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Uncertainties in the value and opportunity costs of pollination services

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Abstract

1. Pollination is an ecosystem service that directly contributes to agricultural production, and can therefore provide a strong incentive to conserve natural habitats that support pollinator populations. However, we have yet to provide consistent and convincing pollination service valuations to effectively slow the conversion of natural habitats.
2. We use coffee in Kodagu, India, to illustrate the uncertainties involved in estimating costs and benefits of pollination services. First, we fully account for the benefits obtained by coffee agroforests that are attributable to pollination from wild bees nesting in forest habitats. Second, we compare these benefits to the opportunity cost of conserving forest habitats and forgoing conversion to coffee production. Throughout, we systematically quantify the uncertainties in our accounting exercise and identify the parameters that contribute most to uncertainty in pollination service valuation.
3. We find the value of pollination services provided by one hectare of forest to be 25% lower than the profits obtained from converting that same surface to coffee production using average values for all parameters. However, our results show this value is not robust to moderate uncertainty in parameter values, particularly that driven by variability in pollinator density.
4. *Synthesis and applications*. Our findings emphasise the need to develop robust estimates of both value and opportunity costs of pollination services that take into account landscape and management variables. Our analysis contributes to strengthening pollination service arguments used to help stakeholders make informed decisions on land-use and conservation practices.

Keywords

Coffee, crop pollination, ecosystem services, forest, opportunity cost, sensitivity analysis, valuation

Resumen (Abstract in Spanish)

1. La polinización es un servicio ecosistémico que contribuye directamente a la productividad agrícola, y que, por tanto, puede suponer un incentivo para conservar los hábitats naturales que albergan poblaciones de polinizadores. Sin embargo, aún no somos capaces de establecer valoraciones consistentes y convincentes de los servicios de polinización que sirvan para frenar la conversión de hábitats naturales.
2. En este artículo, usamos el cultivo de café en el distrito de Kodagu en India para ilustrar la incertidumbre asociada a la estimación de los costes y beneficios de los servicios de polinización. En primer lugar, contabilizamos los beneficios obtenidos en sistemas agroforestales de café que son atribuibles a la polinización por abejas silvestres que anidan en hábitats forestales. En segundo lugar, comparamos estos beneficios con los costes de oportunidad relativos a conservar hábitats forestales al renunciar a la conversión a la producción de café. A lo largo de todo el proceso, cuantificamos sistemáticamente la incertidumbre asociada con nuestro ejercicio de contabilidad e identificamos los parámetros que más contribuyen a la incertidumbre en la valoración del servicio de polinización.
3. Encontramos que, usando valores medios para todos los parámetros, el valor de los servicios de polinización generados por una hectárea de bosque es un 25% más bajo que el beneficio obtenido al convertir esa misma superficie a la producción de café. Sin embargo, nuestros resultados demuestran que este

valor no es robusto a una incertidumbre moderada en los valores de los parámetros, en particular relacionada con la variabilidad en la densidad de polinizadores.

4. *Síntesis y aplicaciones*: Nuestros resultados destacan la necesidad de desarrollar estimas robustas tanto del valor como del coste de oportunidad asociado con los servicios de polinización que tengan en cuenta variables del paisaje y del tipo de manejo. Nuestro análisis contribuye a fortalecer los argumentos sobre los servicios de polinización usados para ayudar a que los diferentes actores involucrados tomen decisiones informadas sobre las prácticas de conservación y el uso de la tierra.

Introduction

Natural ecosystems are exposed to pressures that threaten their biodiversity (Butchart et al., 2010) and the ecosystem services they provide (Díaz et al., 2006). Ecosystem services (ES) are often used to highlight links between conservation and human well-being, as more diverse ecosystems are often considered better providers of ES (Cardinale et al., 2012). Thus, ES are increasingly being used as an argument for biodiversity conservation (Chan et al., 2011).

Pollination is an essential ES linking natural habitats to agricultural landscapes, as 70% of crop species depend to some extent on pollinators (Klein et al., 2007). Yet, many pollinators are exposed to threats that are driving population declines (Vanbergen & The Insect Pollinators Initiative, 2013), such as pesticides, diseases (Potts et al., 2010) or habitat destruction due to land use change (Winfree et al., 2009). The conversion of natural habitats to agricultural land causes the loss of nesting and foraging resources for pollinators, and ultimately leads to a decline in pollinator activity, with potentially serious consequences for crop production (Kremen et al., 2002).

In many farming systems, pollinator scarcity might be overcome by direct pollination management practices, such as renting beehives. For smallholder farmers in the tropics who mainly depend on wild pollinators for crop productivity, this is rarely an option. In those cases, crop pollination services can be valued as the difference between crop profits when wild pollinators provide services, and crop profits with diminished pollinator availability due to habitat loss, for instance. Yet, obtaining consistent valuations of natural habitat as a provider of crop pollination services has proved challenging (Melathopoulos et al., 2015; Winfree et al., 2011).

Two approaches can be used to quantify the value of pollination services. The first one involves the calculation of the cost of replacement using alternative pollination sources (e.g., bee hives, hand-pollination, pollen dusting) (e.g., Allsopp et al., 2008). In coffee, replacement is often difficult, given the loss of many domestic bee colonies to pest and diseases (e.g., in India with *Apis cerana,* Boreux et al., 2013). The second, and most frequently used approach, consists of calculating the increase in crop productivity that results from effective pollination by wild pollinators as compared to no, or reduced, pollination (e.g., Losey & Vaughan 2006; Olschewski et al., 2007). Many of the studies following such approach have relied on the relationship between pollinator visitation rates and distance from habitat (Ricketts et al., 2004). Improvements of this method increase the precision in accounting for production costs, and adjust these costs to production losses in the absence of pollinators, further distinguishing between the contributions of managed and unmanaged bees (Winfree et al., 2011).

However, contributions using both approaches have an important limitation for the support of ES as a conservation argument: they generally only calculate benefits brought by pollination services originating in nearby natural habitats, and thus neglect the opportunity cost of maintaining those habitats rather than converting them to other valuable uses. A second limitation lies in the lack of uncertainty measures for estimated values (Olander et al., 2017) and a robust management of the inherent variability and complexity of pollination processes in complex landscapes. These shortcomings may help explain why the pollination service conservation argument is not effectively reaching decision-makers in developing countries, despite the growth in academic research focusing on pollination services in the 15 years since the seminal paper by Ricketts and Taylor (2004).

Here, we develop an accounting of costs and benefits for pollination services provided to coffee production. Coffee is one the most valuable tropical export crops with a production that has steadily increased during the past decades (FAOstat, 2018); and for which expansion has been done at the expense of forested areas (Meyfroidt et al., 2014). Coffee is also a crop for which pollination biology and agricultural practices are well known (De Beenhouwer et al., 2013; Vandermeer & Perfecto, 2012; Vergara & Badano, 2009), and thus represents a good model crop species to illustrate the uncertainties in estimating the costs and benefits of pollination services.

Specifically, our study seeks (i) to fully account for the benefits accruing to coffee agroforests that are attributable to pollination from wild bees nesting in forest habitats, (ii) to compare these benefits to the opportunity cost of converting forest habitats to coffee production, and (iii) to apply systematic sensitivity analysis to quantify the uncertainty in the accounting exercise, while identifying which of the parameters included in the calculations contribute most to output uncertainty.

Although our model does not explicitly track pollinator diffusion in space and the related problem of coordination among farmers, we argue that we can address the need for robust pollination valuation more effectively by sorting and prioritizing uncertainty and complexity in pollination processes.

Materials and Methods

Our study focuses on Robusta coffee, *Coffea canephora* Pierre ex Froehner, in the agroforestry systems of Kodagu, Karnataka State, in the Western Ghats in India. The Western Ghats is a global biodiversity hotspot within one of the world's megadiverse countries, India (Myers et al., 2000). The district of Kodagu displays a gradient of land covers from primary contiguous forest, to a mix of remnant forest fragments which comprise 46% of the territory, diverse agro-forests covering 32.5% of the area where *C. canephora* is the main crop (72% of all the coffee produced in the area in 2009, Coffee Board, 2014); with the rest being occupied by water bodies (0.5%) and other crops (including paddy 21%). Coffee agroforests are shaded either by a diverse community of native tree species, a monoculture of the fast growing Australian species *Grevillea robusta* (silver oak) or more often a mix of the two in varying proportions. *G. robusta* now accounts for 20% of shade tree individuals in the area (French Institute of Pondicherry, 2012), the result of a rapid adoption driven by low seedling and pruning costs, periodic timber sales (which do not involve elaborate procedures to obtain rights to fell trees as is the case for native trees), and its suitability as trellis for pepper plants, the second major crop within coffee estates (Garcia et al., 2010).

In the study area, coffee is mainly pollinated by three social bee species: *Apis dorsata*, *Apis cerana indica* and *Tetragonula iridipennis* which account for 58%, 23.4% and 18% of the visits respectively, the remaining 0.5% performed by *Apis florea* (Krishnan et al., 2012). Pollination by insects increases fruit set by up to 50% (increasing the proportion of flowers that develop into fruits from 22% when pollinated by wind only to 33% when wind and insects are combined, Krishnan et al., 2012). The persistence of *Apis cerana* is not strictly dependent on natural forests, as it can nest within tree-holes and termite mounds, also present in coffee agroforests. Furthermore, domesticated *A. cerana* hives are actively managed in some coffee estates (Boreux et al., 2013). *Tetragonula iridipennis* prefer to nest in old man-made structures and tree holes in coffee agroforests, as well as in forests. In contrast, *A. dorsata* depend largely on the occurrence of large trees in which they nest, and these trees are mostly found in forest patches, although occasionally, also in agroforests (Pavageau et al., 2018). The activity of *A. dorsata* within coffee agroforests is influenced by both distance to the nearest forest and size of the forest (Boreux et al., 2013). The data available on the distribution and abundance of *T. iridipennis* and *A. cerana* in relation to forest cover is very scarce, and mostly collected through ground surveys, which could increase the possibility of missing colonies located in tree canopies (Krishnan unpublished data). We therefore focus our analyses on the main forest-dependent wild pollinator in the study area, *A. dorsata*, which accounts for the large majority of flower visits, and is a more effective pollinator than the other two species (Krishnan et al., 2012).

Accounting of Cost and Revenues of Coffee Production

We develop an accounting model- both economic and ecological- of pollination services provided by *A. dorsata* bees from native forests. We compare the opportunity costs of conserving native forests in terms of forgone coffee production, against the value of the pollination services that such forests provide. This quantitative comparison is useful to a landowner facing the decision of conserving or converting a forest remnant. The owners of most of the private forest fragments in the study area are farmers, and it is mainly privately-owned forest fragments that have undergone conversion to coffee cultivation (Garcia et al., 2010). Therefore, we use agronomic accounting standards used by farmers and extension services around the world, and coffee production cost and coffee revenues as the focus of our model. We are careful to account for pepper and timber revenues, as these are known to be important to farmers in the area. Finally, we use Monte Carlo simulations to track sources of uncertainty in our estimates by implementing a systematic analysis of sensitivity to parameter values.

We obtained data from three sources: interviews conducted with local farmers, ecological data from previous studies (Boreux et al., 2013; Boreux et al., 2013; Krishnan et al., 2012; World Agroforestry Centre, 2011) and other published literature (e.g., (Wintgens, 2004)).

Farmer interviews were conducted during April 2014 in 34 farms located in the vicinity of Virajpet in Kodagu (12°12'02.55"N 75°47'59.90"E). Fifteen of these farms had silver oak (*G. robusta*) cover exceeding 30% of all shade trees and are therefore considered "exotic" agroforests. The rest had lower values of silver oak and are considered "native" agroforests. Each farmer was questioned about the characteristics of their farm (size, types of crops planted, number of coffee plants, tree shade species identity and abundance), coffee production, the production of other crops (e.g. pepper or bananas), amount and type of timber sold per year, profits obtained from coffee and from other products (other crops and timber), as well as a detailed accounting of the estate management costs (e.g. shade tree pruning, manure or fertilizer application etc., summarized as cultural costs in Table 1).

Using standard agronomic accounting, we calculate the economic returns of two alternative uses of one hectare of natural forest: (i) conservation of native forest for pollination services and (ii) conversion of forest to coffee production.

For a comparable accounting of initial investments and costs or benefits accruing over the lifetime of a coffee agroforest, we calculated net present values (NPVs). We assumed a 50-year horizon to match the maximum productive lifetime of coffee trees, with discount rates ranging from 2 to 8% (Moore et al., 2004). In coffee production, revenues accrue from selling coffee, pepper and timber. Production costs arise from the use of labour and agricultural inputs. We estimated values for both exotic (those where shade tree cover by the exotic species *G. robusta* exceeds 30%) and native coffee systems (those where exotic shade tree cover < 30%), and with and without irrigation (one of the most important inputs in this area, Boreux et al., 2013). Pepper and timber profits are higher in exotic systems as *G. robusta* trees provide better trellis for pepper vines, and state regulations permit harvesting of exotic trees but not native species.

NPV for coffee production is calculated as the sum of the present values (PVs) of coffee ($PV_{R\,sat.}$) at its maximum production value and non-coffee revenues (PV_{NCR}) (all based on 2014 values reported in interviews) minus the present value of total costs (PV_{TC}):

$$NPV_{coffee} = PV_{R\,sat.} + PV_{NCR} - PV_{TC} \qquad \text{[Eq. 1]}$$

$PV_{R\,sat.}$ can be broken into base coffee production (without biotic pollination, $PV_{R\,base}$) and production attributable to pollination ($PV_{R\,attrib.}$) using the relationship between both found in previous studies (Krishnan et al., 2012):

$$PV_{R\,sat.} = PV_{R\,base} + PV_{R\,attrib.} \qquad \text{[Eq. 2]}$$

In turn, $PV_{NCR}$is the present value of non-coffee revenues (NCR), includes pepper and timber revenues for exotic species and accrues every year of the 50-year period:

$$PV_{NCR} = NCR * D_{1\,to\,50} \qquad \text{[Eq. 3]}$$

where $D_{1\,to\,50}$ converts a yearly cash flow for years 1 through 50 discounted into a present value. Discount factors are calculated as sums of R terms of geometric series:

$$D_{1\,to\,5} = \frac{1-R^5}{1-R}\,,\ D_{6\,to\,50} = \frac{R^5-R^{50}}{1-R} \text{ and } D_{1\,to\,50} = \frac{1-R^{50}}{1-R}$$

where R is:

$$R = \frac{1}{1-I_r}$$

and $I_r$is the discount rate, which is fixed for the lifetime of the plantation and drawn from a beta distribution. We use the notation for discount factors $D_{i\,to\,j}$ in the rest of the section.

The term PV_{TC} represents total costs and includes establishment costs (EC), cultural costs for the first five years when coffee is not yet productive (CC_1) as well as for years 6 to 50 when coffee becomes productive (CC_2, Table 1):

$$PV_{TC} = EC + CC_1 * D_{1\,to\,5} + CC_2 * D_{6\,to\,50}\ . \qquad \text{[Eq. 4]}$$

While many cultural costs are mostly independent from coffee yield, a few cost items are related to yield. Harvest costs may vary with yield, and to a lesser extent fertilizer and irrigation costs. Given the lack of detailed information to establish these relationships we assume that costs are fixed, an assumption that is shown to have limited potential consequences on estimates by our sensitivity analysis (see Results section).

Present values for base production ($PV_{R\ base}$) and that attributable to pollination ($PV_{R\ attrib.}$) are simply discounted sums of yearly revenues:

$$PV_{R\ base} = Y_{base} *\ P_r * D_{6\ to\ 50} \qquad \text{[Eq. 5]}$$

$$PV_{R\ attrib.} = Y_{attrib.} *\ P_r * D_{6\ to\ 50} \qquad \text{[Eq. 6]}$$

where Y_{base} and $Y_{attrib.}$ are the yearly coffee yields for base production and attributable to pollination, and P_r the price of coffee (Table 1):

$$Y_{base} = T_h * F_t * FS_{no\ p.} * B_w * (1 - F_{drop})/1000 \qquad \text{[Eq. 7]}$$

$$Y_{sat.} = T_h * F_t * FS_{sat.} * B_w * (1 - F_{drop})/1000 \qquad \text{[Eq. 8]}$$

$$Y_{attrib.} = Y_{sat.} - Y_{base} \qquad \text{[Eq. 9]}$$

where T_h is the number of coffee trees/ha, F_t the number of flowers/tree. $FS_{no.p}$ represents fruit set if there is no insect-mediated pollination (i.e., only wind pollination) and $FS_{sat.}$ fruit-set with pollination. B_w represents berry weight (in grams per berry) and F_{drop} fruit drop of initial fruit set (Table 2). $Y_{sat.}$ is coffee yield at pollination saturation, which in this case is determined by the maximum fruit set obtained in interviews to farmers. The difference between base and saturated yield values is the yield attributable to insect pollination ($Y_{attrib.}$). The division by a thousand converts grams into kilograms to obtain yields in kilograms per hectare.

Calculation of benefits of forest conservation through production increase attributable to pollination

In forest, we account for the value of pollination services provided to surrounding coffee agroforest, i.e., the increase from the base yield without pollinator visits to the yield produced at pollination saturation in monetary terms (Fig. 1). Here, we calculated NPVs as a function of the number of visits to coffee plants provided by the main pollinator for coffee in the study region, *A. dorsata* and the effect of these visits in terms of yield increment. Thus, NPV of forests is calculated as per:

$$NPV_{forest} = R_{sat} * PV_{R\ attrib.} \qquad \text{[Eq. 10]}$$

where $PV_{R\ attrib.}$ is the return attributable to pollination saturation and R_{sat} the coffee surface saturated by the visits from one hectare of forest habitat and which is given by:

$$R_{sat} = \frac{V_f}{V_{sat.}} \quad , \qquad \text{[Eq. 11]}$$

where (V_f) is the number of visits provided per hectare of forest and ($V_{sat.}$) the number of visits required to fully pollinate one hectare of coffee (Fig. S1). Note that R_{sat} can be greater or smaller than 1.

$$V_f = H * I_h * A_h * Tr_d * D_{open} * Fl_{tr} \qquad \text{[Eq. 12]}$$

$$V_{sat.} = T_h * F_t * F_{drop} * V_{sat.fl} \qquad \text{[Eq. 13]}$$

where H represents the number of *A. dorsata* hives within forest fragments, I_h the number of individuals/hive, A_h the percent of foraging individuals, Tr_d the number of trips/day/worker bee, D_{open} the days flowers remain receptive and Fl_{Tr} the number of coffee flowers visited/foraging trip. $V_{sat.fl}$ represents the number of pollinator visits required to saturate a flower with pollen (Table 2). In the case of forest, we have not included any conservation costs because most forest fragments in the area are privately owned and do not directly entail costs to the owner comparable to the ones included in the coffee calculations (i.e., there are no yearly expenses related to the conservation of forest in the area).

Sensitivity analyses

We performed sensitivity analyses to identify the model parameters that contribute most to uncertainty. We use the Latin hypercube sampling generating 1,000 sets of parameter values. Each parameter value is drawn from an independent distribution as specified in Tables 1 and 2. We use rescaled beta distributions for parameters that are bounded on an interval, such as ratios. For parameters that are not bounded, such as a price, or a yield, we use truncated normal distributions in order to rule out negative values. The minimum, maximum, mean and standard deviations, which we obtain from different sources as indicated in the tables, are sufficient to parameterise each distribution. For each model, we generated the cumulative distribution of all model results based on the combination of values of all parameters, as well as means, quartiles and other statistics of the distributions. We also calculated the partial rank correlations coefficients (PRCCs) as indicators of the contribution of one parameter to model output uncertainty, reflecting the importance of that parameter in the model and the variance of the distribution of this parameter. We calculated the PRCCs as the correlation between an input/parameter and model output, controlling for the linear effect of all other inputs. We computed the Pearson correlation coefficient between an input and the residuals of an OLS linear regression of the output on all other inputs. We also calculated PRCCs for the ratio of forest to best coffee NPV in order to enter all parameters into the same uncertainty calculation to be able to compare their different contributions to uncertainty. This ratio also summarizes the comparison of NPVs for forest and coffee agroforests.

Finally, we created scatterplots showing the distribution of all model values in the parameter space sampled by the Latin hypercube showing the sensitivity of model results to the variation in each of the parameters. The value for each parameter is assumed to be constant over the lifetime of the agroforest.

Results

Using average values and other best available estimates for the value of agroecological parameters, we found exotic shade/irrigated coffee had the highest NPV (28.5K EUR/Ha), followed by native shade/irrigation (18.3K EUR/Ha). These discounted profits for coffee production fall on each side of the NPV attributable to pollination services provided by the conservation of forest as habitat for pollinators (21.6K EUR/Ha, vertical dotted lines in Fig. 2). However, the ratio NPVs of forest and shade/irrigated coffee showed a value of 0.75 ± 26.6 (mean ± standard deviation), reflecting that pollination services may not have on average a higher NPV than the best coffee alternative but that uncertainty remains very large.

Sensitivity analyses confirm that the ranking of NPV values was not robust to error propagation when parameter values were allowed to vary over reasonable ranges determined by the variability in each of the parameters. Indeed, the distribution of NPVs for forest conservation showed a wide range of values (boxplots in Fig. 2), which considerably overlap with the distributions of the four coffee alternatives. Forest conservation was potentially a better economic option than some coffee agroforest regimes at low NPVs (<30K) but the probability that forest will provide NPVs >30K EUR/Ha is lower than for coffee (Fig. 2).

The PCCRs for NPVs of coffee production reveal that the parameters contributing the most to uncertainty are fruit drop and fruit set excluding insect pollination, although most parameters have an important contribution (Fig. 3a). Establishment costs (EC in the figure) and cultural costs before maturity (CC1) of coffee were less important contributors to uncertainty as is expected for a 50-year horizon with moderate discount. The uncertainty in the value of pollination services from forests was mainly driven by hive density per hectare (H) and the proportion of fruits dropped (Fdrop).

Results from PCCRs for the ratio of forest to best coffee NPV (Figure 3b, Table S1, Fig. S2) showed that beehive densities per hectare of forest (H) and fruit drop (Fdrop) are the two largest sources of uncertainty in the value of the ratio. Fruit set without pollination (Fsnop) , flowers per tree(Fltr) , trips per day (TRd), days during which flowers are open (Dopen), and the interest rate (Ir) contribute to uncertainty to a lesser extent. The other parameters hardly contribute to the uncertainty in the ratio either because the ratio calculation cancels off their effect on forest and coffee NPVs (e.g. the coffee price or discount rate), or because they have a small impact on either value in the first place (e.g. establishment costs, Fig.S4-S9).

Discussion

The notion that pollination services could justify biodiversity conservation is a topic of current debate, although the initial impetus for the validity of this argument is being questioned (Kleijn et al., 2015). Our results indicate that evaluating the economic benefits of pollination services, and the opportunity costs of conserving pollinator habitat, is highly context-dependent and sensitive to several variables. Quantifying a monetary value for some ES is often necessary to conceptualise the benefits of these services, but it is important to recognize the uncertainties in their calculation (Silvertown, 2018)**.**

We find large disparities in modelled economic values for coffee, despite the fact that coffee pollination is well studied (e.g., Klein et al. 2003b; Ricketts et al. 2004; Krishnan et al. 2012; Boreux et al. 2013a), and that we understand the effect of farm-scale management practices on this service (Boreux et al., 2013). Previous studies suggested that heterogeneity in valuation outcomes might be explained by differences in the estimates of pollinator dependence ratio or market prices (Breeze et al., 2016). This is not the case here, as we have accurate field data on pollinator dependence (Krishnan et al., 2012) and local market prices, as well as a good understanding of management effects (Boreux et al., 2013). Moreover, our study accounts for variables that limit the value of the pollination service, (e.g., fruit drop and resource limitation, Bos et al., 2007) as fruit production is calculated as the number of mature fruits at the end of the season. Despite these advantages, we are still unable to provide a value of pollination services with a high degree of confidence.

While previous studies conducted sensitivity analyses to validate the robustness of their pollination service valuations, these included upper and lower-bound values for only two parameters (Bauer & Sue Wing, 2016). Our study accounts for all 19 parameters measured. Considering all these sources of uncertainty, we show the importance of understanding the local dynamics of ES before being able to generate confident value estimates.

Pollination represents an example of a locally sourced and consumed ES that could aid in the local conservation of habitats by directly linking the service to locally realised economic benefits. This is, however, challenged if we are not able to clarify the actual economic benefit of pollination when set in the full context of agricultural management practices.

At present, given our analyses, the NPV of forest conservation for crop pollination services is not clearly different to the NPV of irrigated coffee production with exotic shade cover. Yet while there are substantial risks for negative returns in all coffee scenarios given the high costs associated to coffee production, there are none for forest as there are no direct annual costs related to forest conservation.

We acknowledge that our study is subject to significant caveats aside from data precision. Since we have no information on the current level of pollination saturation in the area, we assume that the current yields, used as reference in our parameter values, correspond to full saturation. Furthermore, we calculate average values of pollination visits assuming a linear effect until saturation. Every visit before saturation brings the same increase in fruit set and corresponding returns, while all visits after saturation bring no yield increase. This stepwise linear response to pollination visits captures the non-linearity generally observed but fails to capture more complex patterns such as more progressive saturation. However, this simplification is not critical since average values are sufficient to support the notion that forest and coffee values are too uncertain to rank with confidence.

Our analyses focus on a single species, *A. dorsata*, and ignore the contribution of forests to the maintenance of the other two forest-dependent species, *Tetragonula iridipennis* and few feral colonies of *Apis cerana*. However, this should not be greatly affecting the value we give to forests as providers of pollination because the dependence of *T. iridipennis* and *A.cerana* on forests for nesting is much lower than that of *A. dorsata.* In previous surveys, we found 356 colonies of *A. dorsata* within forest ecosystems, while we located only 5 *T. iridipennis* and 23 *A. cerana* colonies using ground surveys in the same region (Krishnan unpublished data). Therefore, *T. iridipennis* and *A. cerana* do not seem to be constrained by the extent of forest, since they also found suitable nesting sites in tree holes and termite mounds or old man made structure within coffee agroforests.

Further, our model does not represent yearly variability and important features such as farmers' management of production or price risk. In fact, the uncertainty of parameters in our analysis does not distinguish between what is inherent variability (e.g. price is largely determined outside the area of the study) and what is actual lack of knowledge (e.g. the number of *A. dorsata* nests in a given forest patch). Our analysis is also based on the data provided for a single year, which represents a typical "boom" year in coffee production, in which coffee prices were on average 10-20% higher than those reported the previous and next years (ICO, 2014).

Furthermore, we assume that pollination services are the same for all coffee plants regardless of their location. This might overestimate the value of pollination services in some cases. Indeed, pollinators generally show a visitation rate that decays with distance from the nest (Ricketts et al., 2004). In some spatial configurations this could result in saturation in coffee plants near nest habitat and no visitation far away. Heterogeneities in the distribution of forest patches could potentially introduce added uncertainty in our analysis, if coffee production responds to the local density of forests. The coffee landscape in Kodagu has, however, a relatively high density of forest fragments throughout the landscape, with a forest remnant every 3 km^2 of the land area (Bhagwat et al., 2005), and substantial tree cover within many agroforests. Moreover, the large majority of coffee agroforests are well within the foraging range of *A. dorsata* (Pavageau et al., 2018). We therefore do not expect substantially different responses of further forest loss among areas of relatively low or high existing forest cover.

Focusing on average pollinator-flower densities, visitation rates, and resulting economic outcomes, we avoid the sizeable challenges of spatially-explicit modelling, although we are aware that pollination is essentially a spatial process. Indeed, a general analysis of the spatial patterns in the optimal landscape is likely unnecessary since we find that the uncertainty in non-spatial parameters already curtails our ability to rank land uses. The distributions of visits and services in space and their possible heterogeneity can be relevant but are unlikely to be as important as management practices, e.g. the use of irrigation (Pavageau et al., 2018). It remains that an explicit spatial accounting exercise exploring the impact of different diffusion assumptions and parameter values on the uncertainty of NPVs represents a useful extension to our analyses.

Another limitation of our analysis stems from our economic and agronomic model being based only on NPV criteria. Land use decisions and adoption of agroecological practices are complex behaviours involving many factors (Burton, 2004; Edwards-Jones, 2006) such as: risk attitudes towards investment (Binswanger, 1980), access to market or farmer's knowledge of alternative practices (DeFries et al., 2004). Our accounting exercise helps identify the information needed to support the claim that internalizing pollination externalities might contribute to forest conservation. Yet, we must acknowledge that the calculation of NPVs is only one early step in the implementation of the ES argument as a conservation tool (Chan et al., 2012).

Finally, our analysis only accounts for pollination services. Forests provide several other services (e.g., carbon storage, pest control) that might greatly increase their value (Ninan & Inoue, 2013). Nonetheless, the main objective of this study was to identify the extent to which we can, with present knowledge, assign robust economic values to pollination services provided by natural ecosystems. The conclusion is that it is very difficult to do so in view of multiple confounding factors and associated uncertainties. However, making tangible the trade-off between ecosystem service value and opportunity cost is particularly pressing in view of the global continued conversion of forestland to crop production.

Data accessibility

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.7f14jt7 (Magrach et al 2019)

Authors' contributions

AM, AC and JG conceived the ideas and designed methodology; AM, SK and VB collected the data; AM and AC analysed the data; AM and AC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Accounting Parameter symbols, values, and sources.

Parameter	**Description**			**Mean**	**Max**	**Min**	**SD**	**Distribution, Source**
Pr	Coffee price (EUR/kg)			0.93	1.13	0.73	0.11	TN, Interviews, Coffee board (2014)
E_C	Establishment costs	Native	No irrigation	124.83	+Inf	0	31.21	TN, Interviews
			Irrigation	1,646.08	+Inf	0	411.52	
		Exotic	No irrigation	124.83	+Inf	0	31.21	
			Irrigation	1,243.29	+Inf	0	310.82	
C_{C1}	Cultural costs years 1-6 (per year)	Native	No irrigation	1,196.26	+Inf	0	299.07	
			Irrigation	1,252.43	+Inf	0	313.11	
		Exotic	No irrigation	1,040.03	+Inf	0	260.01	
			Irrigation	1,068.03	+Inf	0	267.01	
C_{C2}	Cultural costs years 6-50 (per year)	Native	No irrigation	1,233.69	+Inf	0	308.42	
			Irrigation	1,289.86	+Inf	0	322.46	
		Exotic	No irrigation	1,143.17	+Inf	0	285.79	
			Irrigation	1,171.17	+Inf	0	292.79	
NCR	Non-coffee revenues		Native	387.47	800	0	100.00	
			Exotic	557.03	800	0	100.00	
Ir	Discount rate (%)			5.0	8.0	3.0	1.0	RB, Moore 2004

Note: For distributions, TN stands for truncated normal and RB for a rescaled beta distribution. “+Inf” stands for “infinite” and indicates that the distribution is not truncated at high values, allowing in principle for infinitely large values to be drawn.

Table 2. Agroecological parameter symbols, values, and sources.

Parameter	Description			Mean	Max	Min	SD	Distribution, Source
Th	Number of coffee shrubs per ha		Exotic	1160.71	1250	1125	36.08	TN, Interviews
			Native	1178.85	1500	1062.50	126.29	
Ft	Number of flowers per coffee shrub			25,000	30,000	20,000	2,000	RB, (Wintgens, 2004)
D_{open}	Days flowering. Coffee flowering is triggered by the first rains at the end of the dry season, and flowers remain receptive for around two days. Flowering following rainfall occurs synchronously across all affected plantations in the landscape.			2	3	1	0.5	RB, (Boreux et al., 2013)
$Fs_{no.p}$	Fruit set no pollination (only wind)	Native	No irrigation	0.17	0.52	0.11	0.118	TN, (Krishnan et al., 2012)
			Irrigation	0.21	0.55	0.17	0.110	
		Exotic	No irrigation	0.17	0.41	0.16	0.072	
			Irrigation	0.23	0.52	0.20	0.096	
Fs_{sat}	Fruit set with pollination (wind+insect)	Native	No irrigation	0.08	0.16	0.01	0.024	
			Irrigation	0.11	0.22	0.01	0.033	
		Exotic	No irrigation	0.08	0.16	0.01	0.024	
			Irrigation	0.13	0.26	0.01	0.039	
B_w	Berry weight (grams)	Native	No irrigation	0.39	0.57	0.31	0.075	
			Irrigation	0.42	0.55	0.32	0.066	
		Exotic	No irrigation	0.36	0.53	0.35	0.05	
			Irrigation	0.42	0.49	0.35	0.04	
F_d	Proportion of fruits dropped			0.31	0.1	0.9	0.21	RB, (Boreux, 2010)
H	Number of *A. dorsata* hives per forest ha			3.05	18	0.10	5.17	TN, (Krishnan, 2011; Pavageau et al., 2018)
I_h	Number of *A. dorsata* individuals per hive			68,300	100,000	36,600	18,302	TN, (Corlett, 2011; Dyer & Seeley, 1991; Paar, Oldroyd, Huettinger, & Kastberger, 2004)
A_h	Proportion of foraging individuals per hive. There are no exact values for *A. dorsata*, so we use data for a species in the same genus (*A. florea*)			0.17	0.23	0.1	0.037	TN, (Dyer & Seeley, 1991)

Tr_d	Number of foraging trips per day per individual assuming activity occurs 8 AM and 5PM (Krishnan, 2011) Worker bees are normally active for a maximum of ~9 hours each day (Krishnan, 2011), and each worker has been estimated to undertake 1 foraging visit/day (Tr_d) (Dyer & Seeley, 1991). Workers of *Apis florea* are reported to undertake as many as six foraging visits/day (Dyer & Seeley, 1991). Owing to uncertainties regarding these estimates, we used both values to calculate the mean number of visits per day	3.5	6	1	1	RB, (Dyer & Seeley, 1991)
Fl_{tr}	# Flowers visited per trip. There are no data on the number of coffee flowers that *A. dorsata* visits in each foraging trip, although results from Asian cotton in India suggest that each worker might visit up to 94 flowers/foraging trip (Jones, 2005), and studies on *Apis mellifera* suggest they visit up to 100 flowers/trip (Frankel & Galun, 1977).	94	200	20	51.96	TN, (Frankel & Galun, 1977; Jones, 2005)
$V_{sat.fl}$	Number of pollinator visits required to saturate a flower with pollen. Coffee flowers contain two ovules which, when fertilized, produce two coffee beans, known as a 'cherry' fruit. Insufficient pollination results in a 'peaberry' in which one of the seeds is aborted and only one bean develops (Wintgens, 2004). In the case of *C. canephora*, flowers are self-sterile and therefore successful pollination requires that pollen be sourced from a different plant. In theory this could be achieved with a single bee visit, though usually several pollinator visits are required to successfully deliver viable cross pollen (Rosenzweig, Cunningham, & Wirthensohn, n.d.). Given this uncertainty we used values of one and two visits required for full fruit set to account for this uncertainty.	1	2	1		

Note: For distributions, TN stands for truncated normal and RB for a rescaled beta distribution

Figure legends

Figure 1. Diagram showing the relationships between coffee yields (both base in green, i.e., independent of pollinator activity, and those attributable to the effect of pollinator activity and hence dependent on the presence of forest ecosystems in white), prices, costs, profits and other accounting variables for a 50-year horizon of one hectare of coffee under four management regimes: under native canopy trees with and without irrigation (panels a and b), or under *G. robusta* with and without irrigation (c and d). The horizontal axis references the price of coffee adjusted for discounting and the vertical is the yield (kg/hectare/year after first five years). Areas on the graph represent net present value. Boxes in dashed blue lines represents profit. See procedures for detailed calculations.

Figure 2. Top panel: Box plots of simulated distributions (median, 50th percentile, and 95th percentile). Bottom panel: Simulated cumulative distributions for net present values per hectare under the five management regimes. The vertical dotted lines represent the net present values calculated from the best guess of all parameter values.

Figure 3. Partial rank correlation coefficients of model parameters for net present values (a) and ratio of net present values (b).

Fruit drop (F_{drop}), fruit set without pollination (Fs_{nop}),cultural costs for years six to 50 when coffee becomes productive (CC2), berry weight (Bw), hive density per hectare (*H*), price of coffee (Pr), interest rate (*Ir*), flowers per tree (FL_{tr}), number of coffee trees/ha (Th), fruit set attributable to pollination (Fsatt), revenues from pepper and othe non-coffee products (NCR), number of flowers/tree (Ft), number of visits required to saturate one flower (Vsatfl), trips per day (TR_d), days during which flowers are open (D_{open}), cultural costs for the first five years when coffee is not yet productive (CC1), Number of individuals in *Apis dorsata* hives (Ih), individuals of a colony foraging at a given moment (Ah), establishment costs (EC)

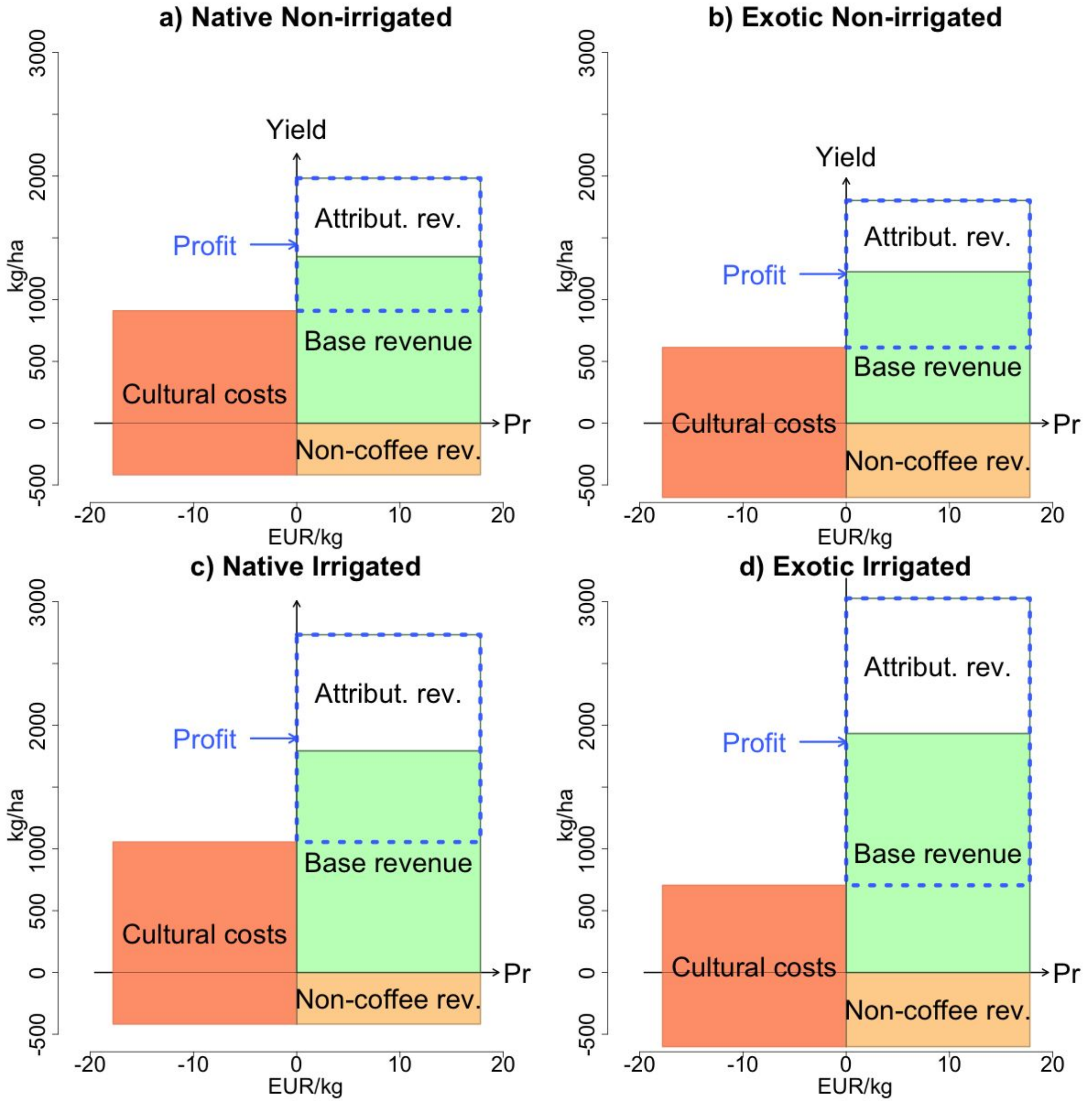

Figure 1.

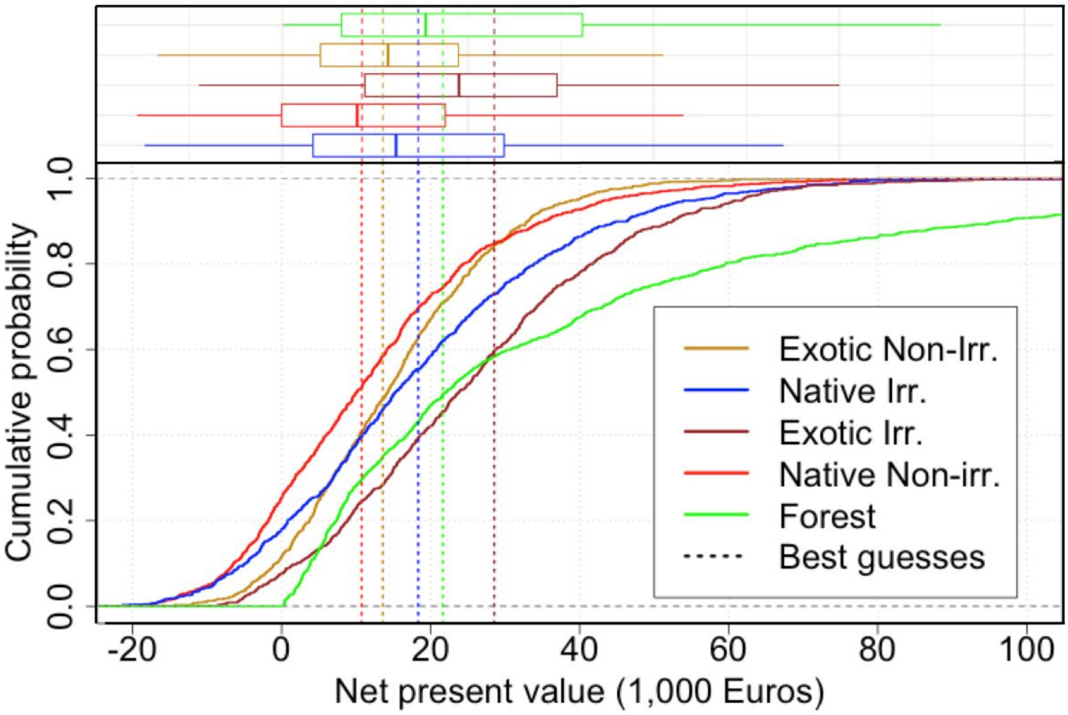
Cumulative probability
0.0
0.2
0.4
0.6
0.8
1.0
-20
0
20
40
60
80
100
Net present value (1,000 Euros)
Exotic Non-Irr.
Native Irr.
Exotic Irr.
Native Non-irr.
Forest
Best guesses

Figure 2.

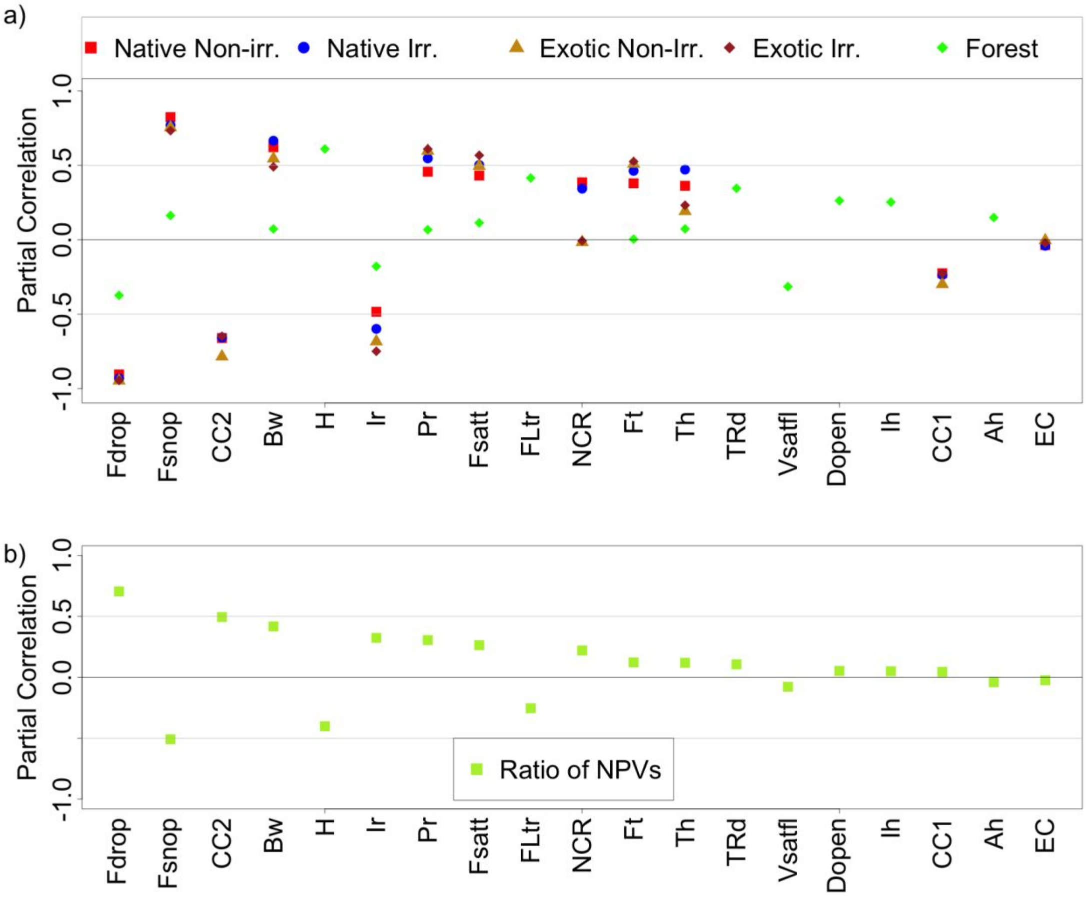
a)
Native Non-irr.
Native Irr.
Exotic Non-Irr.
Exotic Irr.
Forest
Partial Correlation
-1.0
-0.5
0.0
0.5
1.0
Fdrop
Fsnop
CC2
Bw
H
Ir
Pr
Fsatt
FLtr
NCR
Ft
Th
TRd
Vsatfl
Dopen
Ih
CC1
Ah
EC
b)
Partial Correlation
Ratio of NPVs

Figure 3.

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Uncertainties in the value and opportunity costs of pollination services

Short title: Uncertainty in pollination service values

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Keywords
Coffee, crop pollination, ecosystem services, forest, opportunity cost, sensitivity analysis, valuation

Parameter	Coefficient of variation	Partial rank correlation coefficients	Absolute value of PRCC
EC	0.25	-0.0001	0.0001
CC1	0.25	-0.0245	0.0245
CC2	0.25	-0.0232	0.0232
NCR	0.26	-0.0477	0.0477
Ir	0.20	0.0040	0.0040
Pr	0.10	0.0186	0.0186
Th	0.08	-0.0225	0.0225
Ft	0.08	-0.0183	0.0183
Fsatt	0.3	-0.0003	0.0003
Fsnop	0.35	0.0733	0.0733
Bw	0.14	0.0246	0.0246
Fdrop	0.46	-0.1448	0.1448
H	0.67	0.2254	0.2254
Ih	0.22	0.1065	0.1065
Ah	0.18	0.0031	0.0031
TRd	0.29	0.0916	0.0916
Dopen	0.25	0.0834	0.0834
FLtr	0.42	0.0905	0.0905
Vsatfl	0.29	-0.0476	0.0476

Table S1. Coefficients of variation and partial rank correlation coefficients of input parameters for the ratio model output.

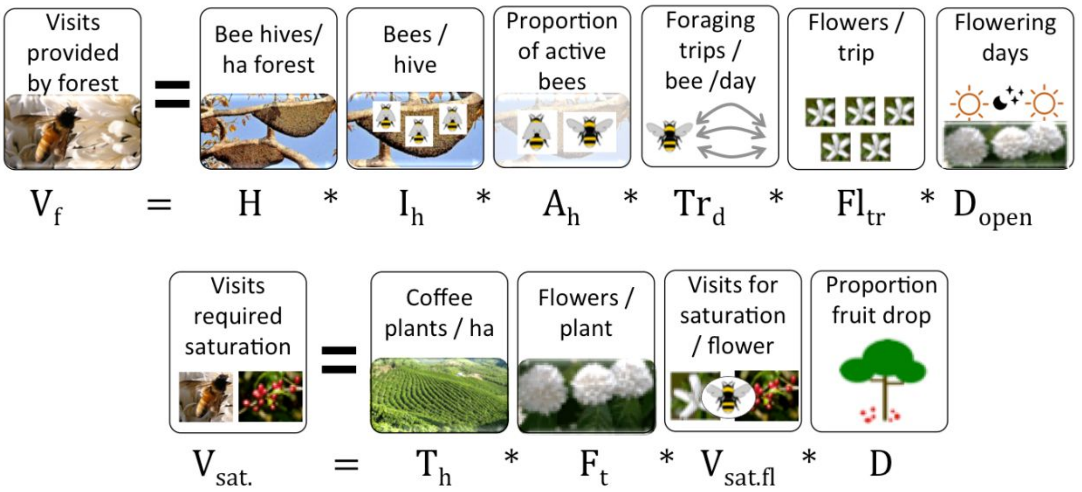


Figure S1. Schematic representation of the pathway followed to calculate V_f, the total number of visits provided by *Apis dorsata* bees per hectare of forest to neighboring coffee plantations and $V_{sat.}$, the number of pollination visits required to reach saturation yield in one hectare of coffee plantation.

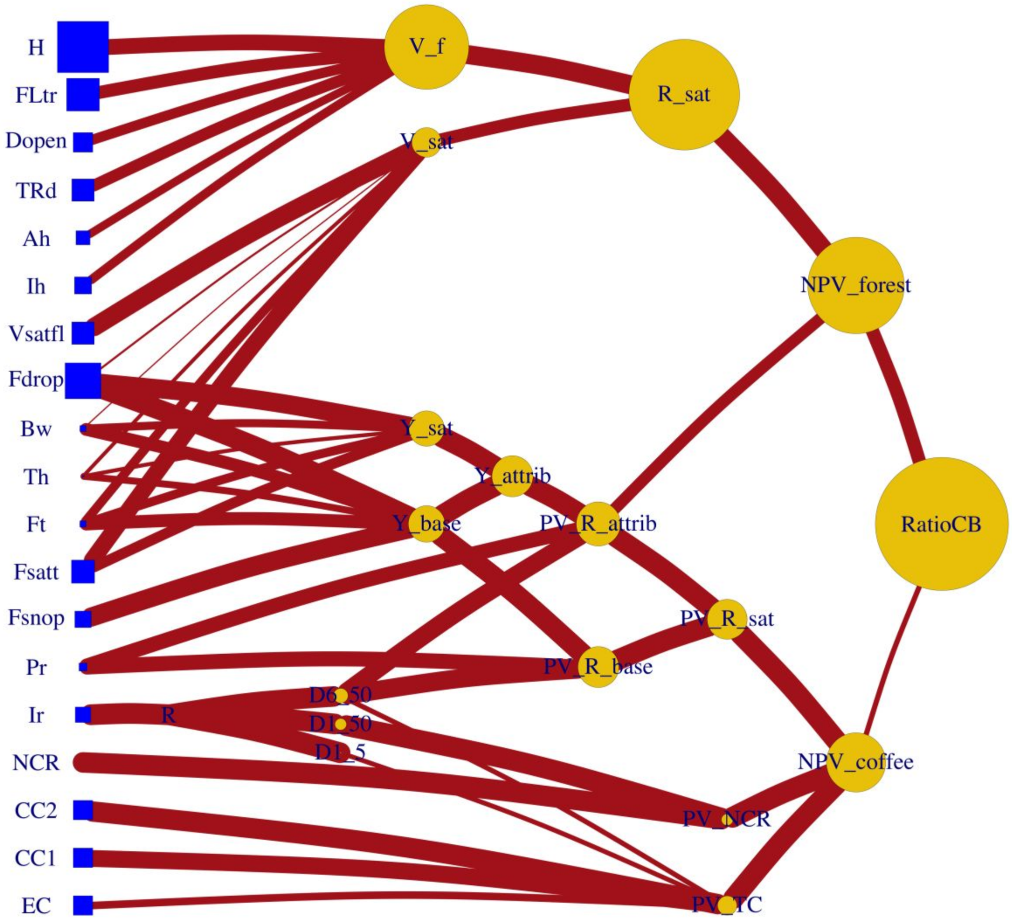
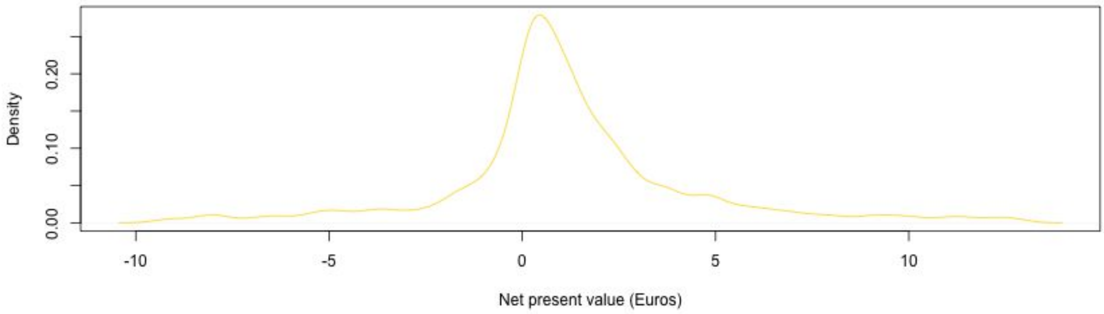


Figure S2. The square nodes on the tree represent parameters while the round ones represent calculations (or model variables). The names of the nodes refer to the parameters and variables listed in Table 1 and 2 and the size of the squares or circles represent the coefficient of variation of each element. The vertices or links connecting the parameters or variables represent the calculation steps and their width represents the contribution of each antecedent to a variable (measured in partial rank correlation coefficients). Calculations go from left to right. This figure corresponds to the exotic irrigation coffee scenario.



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67 **Figure S3.** Density of the simulated distribution of ratio of forest to coffee NPV.

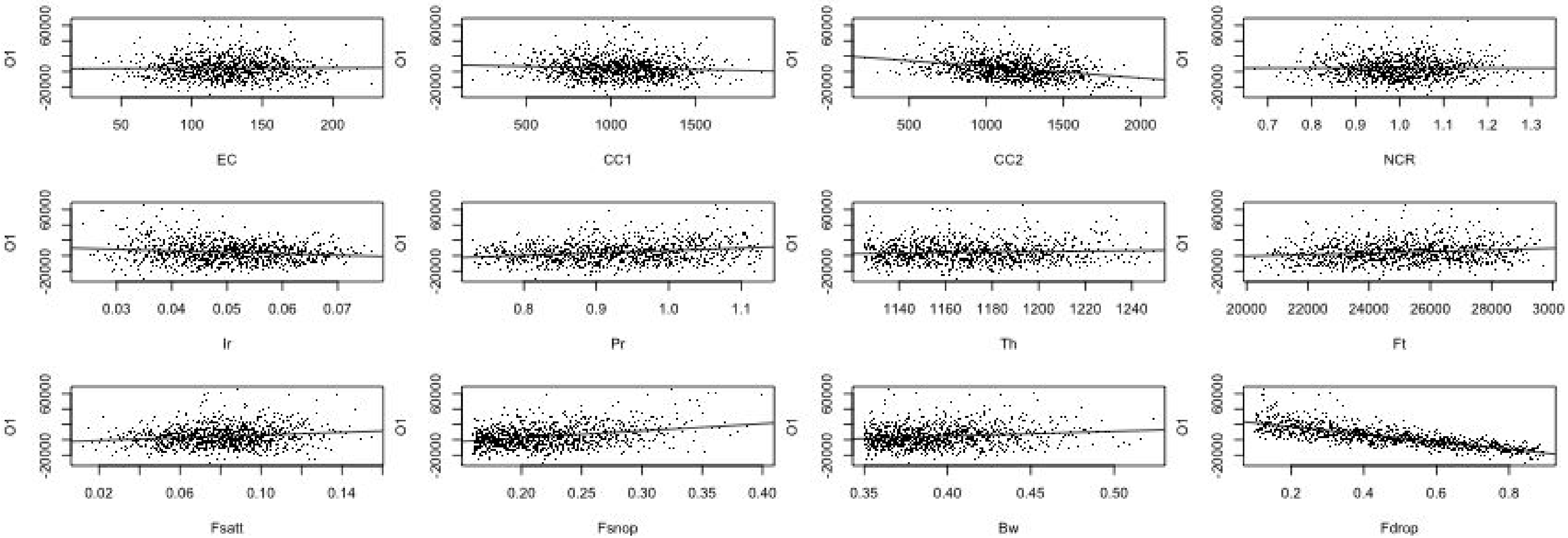


Figure S4 Scatterplots of outputs as a function of input factors: Exotic No-Irrigation

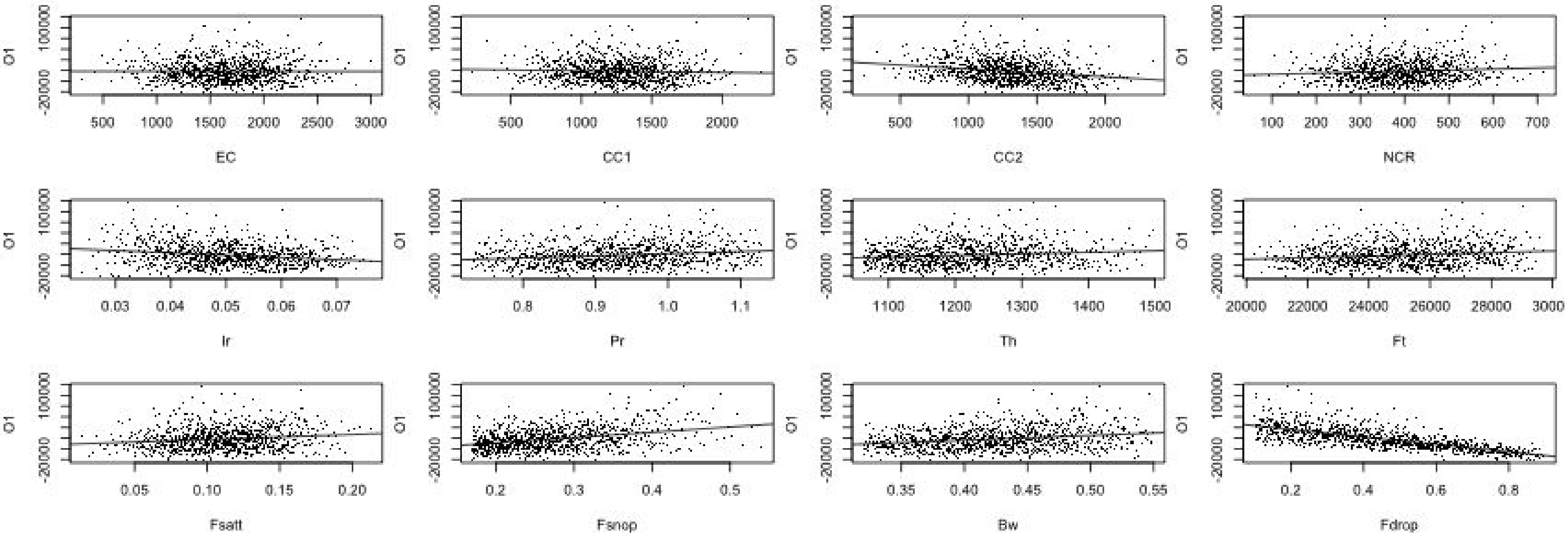


Figure S5 Scatterplots of outputs as a function of input factors: Native No-Irrigation

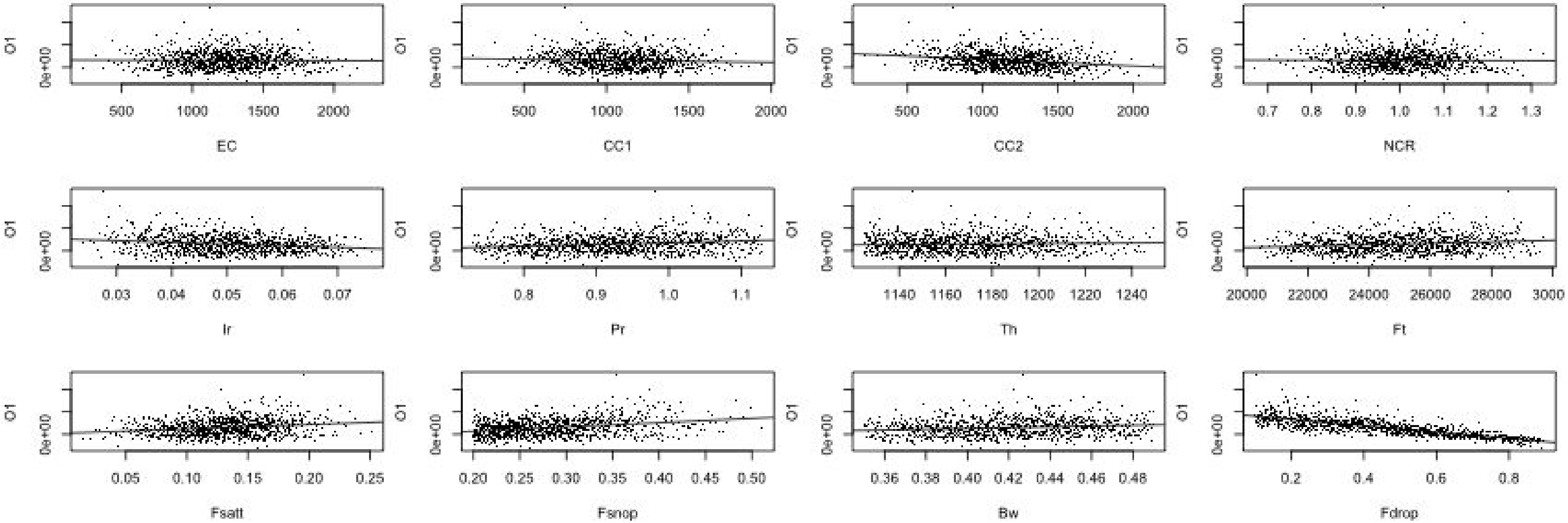


Figure S6 Scatterplots of outputs as a function of input factors: Exotic Irrigation

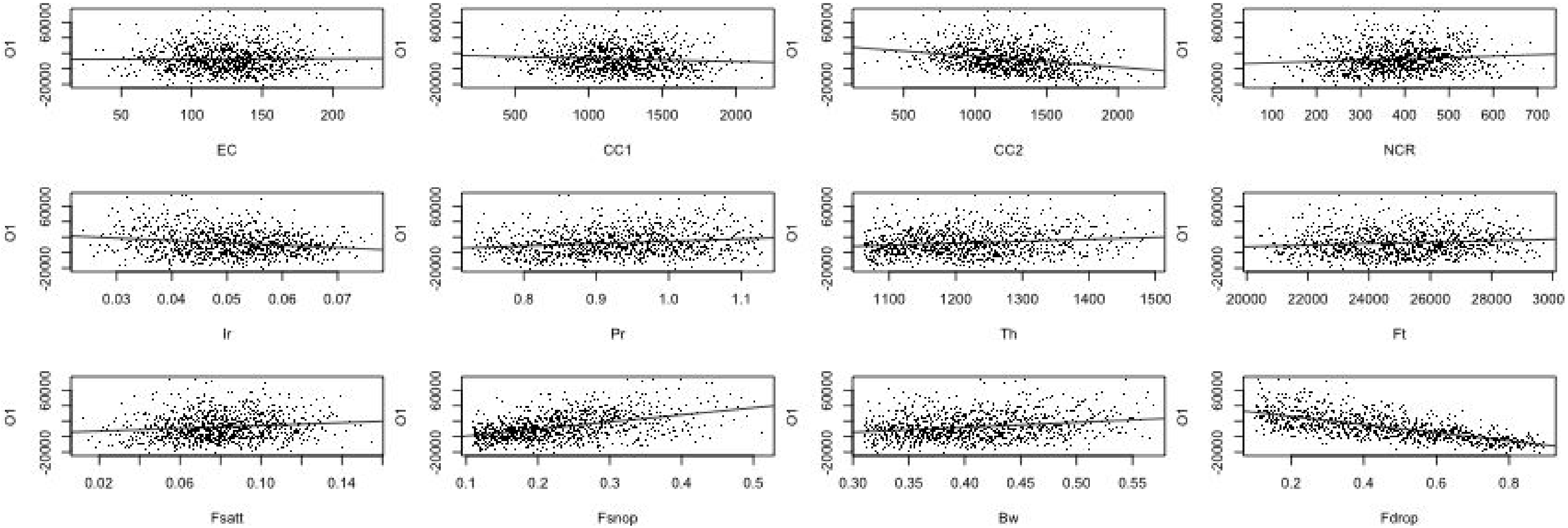


Figure S7 Scatterplots of outputs as a function of input factors: Native Irrigation

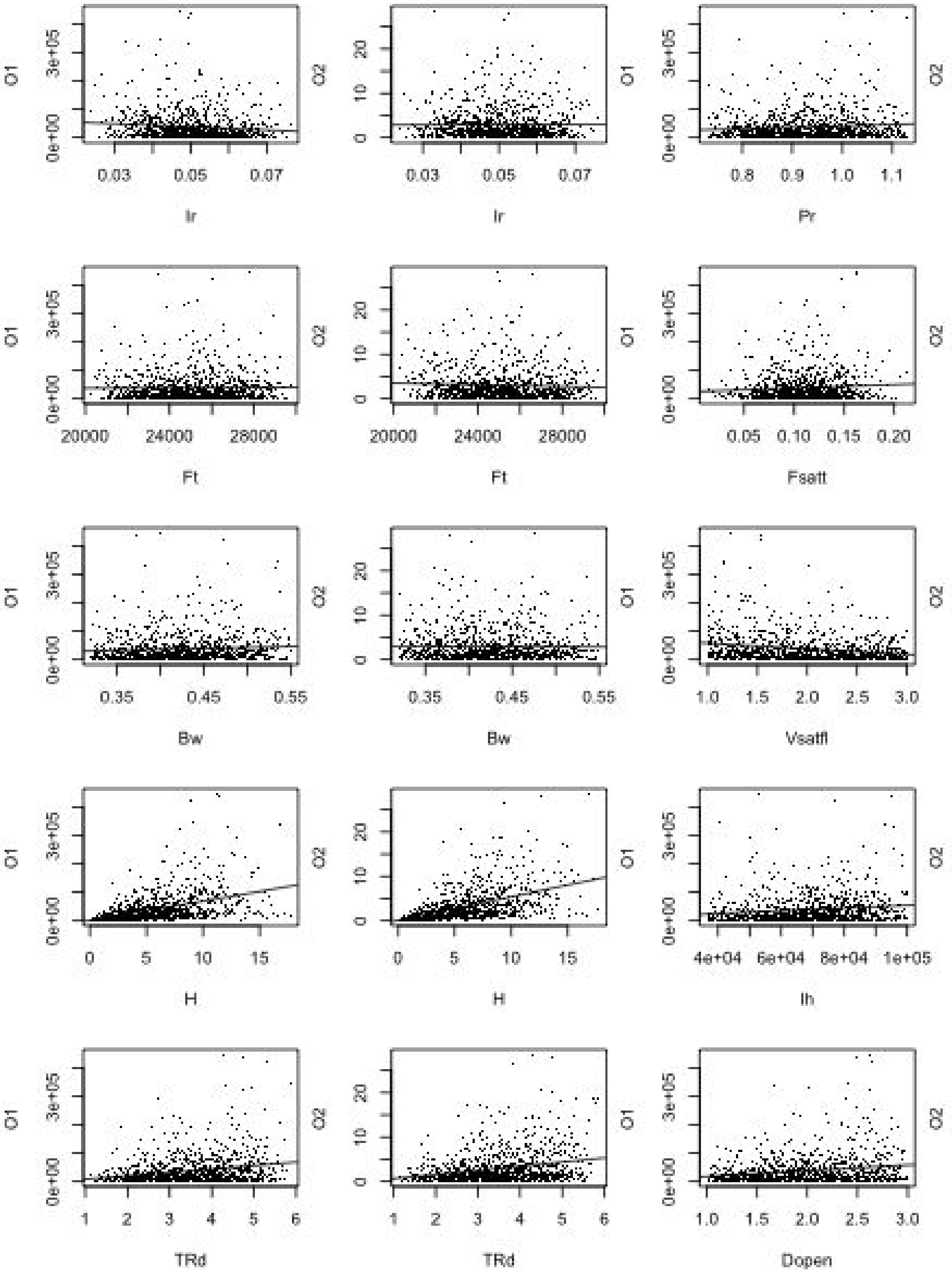


Figure S8 Scatterplots of outputs as a function of input factors: Forest net present value

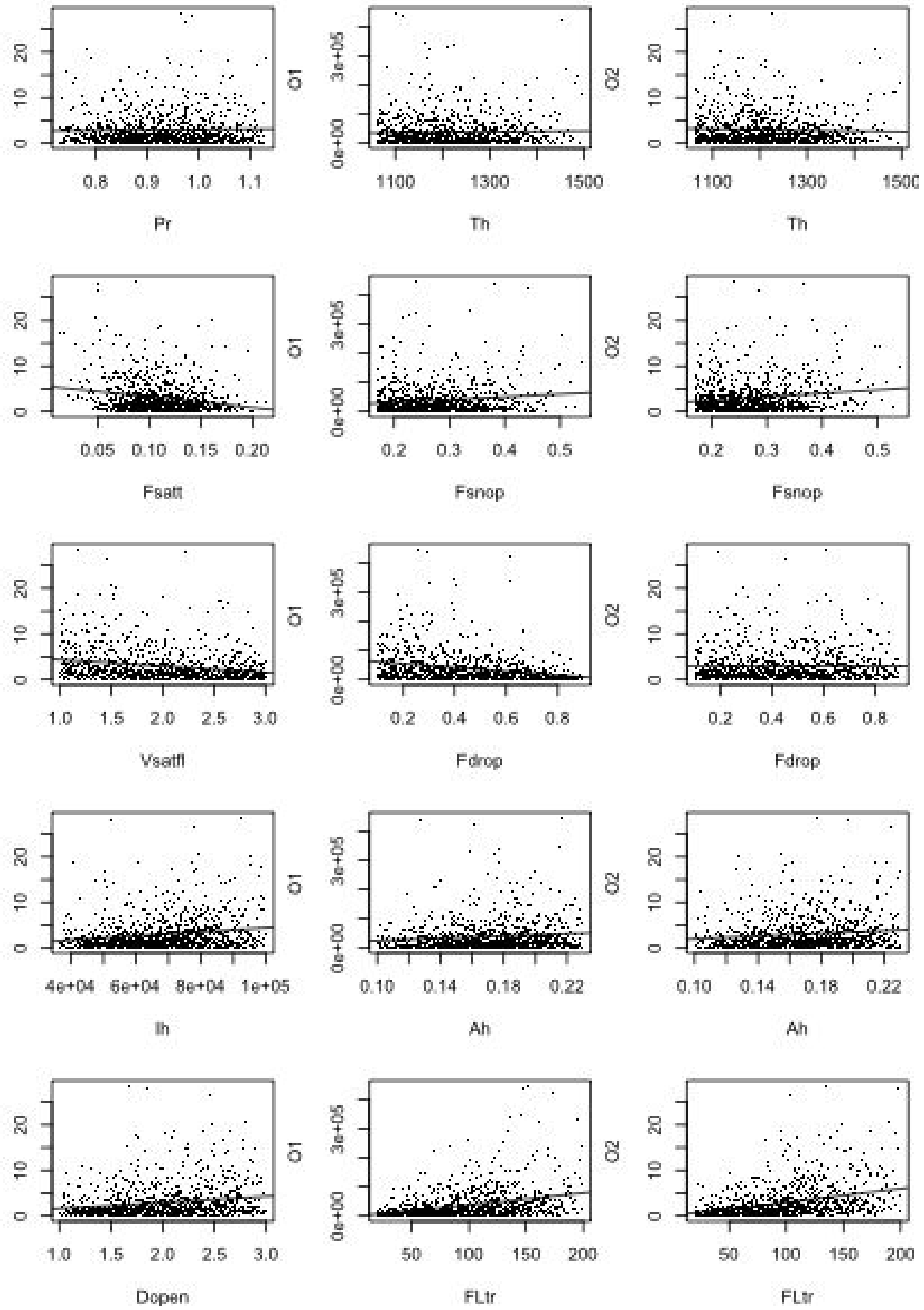


Figure S9 Scatterplots of outputs as a function of input factors: Forest saturation ratio

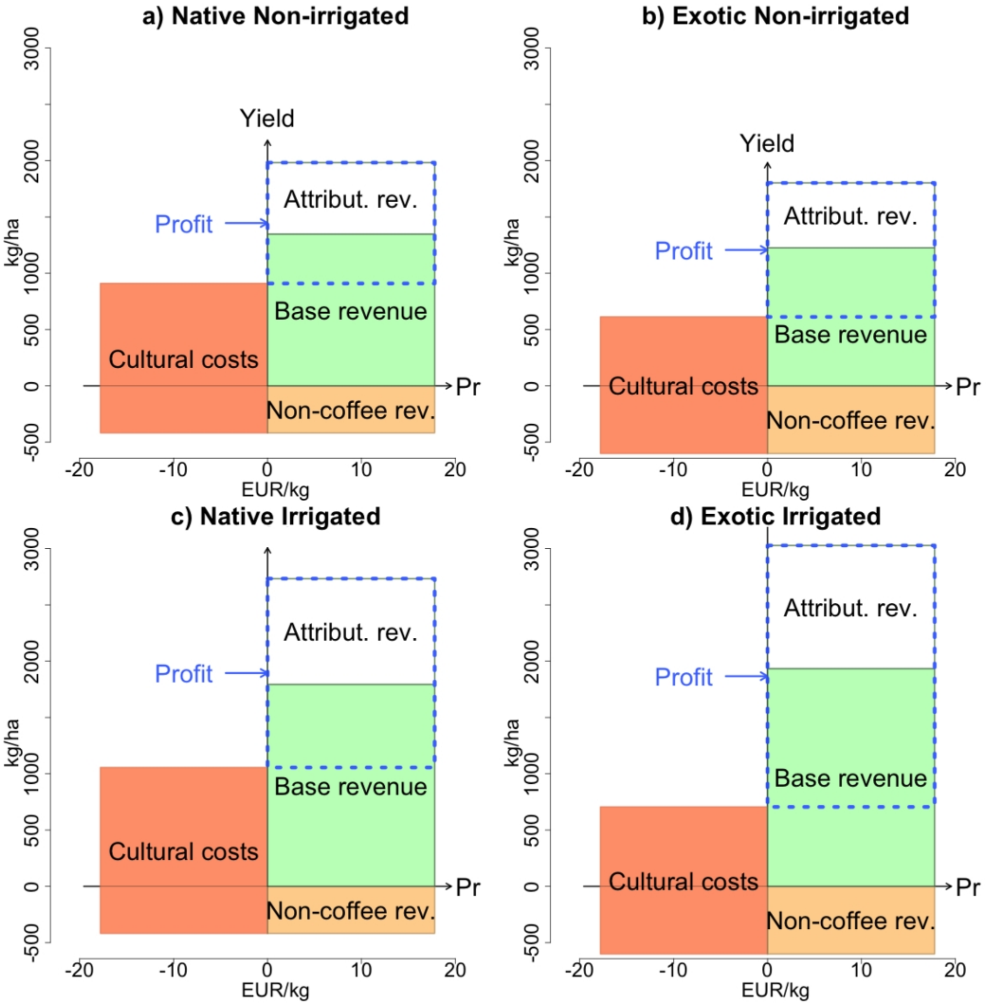
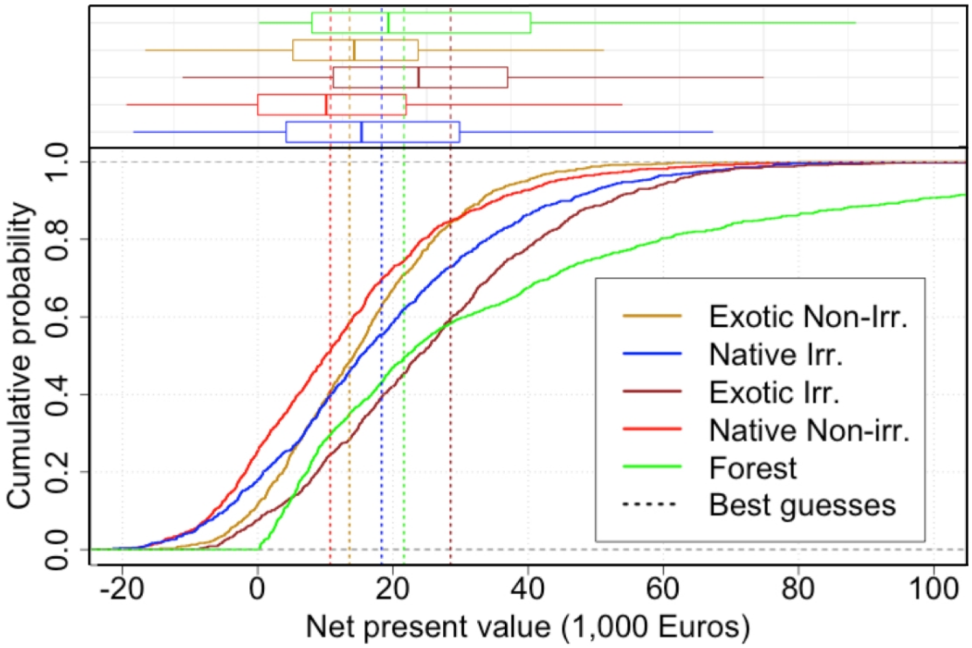


Figure 1. Diagram showing the relationships between coffee yields (both base in green, i.e., independent of pollinator activity, and those attributable to the effect of pollinator activity and hence dependent on the presence of forest ecosystems in white), prices, costs, profits and other accounting variables for a 50-year horizon of one hectare of coffee under four management regimes: under native canopy trees with and without irrigation (panels a and b), or under G. robusta with and without irrigation (c and d). The horizontal axis references the price of coffee adjusted for discounting and the vertical is the yield (kg/hectare/year after first five years). Areas on the graph represent net present value. Boxes in dashed blue lines represents profit. See procedures for detailed calculations.

423x423mm (72 x 72 DPI)



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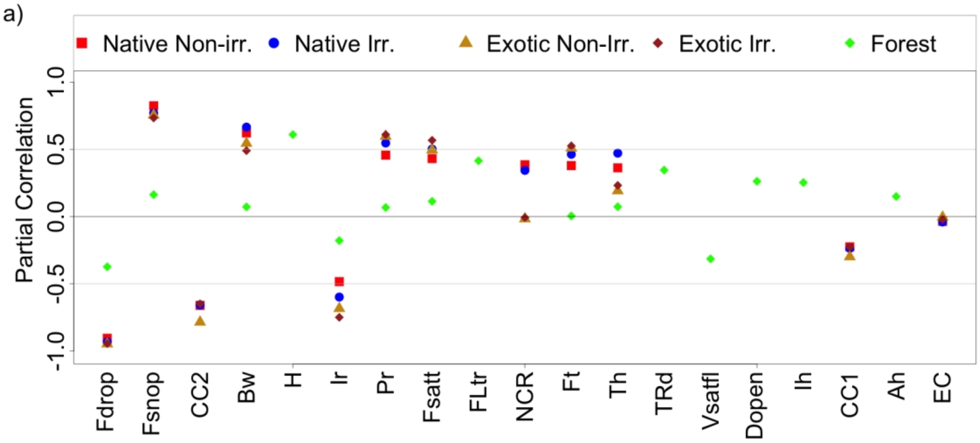
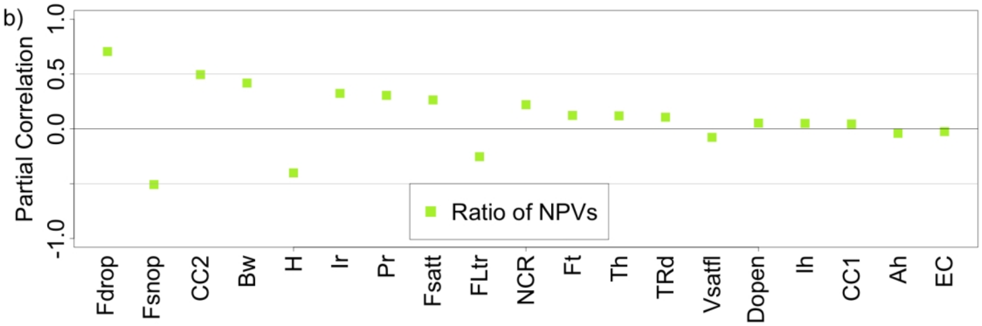


Figure 3. Partial rank correlation coefficients of model parameters for net present values (a) and ratio of net present values (b).

Fruit drop (Fdrop), fruit set without pollination (Fsnop),cultural costs for years six to 50 when coffee becomes productive (CC2), berry weight (Bw), hive density per hectare (H), price of coffee (Pr), interest rate (Ir), flowers per tree (FLtr), number of coffee trees/ha (Th), fruit set attributable to pollination (Fsatt), revenues from pepper and othe non-coffee products (NCR), number of flowers/tree (Ft), number of visits required to saturate one flower (Vsatfl), trips per day (TRd), days during which flowers are open (Dopen), cultural costs for the first five years when coffee is not yet productive (CC1), Number of individuals in Apis dorsata hives (Ih), individuals of a colony foraging at a given moment (Ah), establishment costs (EC)

635x282mm (72 x 72 DPI)



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