A multifunctional approach for achieving simultaneous biodiversity conservation and farmer livelihood in coffee agroecosystems

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**Abstract**

Ecologically complex agroecosystems often provide multiple conservation benefits, yet understanding the agricultural practices that favor biodiversity is often a theoretical task until we simultaneously demonstrate the economic impact of such practices on farmers. We provide a multifunctional analysis of both biodiversity and ecosystem services that influence coffee farm profit in Puerto Rico. We show that the vegetation heterogeneity of an agroecosystem, more so than any one ecological component (e.g. shade), is associated with a higher biodiversity of plants, birds, lizards, bees, ants, and parasitoid wasps. However, a farm’s vegetation heterogeneity does not consistently correlate with profit-related ecosystem services, including coffee yield and biological control of coffee pests and pathogens, due to tradeoffs between services. Therefore, inherent financial incentives that would encourage farmers to manage farms in ways that maintain high associated biodiversity may be lacking. We explored several economic incentives that would allow farms to be simultaneously biodiverse and profitable, which we show is possible through realistic incentive schemes. We found that the combination of a certification premium plus carbon payments (50% premium plus $16 t⁻¹ CO₂e) or a restructuring of agricultural subsidies using currently experienced subsidy amounts may be sufficient to make farms that are more heterogeneous, and therefore more biodiverse, the most profitable option for farmers. If these biodiverse farms can also be profitable, it will open critical opportunities for maintaining rural landscapes that support farmers’ livelihoods, as well as protect the planet’s biodiversity.

1. Introduction

Two evident facts color contemporary concern with food production. First, modern agriculture has homogenized previously heterogeneous environments, seeking and frequently attaining high levels of productivity at the expense of this heterogeneity, which may include structural (e.g., vegetation strata or size), taxonomic, or landscape diversity (Matson et al., 1997; Tscharntke et al., 2005; Robertson et al., 2014). Second, the natural and managed heterogeneity of agroecosystems (i.e., vegetation heterogeneity) has been appreciated for its functional utility in long-term sustainability, provision of ecosystem services, maintenance of biodiversity, and support of farmer livelihoods (Lewis et al., 1997; Perfecto et al., 2009; Tscharntke et al., 2011; van der Ploeg, 2013). These two facts stand in contradiction, yet it is critical that we attain farming systems that can be simultaneously productive and profitable, while also facilitating biodiversity conservation, given that the single largest land use and a primary driver of species extinction is agriculture (Clay, 2004; Ramankutty et al., 2008).

A key stumbling block with resolving this contradiction is that the benefits provided by vegetation heterogeneity—including the diversity of crops as well as the associated plants that are either maintained, allowed to grow, or intentionally planted—to agroecosystems are multidimensional, yet they are commonly treated as individual, isolated issues (Bennett et al., 2009; Gamfeldt et al., 2013). Furthermore,
different organism groups or different ecosystem services often do not respond similarly to different environmental scales or environmental variables (Karp et al., 2018; Peters et al., 2016; Soliveres et al., 2016). Ultimately, in accepting a single organism or ecosystem service framework, we discount the complex relationships (e.g., tradeoffs and synergies) between ecosystem services or biodiversity indicators (Balvanera et al., 2014; Clough et al., 2011; Karp et al., 2015; Kragt and synerges) between ecosystem services or biodiversity indicators (Balvanera et al., 2014; Clough et al., 2011; Karp et al., 2015; Kragt and Robertson, 2014; Krenen and Miles, 2012; Power, 2016; Raudsepp-Hearne et al., 2010), leading to inaccurate conclusions or misguided management recommendations.

A further challenge in valuing vegetation heterogeneity on farms is that the benefits are often realized over the long term. Examples include soil carbon retention, which may take as long as 20 years before its effects are discernible above background noise (Rasmussen et al., 1998), or protection from periodic catastrophic events, such as natural disasters and pest and disease epidemics (Philpott et al., 2008; Avelino et al., 2015). Even so, coincident with a rich literature on biodiversity and ecosystem services, on-farm biodiversity, typically studied as plant diversity, is often positively correlated with farm productivity (Letourneau et al., 2009; Quijas et al., 2010; Cardinale et al., 2012; Iverson et al., 2014). Similarly, structural components of vegetation heterogeneity can be beneficial to farm productivity (Vandermeer, 1989). However, these same studies also highlight a complex relationship—where results are often mixed and tradeoffs between yield and vegetation heterogeneity can be observed on farms. Importantly, in cases where a tradeoff or lack of relationship exists, it is critical to understand if and how these relationships could be altered so as to attain farming systems that can be both productive and heterogeneous—allowing us to achieve dual goals of food production and environmental sustainability.

Although farm productivity is an important component in a farmer’s management decisions, farm profitability may be a more accurate indicator of these decisions, as the former does not measure income directly. Despite valuing long-term sustainability, farmers are often pressured to disproportionately consider short-term profits due to the economically precarious nature of farming. For instance, many coffee farmers experience seasonal periods of food insecurity—the ‘thin months’—due to their reliance on an economically variable commodity that earns them income once per year at harvest time (Morris et al., 2013). This ‘hungry farmer paradox’ may be especially pronounced for coffee farmers, as the product they produce does not directly provide food (Bacon et al., 2014). When confronted with this reality, farmers often face short-term financial pressures and the need to return quick profits. Therefore, if short-term profits do not align with long-term sustainability, the latter tends to suffer, thus compromising future farm profitability and environmental health, including the maintenance of biodiversity. However, if short-term profits can align with long-term sustainability and environmental health, many opportunities may exist for attaining agricultural landscapes that support both farmer livelihoods and biodiversity.

Here, we address how Puerto Rican coffee agroecosystems can be simultaneously profitable in the short-term and retain high levels of biodiversity. To do so, we first quantify the influence of several farm-level and landscape-level environmental variables on the biodiversity of several organism groups and on multiple ecosystem services that directly impact short-term farm profit, including the biocontrol of the major coffee pests and coffee yield. We then assess how farm profitability based on the extant economic situation is related to the environmental variables which most support biodiversity, and we explore several economic scenarios that could lead to both profitable and diverse farms. We use the coffee agroecosystem as a model system; it is replicated around the world, managed in a variety of styles, provides a livelihood for millions of small-scale farmers, and is the economic base for several tropical countries (Daviron and Ponte, 2005; Perfecto and Vandermeer, 2015; Perfecto et al., 2014). Similar to coffee farmers in many other regions of the world, Puerto Rican coffee farmers are often economically constrained; although they receive relatively high governmental support in the form of subsidies, fixed coffee prices, and agricultural extension services, other challenges, such as labor costs and labor shortages, counteract these potential benefits (Borkhataria et al., 2012). As such, most Puerto Rican coffee farmers (> 75% in 2007) rely on off-farm sources of revenue to remain financially viable (Borkhataria et al., 2012). Thus, despite their unique situation of living in an unincorporated territory of the United States, the short-term economic pressures faced by these farmers are similar to those experienced by many coffee farmers around the globe.

2. Materials and methods

2.1. Site description

We selected 36 individual coffee farms (34 conventional and 2 organic) spanning the central western mountains of Puerto Rico (Fig. A1). Coffee is traditionally grown in the understory of a shade tree canopy and the amount of shade is often considered a proxy for intensification (Moguel and Toledo, 1999); our selected farms spanned a gradient ranging from no shade (0%) to high (84%) shade. According to the classification outlined by Moguel and Toledo (1999), the farms that did contain shade were mostly commercial polycultures, with the exception of one traditional polyculture farm. In order to standardize sampling area across farms that differed in size, at each farm we selected an area of 25 × 25 m that was in coffee production and that was representative of the farm’s entire coffee production area to be a plot. In each plot, nine locations that were equidistantly spaced (9 m apart) were utilized for several of the biodiversity surveys and ecosystem service measurements. *Coffea arabica* was the sole coffee species in all plots, and across all farms the mean coffee production area was 5.1 ha (± 1.3 SE, range 0.6 to 39.3 ha). Although some farms had substantial plantings of other crops, such as plantain, coffee composed the majority of the cropped land area on most farms. For a summary of environmental characteristics of sites and details of site selection, see Table A1 and Supplementary material ‘Methods’.

2.2. Ecosystem service and biodiversity sampling

We measured the ecosystem services of biological control, coffee yield, and aboveground tree biomass (carbon storage) in each farm. We assessed multiple measures of biological control through both an enclosure experiment and field surveys. In the enclosure experiment, we assessed vertebrate predation of the coffee berry borer, *Coffea* leafminer, and a flatid planthopper (*Petrusa epilepsis*, Hemiptera: Flatidae). In each plot we selected three pairs of similarly sized and similarly yielding bushes. In each pair we randomly selected one bush to be a bird/bat/anole enclosure, while the other bush of each pair did not receive a mesh enclosure. Exclusions were left in place for 3.5 months, after which we assessed pest presence. For *P. epilepsis*, we visually searched each bush for a period of 3 min. For coffee berry borers, we randomly selected 300 berries (or we censused all berries if < 300) on each bush and recorded borer incidence. On each bush we also sampled 50 leaves (or all leaves if < 50) that had emerged since the implementation of the enclosures and recorded the number of leaves with leafminer damage or general insect herbivory (i.e., primarily herbivorous Coleoptera and Orthoptera).

Through field surveys or field collections, we measured the abundance of the coffee berry borer (*Hypothenemus hampei*, Coleoptera: Curculionidae) and the parasitism rates on the coffee leafminer (*Leucoptera coffeella*, Lepidoptera: Lyonetiidae), which are the two most damaging insect pests of Puerto Rican coffee. We measured coffee leafminer parasitism rates by randomly collecting 100 leafminer pupae, which are usually attached to the underside of coffee leaves, from each plot and rearing them at room temperature in containers. We monitored pupae for 20 d and recorded the number of both unparasitized
leafminers and parasitoids that emerged. We sampled for coffee berry borer abundance by randomly selecting five coffee bushes from each plot (out of approx. 300–350 bushes per plot) and counting the number of bored berries out of 100 total berries per bush from randomly selected branches. Collections of leafminer pupae and surveys of berry borer occurred from 14 May to 22 Jun 2013.

We also assessed the naturally occurring prevalence of coffee leaf rust, *Hemileia vastatrix*, on the nearest non-rust resistant (i.e., no Robusta (*Coffeea canephora*) crosses) coffee bush to each of nine points that were equidistantly spaced 9 m apart in a grid within each plot. We divided each coffee bush into three equally spaced vertical strata that collectively spanned all of the branches, randomly selected branches from each stratum, and scored all leaves (presence/absence) on each selected branch until we reached a total of 100 leaves. We measured aboveground biomass of the shade trees in each coffee farm by measuring each tree's girth and height and applying a biomass formula (see Supplementary Material). Finally, we assessed co-suring each tree's girth and height and applying a biomass formula (see Supplementary Material). To observe the e

For biodiversity, we selected seven different organism clades that represent a broad range of functional and taxonomic diversity: parasitoid wasps, bees, birds, ants, anoles, trees, and groundcover plants. These were chosen based on them potentially providing benefits to the coffee plants through biocontrol (anoles, parasitoid wasps, ants, birds) (Vega et al., 2009; Karp et al., 2013; Monagan et al., 2017; Morris et al., 2018) or pollination (Klein et al., 2003) and, in the case of the plants, that they may provide resources for the aforementioned beneficial organisms. We sampled parasitoid wasps and bees using pan traps, which consisted of three sets of blue, yellow, and white 355 ml plastic bowls affixed 1 m above the ground, individually located 9 m apart in the plot. To sample birds, the same two people performed a 30-min point count in each plot, identifying all birds by sight that were present within the plot plus a 10 m buffer on all sides. We sampled ants in each plot by placing ~1 g of oil-based tuna fish at 25 equidistant ground locations per site (every 4.5 m in a grid). Baits were allowed to sit for 20 min, after which we identified or collected all ant species present. We sampled anole lizards (*Anolis* spp.) by walking two transects measuring 25 × 4 m along a row of coffee bushes within each plot while recording all anoles observed. For tree and shrub richness (hereafter referred to as ‘tree richness’), we counted the number of species > 1.0 cm diameter at breast height present in each plot, whereas for groundcover plants, we measured the number of species in 0.5 m² quadrats, placed on the uphill side of each of the nine equidistant points in the plot. For additional details on how we assessed ecosystem services and biodiversity, see Supplementary Material.

### 2.3. Local and landscape environmental covariates

At a local (farm-level) scale, we selected environmental covariates that, with the exception of elevation, contributed to vegetation heterogeneity and that could be managed by a farmer, so as to allow our results to be applied to farm management recommendations. In addition to the aforementioned variables of groundcover and shade tree species richness, these covariates included shade tree shade density, coffee plant shade density, coverage of groundcover plants, height of groundcover plants, flower abundance on groundcover plants, and elevation. At a landscape scale, we assessed the amount of forest, coffee farms, and open land (including grasslands, non-coffee agriculture, pastures, and barren land) within a 500 m radius of each plot, as well as the distance to the nearest forest. For details on how we measured these covariates and which variables were excluded due to collinearity, see Supplementary Material.

### 2.4. Vegetation heterogeneity

We desired to know the impacts of not just individual vegetation variables considered alone (e.g., shade cover, tree species richness), but of the overall aggregated vegetation heterogeneity of a farm. Therefore, in addition to considering each environmental covariate independently, we condensed the following taxonomic and structural vegetation variables into a vegetation heterogeneity index (VHI): groundcover species richness, groundcover extent (percent cover), groundcover height, shade tree species richness, shade tree biomass, and shade density. To do so, we standardized each variable by calculating the z-score for that variable, then we averaged the z-scores of all six variables for each site to obtain a final vegetation heterogeneity index, where larger numbers equate to higher heterogeneity and smaller numbers equate to lower heterogeneity.

### 2.5. Statistical analysis

#### 2.5.1. Individual ecosystem services and clades

To observe the effects of environmental variables on individual clades and individual ecosystem services, we ran linear mixed-effect models (LMM) or generalized linear mixed-effect models (GLMM), depending on the structure of the data. No biodiversity group or ecosystem service was spatially autocorrelated, according to the Moran’s I statistic. For details on the analyses, please see Supplementary Material.

#### 2.5.2. Multifunctionality analysis

To determine how individual farms can simultaneously provision multiple ecosystem services or simultaneously retain multiple biodiversity clades (i.e., ‘multi-biodiversity’), we performed a multiple threshold analysis (Byrnes et al., 2014). The principle behind this technique is to determine the number of biodiversity clades or ecosystem services that fall above a fixed percentage of the maximum functioning/species richness (i.e. the threshold) that was recorded across all sites. As an example, if a threshold was set at 80% and five ecosystem services were included, we would record the total number of ecosystem services that reached at least 80% of their maximum value found in any one site. If a highly multifunctional plot exists, it will have a value close to five (each ecosystem service is highly functioning—above 80% of the maximum observed value—and is counted).

We then regressed the number of clades/ecosystem services that were counted above a given threshold of species richness or ecosystem service provision in each plot against all ecologically relevant local and landscape environmental variables, including the VHI (see Table A1 for all explanatory variables assessed). A separate regression model was run for each explanatory variable that was assessed. The biodiversity clades included anoles, ants, bees, birds, groundcover plants, parasitoid wasps, and trees. To avoid circularity, when the VHI was used as the explanatory variable, we removed the groundcover plants and shade trees from the biodiversity clades, as they are also components of the VHI. The ecosystem services included rust resistance, coffee berry borer control, coffee leafminer predation, coffee leafminer pupae parasitism, flatid planthopper predation, and shade tree biomass (i.e., carbon storage). Farm profit was also included with the ecosystem services. The biocontrol-related ecosystem services were selected so as to represent the most relevant biocontrol variable for each organism, although two variables (predation and parasitism) were selected for the coffee leafminer, as they pertained to different life stages (predation on adults, parasitism on pupae/larvae) of the moth.

Because choosing a certain threshold is arbitrary, the multiple threshold analysis assesses the degree of multifunctionality across many thresholds (here, all integers from 5 to 99%). From this analysis, we can calculate the range of thresholds for which there is a significant response of an explanatory variable on multifunctionality (i.e. plots which have multiple services ‘functioning’ above or multiple clades being more speciose than a given threshold). Lastly, in order to explore...
which ecosystem services trade-off or are positively correlated, we performed pair-wise regressions among all ecosystem services. Both the multiple threshold analysis and trade-off regressions were done in R version 3.1.2 (R Core Team, 2015), using base R and the package ‘multifunc’ (Byrnes, 2014), respectively.

2.5.3. Value-based weights and incentive scenarios

One disadvantage with using the multiple threshold approach is the difficulty of weighting different ecosystem services, which vary greatly in their value to a farmer. Therefore, in addition to the multiple threshold analysis, we also standardized all ecosystem services (using z-scores) and weighted them according to their potential to benefit farm income (i.e., short-term profit), mostly through the protection of coffee from pests and diseases (Table A2). We calculated this short-term farm profit based on several ecosystem services (including yield) rather than simply using the reported yield value minus costs (i.e., ‘net profit’) for two reasons: 1) many effects of the pests or pathogens (e.g., leaf rust) on yield are not realized until the following year or are not accounted for in overall yield calculations (e.g., damage from coffee berry borer, where yield is assessed prior to discounting infested berries) and 2) including all ecosystem services more accurately estimates future profits that account for risk aversion (e.g., protection against pest outbreaks). We call these profit calculations ‘short-term profit’, because they do not take into account longer-term effects on sustained production through ecological resilience or other environmental benefits (e.g., improved soil fertility).

All ecosystem service weights were based on prior research by the co-authors or other published literature, and represent the potential harm to coffee yield under high infestation rates. For example, we recorded borer berry infestation rates as high as 26% on the most heavily infested farms that we sampled. Therefore, it is realistic that in the absence of biocontrol services, infestation rates could reach values at least this high in any farm. As borers directly decrease yield by drilling into the coffee beans and rendering them unfit for market, we weighted the value of borer predation as 26% that of yield. These may be conservative estimates, given that even the farms that had the highest infestation rates were likely not completely void of biocontrol. An additional biocontrol service, leafminer control, was included in this analysis that was not included in the multifunctionality analysis because in the latter we did not want to include more than one service per life stage of a pest. This redundancy was not an issue when services could be weighted.

Since coffee yield does not equate to farm income, per se, and because our ultimate goal was to calculate an index that most approximates short-term farm profit, we incorporated a term to account for the costs of production (see ‘production costs’ in Table A2). We used this term in addition to a term for coffee yield instead of simply using each farm's reported profit (value of coffee and intercrop yield minus costs of agrochemicals and labor), since all other ecosystem services were valued in relation to their effect on yield; therefore, yield needed to be included as the comparison rather than profit. This comparison to yield was also important to be able to generalize the impact of an ecosystem service across farms. For example, the effect of a given amount of rust on coffee yield will be similar across farms, but the effect of a given amount of rust on farm profit for each farm will vary depending on how much the farmer spends (through inputs) on producing the coffee.

Using these ecosystem-service weighted z-scores that reflect short-term farm profit, we modeled four different economic scenarios by adjusting the weights of certain ecosystem services that relate to each scenario. We adjusted these weights until we reached the point at which the relationship between a farm's vegetation heterogeneity (VHI) and short-term profit became significantly positive (linear regression, $P < 0.05$). These represent situations that economically favor farms that are managed in ways that maintain high vegetation heterogeneity and therefore best conserve biodiversity (for impacts of VHI on biodiversity, see Results). First, we considered the scenario where coffee that was grown in vegetationally heterogeneous farms (VHI > 0.5) received a premium price, representing a certification for wildlife-friendly farming. To calculate the premium, we added a weight to the yield of these high VHI farms (while maintaining the same weights for all other ecosystem services) that was necessary to make the relationship between VHI and profit significantly positive. The ratio of this weighted yield to the observed yield, calculated as a percent increase, was the premium necessary for this relationship to result.

Second, we considered payments for ecosystem services for carbon storage based on each plot's shade tree biomass, which we converted to CO$_2$ equivalents according to calculations outlined in the Supplementary Material. Under this scenario, we sequentially added more weight to the shade tree biomass component of the model (while maintaining the same weights for all other ecosystem services) until the regression of farm profit vs. VHI was significantly positive. All weights were valued in terms of their relationship to coffee yield (set at a weight of 1; Table A2). Therefore, to assign a dollar value to the carbon payment for ecosystem services, we multiplied the weight applied to tree biomass (1.2) by the average profit across all farms ($844$ ha$^{-1}$), so as to convert a yield equivalent (e.g. 1.2 times the value of the yield) to a profit equivalent (e.g. 1.2 times the average profit). We converted to profit instead of yield value, as money added by a payment for ecosystem services would theoretically be additional income (profit), and not simply additional yield value (much of which is lost due to the cost of inputs). We then converted absolute monetary values to SUS t$^{-1}$ CO$_2$e. Third, we considered a combination scenario of farmers receiving both a carbon payment and a certification premium. To do so, we set the premium at a value that is within the range of premiums currently received by farmers (50%), and determined what amount of additional income from carbon payments would be necessary to make the relationship between farm profit and VHI significantly positive.

Lastly, we considered a scenario in which agricultural subsidies were restructured to disincentivize farms contributing the most to environmental degradation (e.g. soil erosion, flooding, landslides, biodiversity loss, climate change, etc.) and to incentivize farms contributing least (i.e., a scenario of internalizing externalities). We structured this last scenario by redirecting subsidies to fund a payment for ecosystem services program for carbon storage. To do so, we simultaneously multiplied a weight (0.63, see below) by the VHI (z-score) of all farms with a VHI < 0 (i.e., the farms that are managed more intensively than the mean level of intensity) and by the shade tree biomass (z-score) of all farms, while maintaining the same weights for all other ecosystem services. The same weight was multiplied by both VHI (for farms with a VHI < 0) and shade tree biomass, since this scenario implies removing subsidies (represented by negative values of VHI) and then re-applying the same monetary amount (represented by the same weight of 0.63) to carbon payments. Negative values of VHI multiplied by this weight decrease the profit of these farms and represent subsidies removed, while positive values of shade tree biomass increase farm profit and represent a payment for ecosystem services. The weight applied to shade tree biomass was based solely on tree biomass; therefore, this subsidy scenario was not influenced by other management practices, such as organic farming. The value that was lost from the intensively managed farms represents a removal of hypothetical subsidies favoring intensified management practices, such as subsidies on fertilizers and pesticides. Because the weight for intensively managed farms was multiplied by the VHI, subsidies were removed in proportion to the management intensity of the farms (i.e., the most intensively managed farms lost the most subsidies). We explored successive values of weights until the relationship between VHI and profit became significantly positive (weight = 0.63). We then converted this weight into a monetary value (SUS ha$^{-1}$) by multiplying the average farm profit (SUS 444 ha$^{-1}$, excluding subsidies) by the weight of 0.63. As weights were standardized in relation to coffee yield of the farm (weight = 1), multiplying the weight by the average farm profit ha$^{-1}$ converted the values from yield equivalents (e.g., 63% of the average yield ha$^{-1}$) to
Table 1
Results from each final LMM/GLMM explaining (A) local and landscape vegetation predictors of biodiversity clades and (B) local/landscape vegetation predictors and relevant biodiversity clades on individual ecosystem services. N = 36 for all services and clades except ants (N = 29), borers control (N = 33), leafminer parasitism (N = 35), coffee yield (N = 35).

A. Biodiversity

<table>
<thead>
<tr>
<th>Taxa¹</th>
<th>Model family</th>
<th>Type of variable</th>
<th>Variable²</th>
<th>Estimate</th>
<th>SE</th>
<th>z/t value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anoles (log)</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Groundcover extent (% cover)</td>
<td>0.011</td>
<td>0.005</td>
<td>2.377</td>
<td>0.023</td>
</tr>
<tr>
<td>Ants (log)</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Flowers on groundcover (log)</td>
<td>−0.084</td>
<td>0.027</td>
<td>−3.134</td>
<td>0.004</td>
</tr>
<tr>
<td>Bees</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Shade tree shade (% canopy cover)</td>
<td>−0.010</td>
<td>0.005</td>
<td>−2.069</td>
<td>0.046</td>
</tr>
<tr>
<td>Birds (sq rt)</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Shade tree shade (% canopy cover)</td>
<td>0.009</td>
<td>0.003</td>
<td>3.119</td>
<td>0.004</td>
</tr>
<tr>
<td>Groundcover plants</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Groundcover extent (% cover)</td>
<td>0.375</td>
<td>0.045</td>
<td>8.378</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Landscape</td>
<td>Open land (% in 500 m radius)</td>
<td></td>
<td>0.131</td>
<td>0.083</td>
<td>1.574</td>
<td>0.127</td>
<td></td>
</tr>
<tr>
<td>Parasitoid wasps (log)</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Groundcover extent (% cover)</td>
<td>0.029</td>
<td>0.009</td>
<td>3.096</td>
<td>0.004</td>
</tr>
<tr>
<td>Trees</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Shade tree shade (% canopy cover)</td>
<td>0.040</td>
<td>0.009</td>
<td>4.574</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

¹ log or sqrt indicates how the data were transformed.

B. Ecosystem services

<table>
<thead>
<tr>
<th>Service³</th>
<th>Model family</th>
<th>Type of variable</th>
<th>Variable²</th>
<th>Estimate</th>
<th>SE</th>
<th>z/t value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Borer control</td>
<td>Poisson</td>
<td>Abiotic</td>
<td>Altitude (m asl)</td>
<td>−0.323</td>
<td>0.104</td>
<td>3.106</td>
<td>0.002</td>
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<tr>
<td></td>
<td></td>
<td>Vegetation structure</td>
<td>Shade tree shade (% canopy cover)</td>
<td>−0.428</td>
<td>0.130</td>
<td>3.294</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Landscape</td>
<td>Distance to nearest forest (m)</td>
<td>0.255</td>
<td>0.110</td>
<td>−2.326</td>
<td>0.020</td>
</tr>
<tr>
<td>Coffee yield (log)</td>
<td>Gaussian</td>
<td>Abiotic</td>
<td>Altitude (m asl)</td>
<td>−0.002</td>
<td>0.001</td>
<td>−3.001</td>
<td>0.003</td>
</tr>
<tr>
<td>Leafminer control (sq rt)</td>
<td>Gaussian</td>
<td>Vegetation structure</td>
<td>Flowers on groundcover (log)</td>
<td>−0.266</td>
<td>0.094</td>
<td>2.814</td>
<td>0.008</td>
</tr>
<tr>
<td>Leafminer parasitism</td>
<td>Binomial</td>
<td>Species richness</td>
<td>Groundcover spp. richness</td>
<td>0.042</td>
<td>0.012</td>
<td>3.369</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Landscape</td>
<td>Groundcover height (cm)</td>
<td>−0.886</td>
<td>0.371</td>
<td>−2.389</td>
<td>0.023</td>
</tr>
<tr>
<td>Plant hopper predation</td>
<td>Gaussian</td>
<td>Birds</td>
<td>Bird abundance</td>
<td>−0.406</td>
<td>0.169</td>
<td>−2.400</td>
<td>0.018</td>
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<tr>
<td></td>
<td></td>
<td>Species richness</td>
<td>Shade tree spp. richness</td>
<td>0.920</td>
<td>0.516</td>
<td>1.783</td>
<td>0.078</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Landscape</td>
<td>Flowers on groundcover (log)</td>
<td>0.328</td>
<td>0.392</td>
<td>0.886</td>
<td>0.371</td>
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<td></td>
<td></td>
<td>Distance to nearest forest (m)</td>
<td>0.027</td>
<td>0.014</td>
<td>1.905</td>
<td>0.060</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forest land (% in 500 m radius)</td>
<td>0.116</td>
<td>0.123</td>
<td>0.940</td>
<td>0.349</td>
<td></td>
</tr>
<tr>
<td>Rust resistance</td>
<td>Binomial</td>
<td>Vegetation structure</td>
<td>Shade tree shade (% canopy cover)</td>
<td>−0.009</td>
<td>0.001</td>
<td>6.458</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shade from coffee plants (%)</td>
<td>−0.006</td>
<td>0.001</td>
<td>4.075</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
</tbody>
</table>

³ log or sqrt indicates how the data were transformed.

3. Results

3.1. Individual ecosystem services and biodiversity clades

We observed a high degree of variation in how the species richness of each organism group was correlated with different environmental variables (Table 1A). For all organisms, only local variables, and not landscape variables, were significant predictors of an organism group’s richness in the best fit models. The species richness of anoles, groundcover plants, and parasitoid wasps was positively correlated with the amount of groundcover on a farm, whereas ant richness responded negatively to the number of groundcover flowers on a farm. Bee richness responded negatively to shade tree shade density, whereas bird and tree richness responded positively to the same variable. To see the abundance and species richness values for all observed biodiversity groups, see Table A3.

The influence of environmental factors on ecosystem service provision also varied depending on the ecosystem service. Local variables, and especially local vegetation structure variables, were most commonly important, although some landscape variables were significant predictors in the best fit models (Table 1B). Coffee yield and coffee berry borers control were highest on lower elevation farms, and borer control was also highest on low-shade farms, where there were fewer groundcover flowers, and where plots were further from a forest. Leafminers were controlled better on farms with fewer groundcover flowers, while their parasitism rates were highest where there were more groundcover species. Leafminer predation was negatively correlated with groundcover plant height, while flatid plant hopper predation was negatively correlated with bird abundance. Finally, rust resistance was negatively correlated with both tree and coffee plant shade density. Complete model selection steps and results are shown in Table A4.

3.2. Multifunctionality analysis

To determine how individual farms can simultaneously provision multiple ecosystem services or simultaneously retain multiple biodiversity clades (i.e., ‘multi-biodiversity’), we performed a multiple threshold analysis (Byrnes et al., 2014). Using the clades and services listed in Table 1, a multiple threshold analysis showed that the vegetation heterogeneity index (VHI) was the best predictor of ‘multi-biodiverse’ farms, more so than any individual environmental predictor alone (Fig. 1A, B, Table A5). Of the individual predictors, only shade and biomass showed any significant correlations with ‘multi-biodiversity’, but the range of significant responses was smaller than when VHI was the predictor (Table A5). A broader range of significant responses signifies that the relationship between ‘multi-biodiversity’ and a response variable is significant across a broader range of thresholds; therefore, this result suggests that VHI is the most influential predictor of ‘multi-diversity’. To understand how the VHI is related to each individual component of the VHI, see Fig. A2.

The outcome observed between VHI and biodiversity is likely conservative because we excluded tree and groundcover species richness from multi-biodiversity to avoid circularity, as these are also components of the VHI. However, tree and groundcover species richness are also likely to respond positively to other components of the VHI (e.g., a...
higher amount of shade cover is associated with a higher species richness of trees). Therefore, it is also useful to consider the relationship between the VHI and multi-biodiversity that includes tree and groundcover richness, although any positive relationship will be artificially high. Here, we found a highly significant positive relationship across all threshold values > 15% (Fig. A3).

The multiple threshold analysis of ecosystem services revealed little significance for individual environmental variables or VHI, where the only significant explanatory variable was the amount of open/cleared land (including grassland, pasture, non-coffee agriculture, and natural barrens at 500 m radius) in the landscape (negative relationship, Fig. 1C, D). The lack of significant relationships in the multiple threshold analysis is reflected by the few relationships between individual ecosystem services that were statistically significant ($P < 0.05$) (Fig. 2). However, both planthopper predation and leafminer control were positively correlated with leafminer predation, while tree biomass was negatively correlated with coffee berry borer and coffee rust control.

### 3.3. Value-based weights and incentive scenarios

When we standardized ecosystem services into z-scores and weighted each according to its potential to benefit short-term farm profit, we found that farm profit was not related to VHI when all coffee farms received the same (market) price for coffee (Fig. 3A). For comparison, the raw profit values (outputs minus inputs) show a similar non-significant relationship (Fig. A4). Using the same z-score summation approach (but unweighted), we found that ‘multi-biodiversity’ was positively correlated with a farm’s vegetation heterogeneity (Fig. A5), corroborating results from the multiple threshold approach.

The non-significant relationship observed between farm profit and VHI suggests that farmers with non-heterogeneous (i.e., intensified) farms may not have an economic incentive to adopt farm management that favors biodiversity conservation. Therefore, we considered how various economic scenarios could sufficiently incentivize farms such that those with a high VHI are the most profitable. We found that if vegetationally heterogeneous farms received a 150% price premium for their coffee, the relationship observed without incentives (Fig. 3A) would shift to being significantly positive (Fig. 3B). If carbon payments were used as the single incentive, payments of $28 t^{-1}$ of CO$_2$ equivalents (CO$_2$e) would result in a positive relationship between profit and VHI (Fig. 3C). We also considered a combination of carbon payments and a certification premium set at a level similar to current premiums that farmers receive. The 1988–2010 price premiums commonly ranged between 25 and 50% for organic, fair trade, or shade coffee, varying in accordance with global coffee market prices (Jaffe, 2012). Therefore, assuming a contemporary price premium of 50% for coffee produced on vegetationally heterogeneous farms, a payment for ecosystem services of $16 t^{-1}$ of CO$_2$e was sufficient to tilt the economic balance significantly in favor of increased vegetation heterogeneity (Fig. 3D).

Lastly, we found that by redirecting subsidies from farms with a low VHI (VHI < 0) and applying them to carbon payments based on shade...
tree biomass, an average redistribution of $532 ha$⁻¹ was sufficient to financially favor vegetationally heterogeneous farms (Fig. 3E).

4. Discussion

We provide evidence that Puerto Rican coffee farms can be both profitable and vegetationally heterogeneous, providing for biodiversity conservation and long-term sustainability, given adequate economic incentives. We show that the conservation of multiple biodiversity groups is highest on heterogeneous farms; therefore, if these same farms are also the most profitable, clear opportunities for conservation and farmer livelihood can exist. However, with payment schedules as currently applied, neither the number of high-functioning ecosystem services nor the short-term economic gain is related to vegetation heterogeneity, reflecting the little covariance observed between individual ecosystem services (Fig. 2) and their varied response to such heterogeneity (Table 1). Importantly, we did not observe a negative relationship between vegetation heterogeneity and net profit (Fig. A4). However, farmers could be pushed in either direction along a vegetation heterogeneity gradient depending on the local political, socioeconomic, or environmental context. Although many farmers place a high value on vegetation heterogeneity through an understanding of long-term sustainability or for aesthetic or cultural reasons, many current agricultural policies may favor farm intensification (Isbell, 2015; Vandermeer et al., 2010). Therefore, opposing forces may be at play in determining the level of vegetation heterogeneity within farms, and if a pre-emptive approach is lacking, the default appears to be pushing farmers in the direction of short-term investments in intensification.

We found that various scenarios of economic restructuring are able to economically favor more vegetationally heterogeneous farms. Although the price at which some schemes would likely be effective are higher than what is currently feasible, some are financially realistic options. In terms of restructuring subsidies, $532 ha$⁻¹ is within the range of current agricultural subsidies provided by the Department of Agriculture to Puerto Rican coffee farmers. These subsidies primarily favor intensified coffee farming through financial incentives for agrochemicals or increased production; some (e.g., fertilizer subsidies) are distributed solely based on coffee yield. Incentives for synthetic fertilizer alone were $55 per 45 kg of green coffee produced in 2013 (Pers. comm. N. López Rivera), which, for the farmers included in this study, would equate to an average value of $608 ha$⁻¹ yr$⁻¹ (± $58 SE).

Aggregates of incentives may be the most plausible mechanism for financially incentivizing vegetationally heterogeneous farm management. We found that by combining a certification premium within the range of currently applied premiums (50% premium above market price) with a carbon payment for ecosystem services, more heterogeneous farms could be economically favored with incentive values that are reflective of the current carbon market. When combined with a 50% premium, a carbon payment value of $16 t$⁻¹ CO₂e is sufficient to economically incentivize heterogeneous farms, compared to $28 t$⁻¹ CO₂e with no associated premiums. Although $16 t$⁻¹ CO₂e is higher than the $7.40 t$⁻¹ CO₂e average payment (in 2014), it is within the range of prices seen in the compliance market, at an average of $12.70 t$⁻¹ CO₂e (Goldstein, 2015), while some payments reach $140 t$⁻¹ CO₂e (World Bank et al., 2017). Carbon payments may be an increasingly effective strategy in the future as carbon markets continue to develop and mature, and as nations attempt to meet international climate agreements (World Bank et al., 2017; Warren-Thomas et al., 2018). As carbon is a function of tree size and not diversity per se, carbon payments that particularly encourage diverse tree assemblages over monocultures would be most beneficial to biodiversity. We did not test the combination of subsidy restructuring plus payment for ecosystem services or certification, although doing so would have also
lowered the necessary incentives of each standalone component.

When considering coffee certification for vegetationally heterogeneous production (i.e., similar to but more rigorous than ‘shade-grown’ production) as the sole economic incentive, a 150% premium is substantially higher than most premiums paid to farmers for specialty coffee. Therefore, a certification-based strategy alone may be insufficient to economically incentivize vegetationally heterogeneous farm management. However, other work on the economic benefits of shade coffee production resulting from bird predation of the coffee berry borer suggest that small price premiums, and sometimes even no premium, may be sufficient to economically incentivize shade production (Hernandez-Aguilera et al., 2019). In the context of our work, a higher premium to farmers, who receive a fraction of the value of the final product, does not necessarily imply an equivalent increase in price to consumers. As much of the price premiums paid by consumers for socially and environmentally responsible coffee often does not trickle down to farmers (Daviron and Ponte, 2005), there may be ripe opportunities to direct a higher share of profits to the farmers without incurring substantial increases in costs to consumers, who are increasingly willing to pay for specialty coffee. Indeed, the consumption of specialty coffee reached over 50% of the total U.S. market share for coffee in 2014 (Specialty Coffee Association of America, 2015). Nevertheless, despite many possible benefits, the impacts of certification on individual farmers and farming communities is complex and may not always translate into desired social outcomes (Getz and Shreck, 2006; Jena et al., 2017; Oya et al., 2018). Therefore, the translation of our expected results into observed reality would inevitably be influenced by human behavior.

We found that a vegetation heterogeneity index that integrates several structural and taxonomic components of the ecosystem is more influential on a farm’s ability to retain high levels of multiple biodiversity groups than any single component comprising the index (e.g. tree shade, tree diversity, groundcover extent). The value of this index over any single environmental variable highlights the diversity of responses based on an organism’s niche. For instance, biodiversity groups tended to respond to diversity within the stratum that they most inhabit; anoles, ants, groundcover plants, and parasitoid wasps responded to variables relating to the groundcover layer, whereas bees, birds, and

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**Fig. 3.** Influence of vegetation heterogeneity on composite ecosystem services. Linear models of weighted composite ecosystem service values (i.e., short-term farm profit) vs. the vegetation heterogeneity of a farm. In (A), all coffee receives the same (market value) price ($R^2 = 0.041, P = 0.128$). In (B), vegetationally heterogeneous (VHI > 0.5) farms receive a premium (150% above market price) for coffee ($R^2 = 0.093, P = 0.042$). In (C), farms receive a carbon payment for ecosystem services (PES) in proportion to the tree biomass on the farm, equating to $28 \text{ t}^{-1}$ of CO$_2$e ($R^2 = 0.087, P = 0.047$). In (D), more vegetationally heterogeneous farms receive a 50% premium for coffee and also a carbon PES, equating to $16 \text{ t}^{-1}$ of CO$_2$e ($R^2 = 0.091, P = 0.044$). In (E), all low heterogeneity farms (VHI < 0) lost subsidies valued at $532 \text{ ha}^{-1}$, which were then applied to a carbon PES ($R^2 = 0.089, P = 0.046$). Gray shading = 95% CI. $N = 35$. 

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trees responded to the amount of shade cover. Interestingly, local vegetation structure variables, rather than taxonomic diversity and landscape variables, were most influential in predicting the species richness of all biodiversity groups. The influence of local variables over landscape variables could reflect that we did not have a large range of forest cover across sites, and forest cover was on average the largest landscape component at sites (mean = 68.3% cover). Furthermore, all sites were located relatively close to a forest (maximum distance = 300 m, mean distance = 98 m). We were unable to include a larger range of forest cover in our site selection, as most of the coffee-growing region in Puerto Rico contains high levels of forest, mostly consisting of post-coffee agriculture secondary forest.

The varied responses to environmental covariates exhibited by different biodiversity groups highlights the value of considering multiple organisms simultaneously and places caution on the extrapolation of results of one organism or organism group to speak generally about impacts on broader biodiversity. We did not gather baseline values from neighboring forests; however, other research has shown that biodiversity levels for some organisms, such as ants and birds, are as high or even higher in high shade coffee than in surrounding forests, although this is not always the case for habitat-specialist species (e.g., forest specialist birds) (Komar, 2006; Philpott et al., 2008a; Buechley et al., 2015). Furthermore, we recorded many endemic species in our surveys, and Puerto Rico constitutes part of the Caribbean Islands biodiversity hotspot (Myers et al., 2000). Taken together, the biodiversity we observed in coffee farms is likely to be important for biodiversity conservation.

Given the importance of the vegetation heterogeneity index, we suggest that coffee certification schemes with intentions of biodiversity conservation should consider these multiple dimensions of vegetation heterogeneity, rather than merely a ‘shade-threshold’ approach, where the amount of shade over the coffee is the sole criterion. Although this type of certification may entail additional assessments of the vegetation, it need not be too cumbersome to be practically applied. Similar to existing certification structures, certification organizations could play a leading role in training farmers on how these certification standards could be met. Some labels, such as the Smithsonian Migratory Bird Center’s Bird Friendly Coffee, do already take into account multiple taxonomic and structural vegetation components of a coffee farm. Furthermore, group certification of cooperatives or associations of coffee growers may provide a more cost-efficient and equitable approach for expanding this type of certification, allowing for greater accessibility especially for small-scale producers (Pinto et al., 2014).

The landscape-level variable of amount of open/non-forested land (including grassland, pasture, non-coffee agriculture, and natural barrens) in a 500 m radius of a farm was negatively related to multiple ecosystem service provision (Fig. 1). These results may reflect enhanced dispersal of pests and pathogens across more open landscapes with fewer physical barriers to impede wind or other dispersal mechanisms (Avelino et al., 2012). Furthermore, these results may reflect how simplified landscapes often have an increased pest and pathogen pressure or a lower diversity or abundance of natural enemies (Rusch et al., 2016; Tschamntke et al., 2012). Maximizing the provision of multiple ecosystem services may thus benefit from the collective responses of farmers, ranchers, or other landowners to maintain more forested land in the landscape.

No single local-scale environmental factor was related to the simultaneous provision of multiple ecosystem services, highlighting the variability in responses to different environmental variables we observed among ecosystem services. For instance, borer control, rust resistance, leaffminer control, and leaffminer predation all responded negatively to local vegetation structure variables (i.e., those related to shade trees and groundcover), but never to the same variable. Conversely, leaffminer parasitism was positively correlated with the species richness of groundcover plants. We also found that bird abundance negatively correlated with planthopper predation; this result suggests that the birds could have been releasing pests from other insect predators upon which the birds were feeding.

Vegetationally heterogeneous farms can provide additional social, economic, and environmental benefits to farmers and surrounding communities that we were not able to incorporate into our study: they retain soil fertility, sequester carbon, protect against drought and disaster, prevent erosion, and shelter workers from the hot tropical sun (Tschamntke et al., 2011). Furthermore, coffee from shaded systems can also be of higher quality (da Silva Neto et al., 2018) and can benefit household food security by providing additional products for consumption or sales, thereby decreasing the risk of relying on a single product and helping to weather the ‘thin months’ (Mendez, 2008; Mendez et al., 2010; Morris et al., 2013). Therefore, our results are likely conservative, signifying that fewer financial incentives than suggested by our economic analyses would be sufficient to encourage more heterogeneous farming systems. For instance, improved soil quality from additional leaf litter deposition and reduced erosion on more heterogeneous farms may cumulatively benefit farm profit through higher yields and reduced fertilizer needs. Social benefits could result from improved working conditions under shade, potentially translating into improved worker retention, efficiency, and contentment. Broadly speaking, having more trees in the landscape could benefit local and/or global communities through decreased erosion (including landslides), improved water quality, moderated temperatures, and climate change mitigation (Tschamntke et al., 2011). Thus, many long-term benefits may accrue from farming practices that also encourage biodiversity, and these practices may ultimately buffer farmers from economic instability in comparison to management practices that are reliant on expensive and economically volatile synthetic inputs.

4.1. Limitations

The goal of our study was to incorporate as many relevant ecosystem services and biodiversity groups as possible. However, we recognize that this approach did not allow us to sample the selected biodiversity groups or services with multiple temporal replicates. Although the ecosystem services were assessed at a point in time when pest damage or disease incidence would be indicative of the damage/incidence for the entire season, it is likely that biodiversity groups would vary seasonally. Therefore, our assessment provides a broad comparison of biodiversity at a given point in time, but our results could differ if we were able to sample with greater temporal or seasonal replication. With greater replication, we may also have been able to detect a greater number of tradeoffs or synergies between organism groups or ecosystem services. Furthermore, in order to limit the scope of an already broad analysis, we also chose to focus on species richness as a measure of diversity; however, given the known importance of other measures of diversity on ecosystem services and ecosystem functioning (Gagic et al., 2015; Grab et al., 2019), it is possible that our results would differ had we considered these other measures. Despite these limitations, we offer a novel methodological approach to address the challenge of incorporating multiple biodiversity groups, ecosystem services, and their influence on farm profit.

5. Conclusions

Managing farms for both biodiversity conservation and farmer livelihood inherently demands us to consider a socio-ecological approach, where we acknowledge that agricultural management is not a function of the ecological outcome alone, but exists in relationship with the social systems that ultimately determine practices (Lescourret et al., 2015). Here, we show that opportunities exist for incentivizing vegetationally heterogeneous farms in Puerto Rico that create a win-win result between farm profit and biodiversity—a synergy that is not probable under regular market conditions. If this scenario is achieved,
great opportunities for biodiversity conservation in agricultural landscapes can emerge. This outcome is critical for conservation, as agricultural lands represent the largest land use globally (Ramanukutty et al., 2008) and, as such, provide critical habitat and serve as conduits between natural areas in mosaics of mixed land use (Perfecto et al., 2009). We use the example of Puerto Rican coffee, yet our findings and approach pertain to many agricultural systems, where tradeoffs within and between biodiversity and ecosystem services are common. Our research is not meant to be a prescription for management, as particular values for ecosystem services and biodiversity will vary across different contexts. Rather, we hope our research shows the value of considering multiple biodiversity groups and ecosystem services within an integrated framework. Furthermore, our research supports the notion that incentive schemes that encourage multi-level (structural and taxonomic) vegetation heterogeneity are the most probable to benefit multiple biodiversity groups. As many countries are implementing agricultural incentive schemes aimed at promoting both biodiversity and human livelihood, the principles of our analysis will likely be useful to determine what type and what quantity of incentives may be necessary to achieve desired outcomes.

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Appendix A. Supplementary material

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