higher shade tree diversity tended to have a more positive likelihood of agreement between the ranks, as compared to farmers with younger plants.

In contrast, higher reported fertilizer use was associated with lower agreement between the respondent-identified and empirically-defined ranks (Table 4).

Leaf colour

Farmer and farm-level attributes that best predict the agreement between a respondent-identified and empirical-defined rank of leaf colour to soil nutrient status, were farm size (L) and the sum of all practices (P), based on the most parsimonious AIC selected model ($r^2 = 0.170$; Table 4). Farm size (L) was significantly negatively associated with the agreement between ranks, such that the smaller the farm, the higher likelihood a farmer will match observed leaf nutrition requirements to documented leaf nutritional deficiencies. The number of practices was positively related to the proportion of agreement between the ranks (Table 4).

Yield potential

The correlation between a respondent-identified ranking of leaves in relation to yield potential, and an established ranking of leaves based on empirically assessed relationships between leaf traits and yield, was most parsimoniously predicted by the number of varieties (V), the number of years farming (Y), the sum of practices (P) and the shade class ($r^2 = 0.263$; Table 4). There was a significantly negative association between overall number of practices and the agreement of the two rankings; the less practices a farmer reported using, the stronger the correlation (Table 4).

Effects of farm size

The first two PCA axes explained 79.3% of the variation in the four response variables (Fig. 2). PCA axis 1 explained the majority of this variation (46.5%), while PCA axis 2 explained a further 32.8% of the variation in the four response variables. PCA axis 1 scores were significantly related to three of four responses including the agreement between farmer rankings and empirical rankings of i) leaf area, ii) leaf thickness, and iii) leaf colour ($r^2 = 0.80$, 0.59, and 0.41, respectively, and $p < 0.001$ in all cases, as per linear regression analyses performed between these variables and PCA axis 1 scores). PCA axis 2 was significantly related to the agreement between farmers and empirical rankings of yield potential ($r^2 = 0.80$, $p < 0.001$; Fig. 2). PCA 1 axis scores differed significantly across small and large farms (one-tailed $t = 1.92$, $p = 0.035$), indicating that respondents with smaller farms generally showed higher agreement between their ranking of leaves and the empirical ranking of leaves (Fig. 2).

Discussion

The breadth and depth of farmer knowledge on ITV

There is increasing interest in using plant functional traits to better understand the causes and consequences of environmental change on plants in agroecosystems (Garnier & Navas 2012; Martin & Isaac 2015; Wood *et al*. 2015). We contribute to this growing literature with an examination of farmer use of plant traits, namely, the use of ITV in LES traits for on-farm evaluation and decision-making. While farmer selection of shade trees traits in coffee agroforestry systems is well documented (Cerdán *et al*. 2012; Valencia *et al*. 2015), we show that leaf ITV in coffee is also recognized by farmers, and employed in farm management. In our study, the majority of farmers demonstrated a developed system of utilizing coffee leaf and whole-plant ITV as response indicators of management practices.

To be relevant for management, LES traits or their proxies must be visible and distinguishable by a manager, insofar as they are physical, mutable and tractable. The “soft” traits that comprise part of the LES (cf. Wright *et al*. 2010), namely LMA and (arguably) leaf N, are not immediately analogous with those visible traits described as important by farmers, but LMA does represent certain proxies of observable leaf traits such as leaf size and thickness trade-offs. However, leaf colour was identified as the most important leaf ITV characteristic used as an indicator of crop response to environmental and management conditions (Table 2). This is not unexpected as farmers typically use leaf colour to identify both systemic issues (e.g. nutrient deficiencies) and localized issues (e.g. disease).

Agreement between the LES and the FES

The range of agreement between the LES and the FES (Table 3) highlights the discrete nature of the perception and use of leaf traits in farm management. Our predictive models provide evidence that differences among farmers in how they evaluate leaf traits in response to environmental and management conditions, is at least partially explained by systematic differences in farmer- and farm attributes (Table 4). Though the size of the farm, the sum of practices, and the number of coffee varieties appear as significant predictors in several predictive models, no one farmer- or farm attribute was consistently retained in all AIC-selected models across all traits (Table 4).

Given the established axis of resource acquisition to resource conservation hypothesized by the LES, leaf traits that are observable by farmers may be used to diagnose the relationship with agroecological processes. While a farmer-defined FES was evident, for instance relatively larger leaves were widely associated with a high shade environment (Table 3), our study demonstrates that an understanding of how plants respond to environmental conditions in scientific literature does not necessarily correspond to how farmers or managers interpret ITV or plant ecological strategies. For instance, respondents associated thick leaves with high shade environments (Table 3). However, peer-reviewed studies suggest coffee leaf thickness decreases with increasing shade due to increase size of palisade and spongy parenchyma tissue under sun conditions (Martins *et al*. 2014; Fahl *et al*. 1994). Therefore, though 68% of respondents allocated thick leaves to shade conditions, thus defining an FES for leaf thickness, it is not in accordance with empirically derived relationships between leaf thickness and light availability in, specifically, coffee (Martins *et al*. 2014).

The size of farm appears as significant in multiple models and was consistently associated with the agreement between the rankings: respondents with smaller farms (<1 ha) showed higher coordination between the LES and their FES, as compared to respondents on larger farms (≥ 1ha) (Table 4; Fig. 2). Notably, this PCA axis 1 was significantly related to three of the four response variables and was linked with farm size (Fig. 2). Whether this is a function of i) experience – those with smaller farms have more opportunity to engage with coffee plants, – or ii) labour – those with larger farms are more likely to hire labour, or are burdened with administrative management, and therefore reduce their engagement with coffee plants (Laffourcade 2012; Hugøy 2016) – demands further exploration. In most cases, when farmers are less engaged on larger farms, standardized management protocols were used. Specifically, the agriculture ministry in the Turrialba region deploys messages that recommend broadly applicable spraying and fertilizing schedules.

As expected, physical engagement with coffee plants was retained as a predictor in terms of how farmers ranked leaf thickness in relation to light environment (Table 4).

Unlike leaf size, which is visually observable, leaf thickness requires a physical engagement with the plant. However, despite potential benefits of doing so, not all farmers reported physically engaging with plants to assess leaf attributes. Farmers who report touching their leaves during farm inspection also tended to rank leaf thickness in agreement with the empirically-defined rank for coffee leaf thickness. This finding supports Ingold's (1992) assertion that knowledge production of the environment is formed through action. Farmer perception of leaf traits is presumably formed through action, seeing, or being engaged in the experience with plants, as described by Ingold (1992), Okely (2001), and Hugøy (2016). Farmers have clear and coherent ways of understanding the diversity, services, and yield potential on their coffee farms (Cerdán *et al*. 2012). Based on our results here, this knowledge is at least partly derived from a physical engagement with the plant.

The role of plant characteristics in management actions

We make the case here that farmers use crop ITV in leaves as "response traits" that are indicators of how the coffee plant is responding to the agroecological environment. The accumulation of farm management (here represented as fertilizers inputs, pesticide and herbicide application, weeding, and pruning of coffee and shade trees) synchronizes farmers along an axis of agricultural intensification. This characteristic is a significant negative predictor of the correlation of leaf ranking for yield potential (Table 4); in other words, farmers with less intensified farms matched the LES and the FES for yield potential, as compared to those with more intensified farms. Such low input agricultural systems are repeatedly linked with higher diversity (Tscharntke *et al*. 2005), given that species interactions often replace external inputs. For instance, in our study region, Cerda *et al.* (2017) found that diversified coffee agroforestry systems maintain higher soil potassium content than either simple coffee agroforestry systems (e.g. one shade tree species only) and coffee monocultures, and some of these shade trees are leguminous species, contributing to soil fertility. Here, we show that farmers in this region with such highly diverse farms use a well-structured system of leaf ITV as a response indicator to management.

Employing ITV as indicators of management may result in action. For instance, in the shade tree stratum, farmers typically reduce shade cover via pruning of shade trees, at the beginning of coffee flowering and at the beginning of harvest; however, farmers also reduce shade when coffee plants exhibit signs of small leaves or otherwise stunted growth. Consequently, under heterogeneous light environments, coffee leaf ITV is recognized as changes in leaf size and is used to assess shade tree success in the provisioning of optimal conditions for yield. In this study, we show that farmers deem coffee plant canopy radius as a more important indicator for management decision-making than coffee plant height (Table 3). DaMatta (2004) identified coffee crown architecture as a leading whole-plant trait in the selection of coffee cultivars, particularly in water limited environments. Though coffee planting density is typically a fixed variable, the space between crowns is managed with pruning practices, which in turn can affect canopy "lushness", or the amount of leaves on a given plant. All reported explanations for canopy radius as the most important indicator of a coffee plant success were related to plant requirements – a larger canopy radius requires less fertilizer, and simultaneously produces greater yield – and a farmers' ability to change the canopy radius and lushness via pruning.

Trait trade-offs and trait typologies

The LES is constructed from leaf-level trade-offs among traits (Wright *et al*. 2004), for instance, leaf mass per area (LMA) trade-offs with mass-based photosynthesis and leaf N concentration. Yet, there remains uncertainty as to whether these strong global correlations among and between LES traits also function at the local scale (Wright & Sutton-Grier 2012). For instance, trait expression and the strength of trade-offs are affected by soil fertility (Ordoñez *et al*. 2009), climate (Sandel *et al*. 2010), and in crops, a history of domestication (Milla *et al*. 2014; Martin *et al*. 2017), and therefore may follow other drivers that influence the degree, or even presence, of trade-offs.

From an applied perspective, what remains unresolved is if farmers also perceive, and make decisions based on, trade-offs among traits, which may consciously result in certain ecosystem functions being optimized at the expense of others. For instance, Mason & Donovan (2015) report that allocation to leaf defense may stimulate conservative leaf strategies. Similarly, in this study the ranking of leaf size or thickness to light environments often resulted in farmer references to leaf disease. A thick, dark, small leaf, for example, may be identified as situated under an excess of shade, but discussions of such trait syndromes often triggered supplementary comments by farmers on leaf susceptible to disease, most notably, coffee rust. Alternatively, in several cases the inverse was stated: the presence of some specific diseases or fungus indicated an excess of shade. Several respondents identified the second largest leaf as the most productive in the yield potential ranking, given that the largest leaf "…*needs more fertilizer to maintain*": an identified management trade-off between nutrient acquisition and leaf area.

Respondents often defined leaf- and whole-plant characteristics as indicative of plant health, and occasionally in terms of human health, supporting previous work that identified the tendency of farmers to compare coffee plant health to human health when managing farms (Hugøy 2016). Leaves appeared "*poisoned*" ("*intoxicado*") due to an excess of fertilizer inputs or *"wilted/sad*" (*"somayadita"*) due to insufficient shade or an excess of light. Based on leaf size and colour, one respondent identified leaves as being on "*…a branch who has no future*". Trait trade-offs in the strictest ecological sense were not at the forefront of respondent ranking of leaves, however, upon further exploration of multiple leaf properties or trait syndromes, respondents clearly perceived trade-offs between leaf size, thickness, nutrition, and disease resistance. This has been previously reported as the concept '*hielo'*, or the tendency to group a variety of symptoms related to plant disease, water imbalances, and nutritional deficiencies together (Bentley 1990).

Implications

The application of ecological theory to agricultural systems, for instance the use of trait-based approaches in agroecology, needs to consciously take into account existing on-farm practices. Just as the LES offers a framework to understand the traits underpinning variation in plant ecological strategies, an FES can provide structure to understanding farmer knowledge on plant trait expression and ITV, and the use of traits that are not strictly related to yield in management decision-making. Our findings show both commonality in knowledge of leaf traits between the scientific literature and farmers, as well as apparent disconnects. It should be noted that given proximity to an agricultural training research station, respondents in this study might have a distinctive agricultural knowledge base than those in the surrounding regions. Regardless though, our findings open an opportunity for mutually beneficial exchange on the role of functional traits in agroecosystems that may advance management prescriptions that are consistent with contemporary scientific knowledge, and practical understandings of agroecological systems. Specifically, traits can be used to assess the success of a range of management practices including shade-tree species selection and abundance, crop- and shade-tree pruning regimes, and fertilization treatments. Furthermore, several emerging areas of agroecological management, including the implementation of new crop genotypes, control of novel pests and pathogens, and climate change mitigation strategies, demand a highly robust and diverse array of ecological knowledge. Given environmental change in many agriculture regions, coordination between scientific- and local knowledge systems is increasingly required to effectively adapt management practices to changing conditions.

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Table 1. Mean (± s.d.) and range of farm-level variables attributes. In all cases $n = 25$ farms, and acronyms in brackets correspond to how they appear in Equation 1.

Predictor variables	Mean (± s.d.)	Range
Land under coffee (L)	0.89 ± 0.92	0.1-4.0
Coffee Age (A)	15.76 ±10.04	2-35
Coffee Density (D)	5094.6 ± 1189.9	3464-8069
Years farming (Y)	36.1 ±16.7	4-86
Variety number (V)	2.8 ± 2.1	0-11
Engagement with plants (E)	0.6 ± 0.5	0-1
Fertilizer use (F)	1.52 ± 0.92	0-3
Sum of practices (P)	17.08 ± 4.95	1-23
Shannon Index (*H*)	0.84 ± 0.55	0-1.611
Simpson Index (*D*)	0.38 ± 0.29	0-1
Shade class (S)	2.52 ± 0.71	1-3

Table 2. Ranking of leaf (colour, size, and thickness) and whole-plant (canopy radius, coffee plant height, and coffee sprout diameter) trait importance for on-farm decision-making. Values following the name of each trait denote the average ranking of that trait (with 1 representing the highest importance, and three representing the least important), based on interviews with $n = 25$ respondents.

Ranking	Leaf traits	Whole-plant traits
1st rank	Colour = 1.4 ± 0.71	Canopy radius = 1.16 ± 0.37
2nd rank	Size = 2.04 ± 0.68	Coffee height = 2.28 ± 0.61
3rd rank	Thickness = 2.52 ± 0.65	Sprout diameter = 2.52 ± 0.71

Table 3. Mean (± s.d.) proportion of agreement for response variables, as well as the most frequently identified trait under three management scenarios: light environment (high and low light), nutrient status (sufficient and deficient nutrition) and yielding potential (high yield and low yield). All values are based on $n = 25$ responses.

Response variables	Mean proportion (± s.d.)	Most frequently identified trait (% of respondents)	
		High light	Low light
Proportion of agreement for leaf size	0.55 ± 0.32	Smallest leaf (56%)	Largest leaf (64%)
Proportion of agreement for leaf thickness	0.39 ± 0.26	Thinnest leaf (36%)	Thickest leaf (68%)
		Sufficient nutrients	Deficient nutrients
Proportion of agreement for leaf colour	0.66 ± 0.34	Large green leaf (80%)	Small yellow leaf (68%)
		High yield	Low yield
Correlation for yield potential	0.47 ± 0.27	Largest green leaf (64%)	Small yellow leaf (32%)

Table 4. Step-wise and multiple regression model analysis evaluating which farm-level characteristics best predict the agreement between i) a famer's ranking of leaf traits to light environments (size and thickness), soil fertility (colour) and reproduction (yield potential), and ii) an empirical ranking of leaf traits. AIC values for both the full model and the most parsimonious model are presented, with ΔAIC values representing the difference between the two. Parameter estimates (and *p*-values in brackets) are shown only for those parameters retained in the AIC-selected model. Parameters highlighted in bold are those that were significant ($p < 0.05$) in a multiple regression analysis, and acronyms and associated β values (in brackets) correspond to Table 1 and Equation 1. Also shown for each AIC-model are is explained variance, where n =25 for each model.

Model	AIC-retained parameters (β values in Equation 1)	Coefficient (*p*-value)	Full AIC	AIC	Delta AIC	Model r^2 (*p*-value)
Leaf size	Intercept (β_0)	**0.47 (<0.001)**	-44.77	-58.97	14.2	**0.146 (0.033)**
	log-L (β_1)	**-0.149 (0.03)**	-	-	-	-
Leaf thickness	Intercept (β_0)	**0.934 (0.031)**	-50.92	-54.97	4.05	0.213 (0.148)
	A (β_2)	**0.009 (0.0187)**	-	-	-	-
	D (β_3)	-0.0001 (0.091)	-	-	-	-
	log-V (β_5)	-0.145 (0.255)	-	-	-	-
	E (β_6)	0.302 (0.058)	-	-	-	-
	F (β_7)	-0.142 (0.056)	-	-	-	-
	H (β_9)	-0.398 (0.165)	-	-	-	-
	D (β_{10})	-0.581 (0.091)	-	-	-	-

	S (β_{11})	0.272 (0.195)	-	-	-	-
Leaf colour	Intercept (β_0)	0.24 (0.323)	-45.7	-56.5	10.8	**0.170 (0.049)**
	log-L (β_1)	**-1.66 (0.026)**	-	-	-	-
	P (β_8)	0.02 (0.141)	-	-	-	-
Yield potential	Intercept (β_0)	**1.231 (<0.001)**	-61.6	-69.0	7.45	**0.263 (0.037)**
	log-V (β_5)	**0.327 (0.007)**	-	-	-	-
	Y (β_4)	-0.004 (0.206)	-	-	-	-
	P (β_8)	**-0.034 (0.006)**	-	-	-	-
	S (β_{11})	-0.119 (0.139)	-	-	-	-

Figure 1. The “leaf book”, a visual elicitation tool based on empirically framed researcher-created visual data for ranges of coffee leaf traits. See Materials and Methods for description of the collection and presentation of leaves in the book.

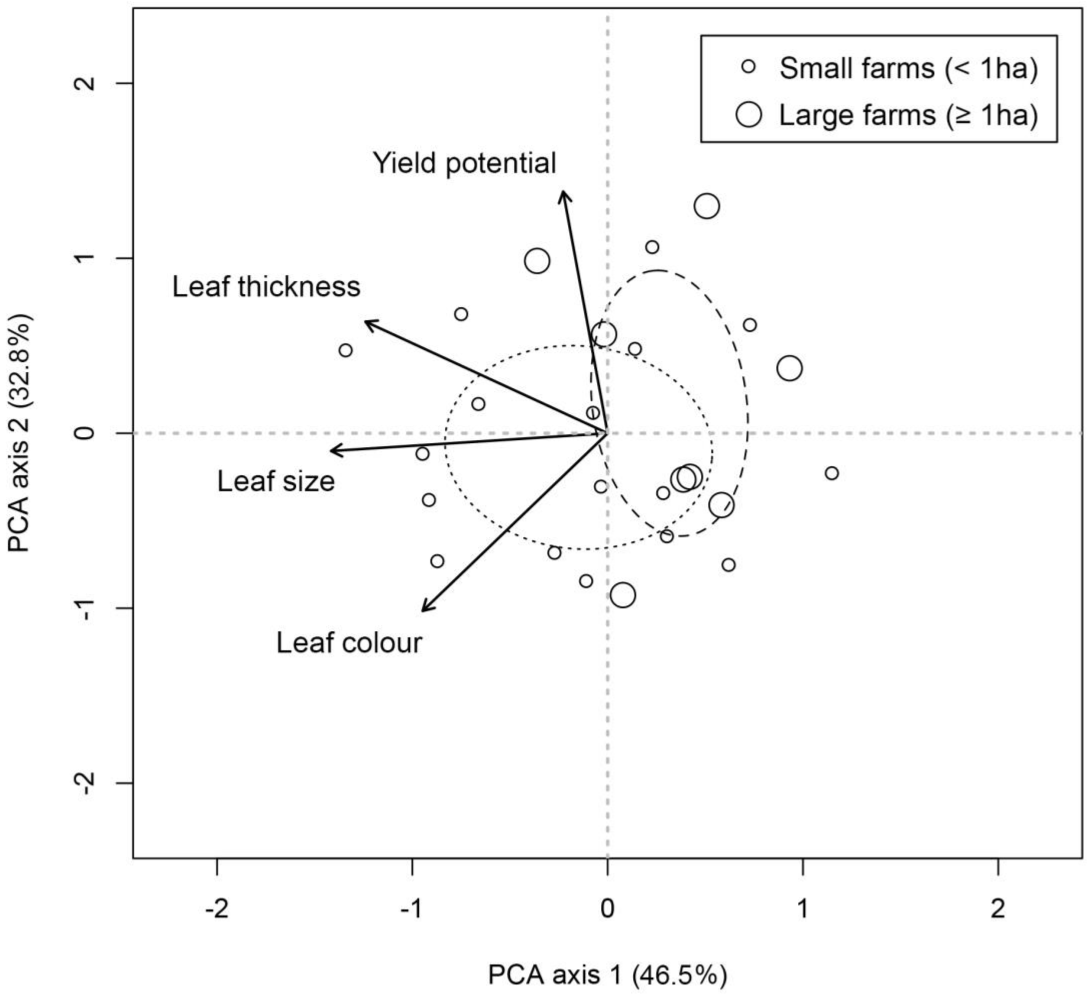

Figure 2. Principal components analysis assessing relationships among the proportion of agreement between respondent-identified ranking of leaves and an empirically assessed ranking of leaves for i) leaf size, ii) leaf thickness, iii) leaf colour, and iv) yield potential). Small circles represent small farms <1 ha in size, while large circles represent farms ≥ 1 ha in size. Dotted and dashed circles represent 95% confidence ellipses surrounding small and large farms, respectively, which differed significantly across PCA axis 1 (one-tailed *t*-test $p = 0.035$).