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6

7 **Title:** **Shade-tree rehabilitation in vanilla agroforests is yield neutral and**  
8 **may translate into landscape-scale canopy cover gains**

9 **Short title:** Tree rehabilitation in vanilla agroforests

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43 analysis. DAM, AW, and KO coordinated the data collection; TR led  
44 the field team; DAM analysed and visualized the data; DAM led the  
45 writing of the manuscript. All authors contributed to the writing  
46 and gave final approval for publication.

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58 **Manuscript highlights:** - Shade-trees in agroforests are commonly cut due to trade-offs  
59 between shade and yields  
60 - Across a chronosequence with 209 vanilla agroforests, we do not  
61 find such trade-offs  
62 - The lack of this trade-off offers an opportunity for yield-neutral  
63 tree rehabilitation

64 **Keywords:** agroecology, agroforestry, canopy cover, ecosystem services, land-  
65 use history, Madagascar, rehabilitation, restoration, vanilla, yield  
66

## 67 **Abstract**

68 Agroforestry can contribute to an increase in tree cover in historically forested tropical  
69 landscapes with associated gains in biodiversity and ecosystem functioning, but only if  
70 established on open land instead of underneath a forest canopy. However, declines in yields  
71 with increasing shade are common across agroforestry crops, driving shade-tree removal in  
72 forest-derived agroforests and hindering tree regrowth in open-land-derived agroforests. To  
73 understand trajectories of change in tree cover in forest- and open-land-derived agroforests  
74 and the impacts of tree cover on vanilla yields, we studied 209 vanilla agroforests along an  
75 88-year chronosequence in Madagascar. Additionally, we used remotely-sensed canopy  
76 cover data to investigate tree cover change in the agricultural landscape. We found yields to  
77 vary widely but independently of canopy cover and land-use history (forest- vs. open-land-  
78 derived), averaging at  $154.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$  ( $SD = 186.9$ ). Furthermore, we found that forest- and  
79 open-land-derived vanilla agroforests gained canopy cover over time, but that only open-  
80 land-derived agroforests gained canopy height. Canopy cover increased also at the landscape  
81 scale: areas in the agricultural landscape with medium initial canopy cover gained 6.4%  
82 canopy cover over 10 years, but canopy cover decreased in areas with high initial canopy  
83 cover. These opposing trends suggest tree cover rehabilitation across areas covered by vanilla  
84 agroforests, whereas remnant forest fragments in the agricultural landscape were  
85 transformed or degraded. Our results indicate that yield-neutral tree rehabilitation through  
86 open-land-derived agroforestry could, if coupled with effective forest protection, provide  
87 mutually beneficial outcomes for ecosystem functions and agricultural production in a  
88 smallholder-dominated agricultural landscape.

## 89 Introduction

90 Rehabilitation of historically forested open land is widely advocated to re-establish  
91 connectivity and increase ecosystem functions in tropical rainforest landscapes (Bastin and  
92 others, 2019; Chazdon, 2003). To date, governments and institutions have pledged to restore  
93 140 million hectares of land in the tropics (Brancalion and others, 2019). However, realizing  
94 those pledges could jeopardize food security if tree cover restoration replaces cropland,  
95 questioning how feasible (Eitelberg and others, 2016) and indeed desirable (Holl &  
96 Brancalion, 2020) their fulfilment is. In this light, agroforests may provide an opportunity to  
97 combine trees with agricultural production on the same land (De Beenhouwer and others,  
98 2016; FAO, 2017). Agroforests that are established on historically forested open-land hold a  
99 particularly large potential, because open-land-derived agroforests rehabilitate selected  
100 ecosystem functions like erosion control or carbon storage on open land (Martin, Osen, and  
101 others, 2020). To describe this process, we specifically use the word ‘tree rehabilitation’ based  
102 on Chazdon and others (2016), as the focus lies on the rehabilitation of ecosystem functions,  
103 without necessarily restoring ecological integrity. In contrast to this, agroforests planted  
104 under the canopy of existing forests typically contribute to forest degradation (Martin, Osen,  
105 and others, 2020), thus hampering ecosystem functioning and ecological integrity (Coe and  
106 others, 2013; McDowell and others, 2020).

107 Nonetheless, trade-offs between shade cover and yields are common across many key  
108 agroforestry crops (Tscharntke and others, 2011), limiting the potential of these agroforestry  
109 systems to contribute to tree rehabilitation in tropical rainforest landscapes. Such shade-yield  
110 trade-offs are exemplified in coffee and cacao agroforests (Blaser and others, 2018; Steffan-  
111 Dewenter and others, 2007), where felling trees is typically beneficial to farmers aiming at

112 optimizing yields. Finding a balance between ecosystem services, biodiversity and profitability  
113 thus requires targeted incentives (Tscharntke and others, 2014). In their absence, a decrease  
114 in canopy cover and tree height over time commonly occurs (Tscharntke and others, 2011),  
115 but time series or chronosequences, which are necessary to identify trends, are rare (see  
116 Nijmeijer and others (2019) for an exception). Finding farming techniques or crops where  
117 such trade-offs do not inherently occur would, on the other hand, offers an opportunity to  
118 profitably farm crops in high-shade agroforestry systems without the need for further  
119 incentives.

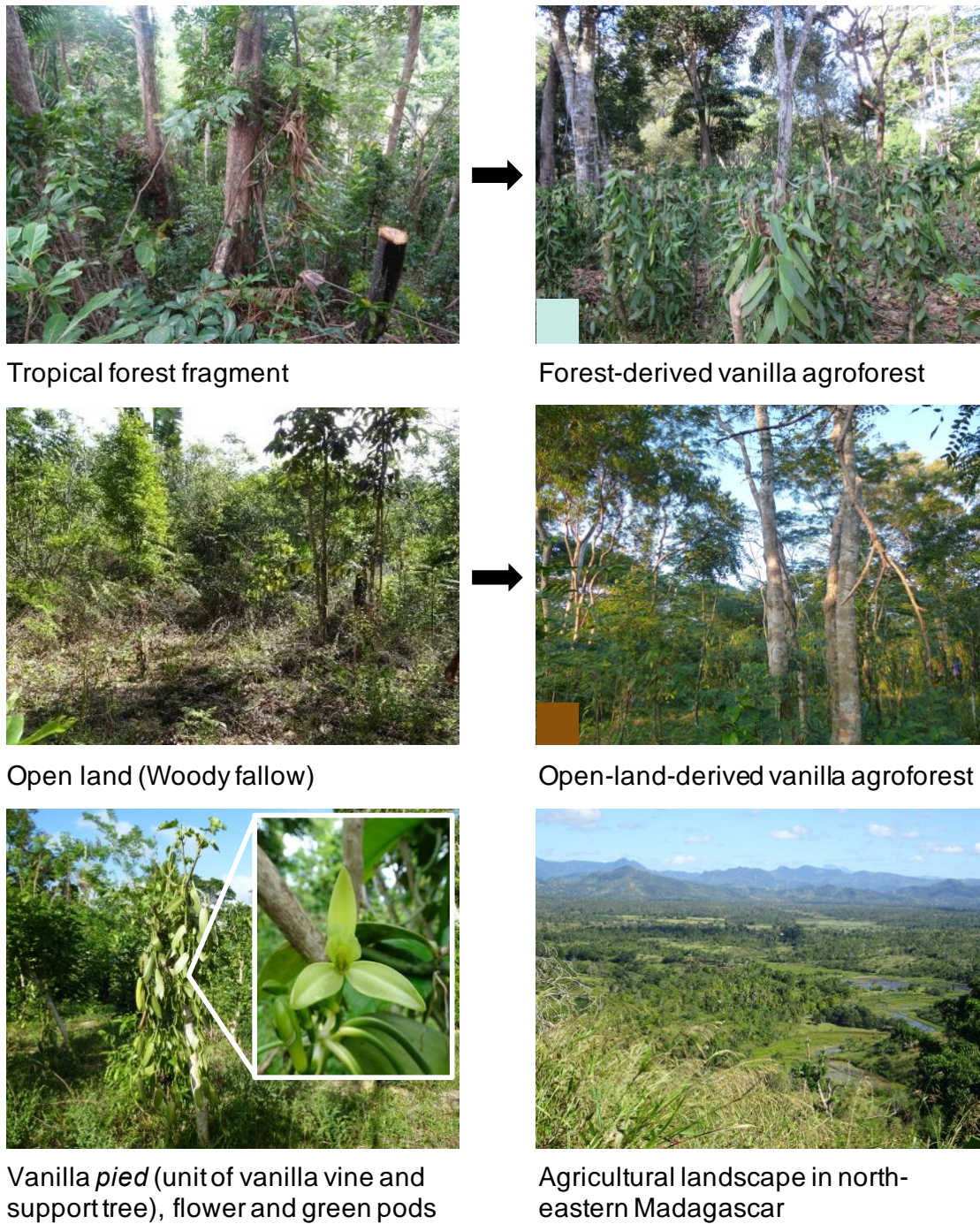
120 One candidate crop where shade-yield trade-offs are currently unknown is the spice vanilla.  
121 When farmed in agroforestry systems, the vanilla orchid (*Vanilla planifolia*) is typically hung  
122 up on support trees which give support to the non-woody vine (Correll, 1953). Vanilla flowers  
123 are then hand pollinated and green pods are harvested nine months later. The green pods  
124 are subsequently cured, thereby developing their distinct flavour and black colouration while  
125 losing roughly 80% of their weight (Havkin-Frenkel & Belanger, 2018). The resulting black  
126 vanilla has strongly increased in price from 2012 to 2019, triggering the expansion of vanilla  
127 farming in Madagascar (Hänke and others 2018; Llopis and others 2019, Supplementary  
128 Material Figure 1).

129 In north-eastern Madagascar, vanilla is the main cash crop for smallholder farmers (Hänke  
130 and others, 2018) who farm the bulk of Madagascar's 40% share on the world market (FAO,  
131 2020). Here, vanilla is almost exclusively produced in rather extensively managed agroforestry  
132 systems without the application of fertilizers, herbicides and pesticides. This is partly in  
133 contrast to other production areas, such as La Réunion or Mexico, where artificial shade  
134 houses are common (Havkin-Frenkel & Belanger, 2018). These extensively managed vanilla  
135 agroforests also have value for biodiversity: various endemic lemur species live in diverse

136 agroforests (Hending and others, 2018). Vanilla agroforests also have a more diverse avifauna  
137 than open land uses (Martin, Andriafanomezantsoa, and others, 2020). Other prominent land  
138 uses in the Malagasy vanilla region include remnant forest fragments, irrigated rice paddies  
139 and hill rice fields with the associated herbaceous and woody fallows, that form part of the  
140 shifting cultivation cycle, locally known as *tavy* (Martin, Andriafanomezantsoa, and others,  
141 2020; Styger and others, 2007). The first cycle of shifting cultivation, where fire is used to  
142 convert forest into hill rice fields, is the main reason for forest loss in the region (Schüßler and  
143 others, 2020; Zaehring and others, 2015). This dynamic is consistent with trends across  
144 most of Africa, but contrasts with trends in the remaining tropics (Curtis and others, 2018;  
145 van Vliet and others, 2012).

146 Vanilla agroforests may be established inside forest fragments or on open fallow land, thereby  
147 differing in land-use history (Martin, Osen, and others, 2020). Forest-derived vanilla  
148 agroforests degrade the forest they are established in but will typically outperform shifting  
149 cultivation, i.e. the replacement of forest with hill rice cultivation, for ecosystem functions  
150 and biodiversity (Martin, Osen, and others, 2020). Open-land-derived agroforests may  
151 instead restore land formerly under hill rice cultivation by rehabilitating tree cover and  
152 preventing the re-occurring fires which characterize the shifting hill rice cultivation system  
153 (Holloway, 2004; Styger and others, 2007). In north-eastern Madagascar, 30% of vanilla  
154 agroforests are forest-derived while 70% are open-land-derived (Hänke and others, 2018),  
155 further underlining the rehabilitation opportunity offered by open-land-derived agroforestry.  
156 The high potential for tree rehabilitation and habitat restoration in Madagascar is also  
157 recognized in a recent study by Brancalion and others (2019), who attribute the 4<sup>th</sup> largest  
158 restoration opportunity area (in terms of benefits and feasibility) of lowland tropical  
159 rainforest to Madagascar. Simultaneously, the country is characterized by high levels of

160 endemism (Goodman & Benstead, 2005) and high deforestation rates (Vieilledent and others,  
 161 2018) and qualifies as a biodiversity hotspot (Myers and others, 2000). This exacerbates the  
 162 need for both effective biodiversity conservation within the existing protected areas as well  
 163 as restoration within the agricultural landscape.



164

165 **Figure 1:** Top row: Forest-derived vanilla agroforests are directly established inside forest.  
 166 Middle row: Open-land-derived vanilla agroforest are established on open land, typically



167 *woody fallow. Bottom row: Vanilla pied (unit of vanilla vine and support tree) and agricultural*  
168 *landscape in north-eastern Madagascar where the study took place. Colour labels indicate*  
169 *contrasting land-use history of vanilla agroforests and are used throughout the manuscript.*  
170 *All photos by the authors.*

171 In this study, we 1) examined how land-use history, canopy cover, agroforest age, planting  
172 density and precipitation influence vanilla yields, 2) assessed tree rehabilitation dynamics  
173 across vanilla agroforests of different age and of contrasting land-use history, and 3)  
174 investigated how tree rehabilitation within vanilla agroforests may transform the landscape  
175 as a whole. To this end, we assessed vanilla yields, canopy cover and canopy height in 209  
176 vanilla agroforests of contrasting land-use history and of different age (0 – 88 years), thus  
177 representing an 88-year chronosequence. Subsequently, we used remotely sensed canopy  
178 cover data to study canopy cover change from 2000-2010 on the landscape-scale. Based on  
179 previous studies from cocoa and coffee agroforests (Blaser and others, 2018; Jezeer and  
180 others, 2017; Perfecto and others, 2005), we expected vanilla yields to decline with increasing  
181 canopy cover. We further anticipated canopy cover and canopy height to decline with  
182 increasing age of forest-derived agroforests, but expected both variables to increase with age  
183 in open-land-derived agroforests, in line with the predictions by Martin, Osen, and others  
184 (2020). At the landscape-scale, we presumed that the ongoing transformation of open fallow  
185 land into open-land-derived agroforests may positively influence canopy cover around the  
186 villages.

## 187 **Methods**

### 188 **Study region**

189 The SAVA region (25 518 km<sup>2</sup> / Latitude: 14° 16' S, Longitude: 50° 10' E) of north-eastern  
190 Madagascar is the historic (Correll, 1953) and current (Hänke and others, 2018) center of

191 global vanilla production and a biodiversity hotspot (Myers and others, 2000). Mean annual  
192 temperature is 23.7 °C and annual rainfall averages at 2238 mm (Mean across 209 focal  
193 agroforests; data from CHELSA climatologies (Karger and others, 2017)). In the southern part  
194 of the SAVA region, where we collected the data (SM Figure 2), the natural vegetation is  
195 tropical rainforest (Vieilledent and others, 2018), but only 35% forest cover remains across  
196 the SAVA region (Ferreira Arruda, 2018).

### 197 **Selection of vanilla agroforests**

198 We first selected 60 villages in a stratified-random way for a previous study (Hänke and  
199 others, 2018). From those 60, we selected 10 villages in a nested stratified-random way that  
200 controlled for village size. Specifically, we randomly selected two villages per village size  
201 category (0-1000 people, 1001-2000 people, 2001-3000 people, 3000-4000 people, > 4000  
202 people). Within each village, we chose 14 households randomly from the 30 households  
203 included in Hänke and others (2018); however, 20 households opted out, leaving us with 120  
204 households.

205 We then visited accessible (< 4h walking return) vanilla agroforests; 33 households did not  
206 own any accessible vanilla agroforests and 27 had more than one agroforest, resulting in a  
207 sample of 123 agroforests owned by 87 households. After collecting data from those  
208 agroforests, but before doing any data analysis, we checked the number of forest-  
209 respectively open-land-derived agroforests in the sample and realised that the number was  
210 uneven (36 vs. 87).

211 We thus decided to include four additional villages from the stratified random sample of 60  
212 villages. For those villages, we knew based on Hänke and others (2018) that their proportion  
213 of forest-derived vanilla agroforests would be high, resulting in roughly even numbers of

214 forest- and open-land-derived agroforests in the final sample. In those four villages, we visited  
215 65 households included in Hänke and others (2018). Those households owned 86 additional  
216 accessible agroforests (7 open-land-derived, 79 forest-derived). This led to a total sample of  
217 115 forest-derived and 94 open-land-derived agroforests (209 in total) owned by 152  
218 households across 14 villages. SM Figure 2 shows all 14 villages with field data and the 60  
219 villages from the initial sample.

### 220 **Data collection in agroforests**

221 We collected field data between July and October 2018 after the 2018 vanilla harvest.  
222 During visits to the agroforest, we asked vanilla agroforest owners in Malagasy about 1) the  
223 realized yield of green vanilla in 2017 and 2018 [kg agroforest<sup>-1</sup>], 2) estimated green vanilla  
224 theft from the agroforest before harvest in 2017 and 2018 [kg agroforest<sup>-1</sup>], 3) the number of  
225 *pieds* (combination of vanilla vine and support tree; **Figure 1**) in the agroforest, 4) the year in  
226 which the agroforest was established, and 5) whether the agroforest was forest- or open-  
227 land-derived (*sensu* Martin and others 2020). Vanilla yields are commonly reported as the  
228 weight of green rather than black pods, since green pod weight is independent of the curing  
229 technique (Havkin-Frenkel & Belanger, 2018). We subsequently added estimated theft to the  
230 realized yields as we were interested in the productivity of the agroforests rather than the  
231 farmers' income. We measured agroforest size during perimeter walks using handheld GPS  
232 devices and applied a slope correction (based on the digital surface model 'ALOS World 3D'  
233 (Japan Aerospace Exploration Agency, 2018)) to account for different steepness of the terrain.  
234 By combining yield data and the slope-corrected agroforest size, we calculated mean green  
235 vanilla yield per hectare [kg ha<sup>-1</sup> year<sup>-1</sup>] across the two years for further analysis. Based on

236 slope-corrected agroforest size and number of *pieds*, we calculated planting density [*pieds*  
237 ha<sup>-1</sup>].

238 We used tablets to assess canopy cover, as photos from mobile devices have been found to  
239 be an adequate, cheap and fast technique to assess canopy cover (Bianchi and others, 2017;  
240 Tichý, 2016). Observers held the tablet (Lenovo YT3-850F) above their head (circa 190 cm)  
241 and used the built-in camera (Lenovo 5C28C02840) with the standard lens and auto-exposure  
242 to take a photo in azimuthal direction. We repeated this procedure at nine locations per plot  
243 (see Supplementary Materials), resulting in 1881 photos from 209 agroforests. We then  
244 classified all photos into vegetation/sky using the R-Package *caiman* (Diaz and Lencinas 2015;  
245 more details on canopy cover classification in Supplementary Materials) and calculated mean  
246 canopy cover across all 9 photos to derive one value per agroforest. Additionally, the observer  
247 estimated the highest point of vegetation above each camera position, enabling us to  
248 calculate the mean canopy height across 9 locations for each agroforest.

249 Some farmers did not know the number of *pieds* and/or the year of establishment of their  
250 agroforest, leading to missing data for planting density and agroforest age in 8 and 3 cases,  
251 respectively (out of 209). We imputed this data for the linear mixed effect models using the  
252 mean of each respective variable.

### 253 **Data extraction from raster layers**

254 To investigate how precipitation and temperature influenced vanilla yields, we extracted  
255 annual mean temperature and annual precipitation for each agroforest from the CHELSA  
256 climatologies with a resolution of 30 arc sec (Karger and others, 2017) using the plot center  
257 as a reference point. Due to the strong correlation of annual mean temperature and annual  
258 precipitation (-0.76, Pearson correlation coefficient), we only used annual precipitation for

259 further analysis. Analogously, we obtained the elevation of each agroforest from the digital  
260 surface model 'ALOS World 3D' (Japan Aerospace Exploration Agency, 2018). Lastly, we  
261 extracted the percentage landscape forest cover in a radius of 250 m around plot centres  
262 using published binary forest cover data for the year 2017 (Vieilledent and others, 2018).

### 263 **Analysis of vanilla yields, canopy cover and canopy height**

264 We used three linear mixed-effects models to analyse variation in vanilla yields, canopy cover  
265 and canopy height, with 'household' (owner of agroforest, N= 152) and 'village' (N=14) as  
266 random effects in all models. We fitted all models using the R-Package *lme4* version 1.1.21  
267 (Bates, 2014) and scaled all explanatory and response variables to zero mean and unit  
268 variance, allowing for direct comparison of effect sizes within and across models (Harrison  
269 and others, 2018). We used an alpha level of 0.05 and calculated marginal and conditional R<sup>2</sup>-  
270 values for all models (Nakagawa & Schielzeth, 2013). We used QQ-plots to assess normality  
271 of model residuals and tested for variable inflation; none of the models had significant  
272 deviations in the QQ-plots or variable inflation values above 1.5.

273 In a first model, we assessed the variation of green vanilla yield [kg ha<sup>-1</sup>] in relation to land-  
274 use history (forest vs. open-land-derived; coded as 1 vs. 0), canopy cover, age of agroforest,  
275 planting density and annual precipitation. To reach normality of model residuals, we applied  
276 a Box-Cox transformation to the response variable (Box & Cox, 1964). We determined a  
277 lambda of 0.25 to be suitable for the transformation using the *boxcox* function of the R-  
278 package *mass* version 7.3.51.4 (Ripley and others, 2013). Due to the highly right-skewed  
279 nature of the age and planting density data, we square root transformed these two variables.  
280 We additionally included interactions between land-use history and all explanatory variables  
281 to test whether responses would differ between forest- and open-land-derived agroforests.

282 Statistically speaking, the full yield model read: green vanilla yield  $\sim$  land-use history + canopy  
283 cover + age of agroforest + planting density + annual precipitation + land-use history \* canopy  
284 cover + land-use history \* age of agroforest + land-use history \* planting density + land-use  
285 history \* annual precipitation + (1 | village / household).

286 In a second and third model, we assessed factors influencing canopy cover (untransformed)  
287 and canopy height (Box-Cox-transformed with lambda 0.35), respectively. We used land-use  
288 history, age of agroforest, elevation, landscape forest cover and planting density as  
289 explanatory variables. Again, we square root transformed the age and planting density data  
290 and included interactions between land-use history and all explanatory variables. Statistically  
291 speaking, the full canopy cover model read: canopy cover  $\sim$  land-use history + age of  
292 agroforest + elevation + landscape forest cover + planting density + land-use history \* age of  
293 agroforest + land-use history \* elevation + land-use history \* landscape forest cover + land-  
294 use history \* planting density + (1 | village / household). The full canopy height model was  
295 exactly the same, except for the response variable.

296 In the yield and canopy cover model, none of the interactions were significant, prompting us  
297 to present the reduced model without interactions. In the canopy height model, only the  
298 interaction between age and land-use history was significant at the  $p < 0.05$  level. We thus only  
299 kept this interaction in the reduced model. All models are presented in full and reduced (i.e.  
300 final) form in the Supplementary Materials (SM Tables 1-3).

301 To visualize the models, we calculated estimated marginal means and their 95% confidence  
302 intervals using the R-Package *emmeans* version 1.4.5 (Length and others, 2018). We further  
303 back-transformed the estimated marginal means to the original distributions to facilitate the  
304 interpretation of model results.

## 305 **Analysis of canopy cover dynamics in the agricultural landscape**

306 We used remotely sensed canopy cover data to explore how observed tree rehabilitation  
307 within agroforests translated to the landscape scale. We obtained canopy cover data for the  
308 year 2000 and 2010 from a Landsat-derived product of continuous canopy cover values with  
309 30 m resolution (Hansen and others, 2013). Using the *raster* R-package version 3.0.12  
310 (Hijmans and others, 2019), we subtracted the 2000 layer from the 2010 layer to obtain a new  
311 raster layer with tree cover gains and losses, respectively (change of canopy cover between  
312 2000 and 2010 [%]). We restricted both layers to an area of 2 km around the centers of 60  
313 focal villages (excluding any offshore areas), for which we knew that vanilla farming was  
314 common and from which we selected the villages for the plot-based part of this study (Village  
315 selection described in Hänke and others, 2018). We chose 2 km because agroforests in this  
316 range will typically belong to the focal village (*personal observation*). We then fitted a  
317 generalized additive mixed model (GAMM) using the R-package *mgcv* version 1.8-28 (Wood,  
318 2012) to evaluate how the dependent variable ‘initial canopy cover in the year 2000’  
319 determined the independent variable ‘change in canopy cover from 2000 to 2010’. We  
320 included ‘village’ as a random effect and also included longitude and latitude of each raster  
321 cell as random effects to control for spatial autocorrelation. Therefore, the model read:  
322 change in canopy cover ~ initial canopy cover + (1 | village) + (1 | longitude) + (1 | latitude).  
323 We further ran the model on the basis dimension  $k = 8$ . We checked model assumptions using  
324 the *gam.check* function of the *mgcv* R-package which demonstrated  $k=8$  to be adequate and  
325 a near-normal distribution of residuals.

326 We analysed all data in R version 3.6.0 (R Core Team, 2019). The underlying data and R-code  
327 are publicly available (see data availability statement).

## 328 Results

### 329 Determinants of vanilla yields

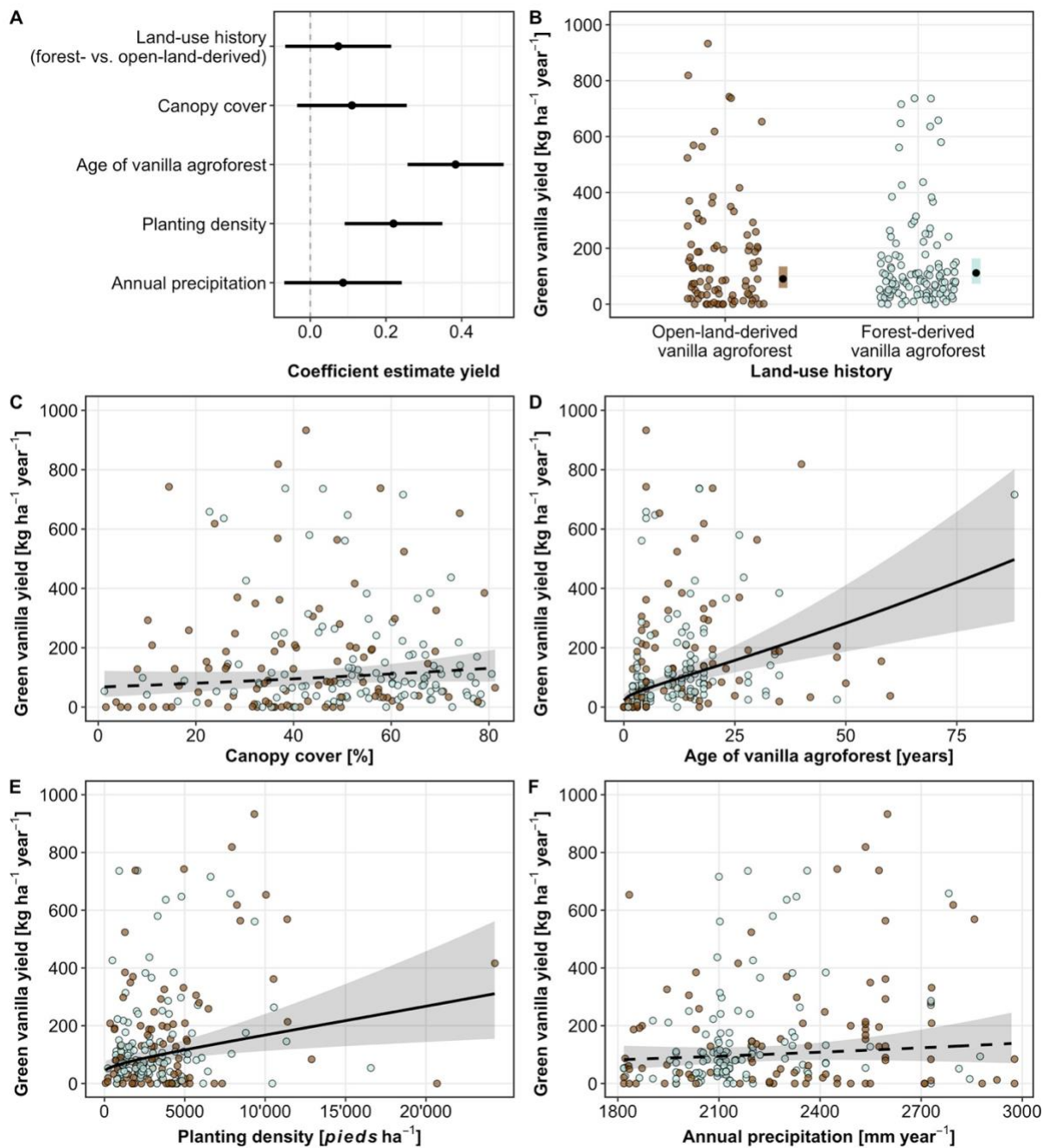
330 Green vanilla yield per *ped* varied strongly and ranged from 0 – 860 g *ped*<sup>-1</sup> year<sup>-1</sup> with an  
331 average of 69.9 g *ped*<sup>-1</sup> year<sup>-1</sup> (*SD* = 112.3; N = 209 agroforests; mean from 2017 and 2018).

332 Note that this estimate includes *ped*s without any yield as it is calculated by dividing the total  
333 yield by the number of *ped*s in each agroforest. Similarly, green vanilla yields differed strongly  
334 across agroforests, ranging from 0 - 932.7 kg ha<sup>-1</sup> year<sup>-1</sup> with an average of 154.6 kg ha<sup>-1</sup> year<sup>-1</sup>  
335 (*SD* = 186.9; N= 209 agroforests; mean of 2017 and 2018). Using farmgate vanilla prices for  
336 the year 2017 (Hänke and others, 2018), this average yield translates into gross earnings of  
337 4684 € ha<sup>-1</sup>. However, a household in this dataset only farmed 0.46 ha (*SD* = 0.42; N=152) of  
338 accessible vanilla agroforests in average. The difference in green vanilla yield per ha between  
339 the two years was small (2017: 158.8 kg ha<sup>-1</sup> (*SD* = 200.1); 2018: 150.2 kg ha<sup>-1</sup> (*SD* = 202.6))  
340 and a Wilcoxon rank sum test revealed no significant differences between years (*W* = 21267,  
341 *p* = 0.642, N = 209 agroforests). Farmers reported green vanilla theft in 26 agroforests (12.4%)  
342 for 2017 and in 25 agroforests (12.0%) for 2018. Farmers who reported theft, stated that they  
343 lost on average 9.15 kg (*SD* = 15.3) green vanilla per agroforest in 2017 and 8.72 kg (*SD* = 8.7)  
344 per agroforest in 2018.

345 Our yield model (**Figure 2**, SM Table 1) revealed that vanilla yields varied independently of  
346 land-use history, i.e. whether an agroforest was forest- or open-land-derived. Yields were  
347 furthermore not significantly related to canopy cover and annual precipitation. Yields rose  
348 with increasing agroforest age and planting density. Overall, the marginal R<sup>2</sup>-value of the  
349 model was 0.216 while the conditional R<sup>2</sup>-value was 0.450. The difference between the two  
350 values was mainly driven by the random intercept variance for the random effect 'household'



351 ( $\tau_{00} = 0.26$ ); the random intercept variance for the random effect 'village' was negligible ( $\tau_{00} =$   
 352 0.03)



353

354 **Figure 2:** Results of a linear mixed effect model explaining green vanilla yield [kg ha<sup>-1</sup> yr<sup>-1</sup>]  
 355 across 209 agroforests. **A:** Scaled effect plot of the reduced yield model for all five predictors.  
 356 **B-F:** Green vanilla yields as a function of land-use history (**B**), canopy cover [%] (**C**), age of  
 357 vanilla agroforest [years] (**D**), planting density [pieds ha<sup>-1</sup>] (**E**) and annual precipitation [mm  
 358 year<sup>-1</sup>] (**F**). Green vanilla yields were independent of land-use history and positively associated  
 359 with all four continuous variables, but the relationships between canopy cover and yields as  
 360 well as annual precipitation and yields were not significant. Lines and black dots respectively

361 *show back-transformed estimated marginal means based on the linear mixed-effect model*  
362 *and shaded areas depict 95% confidence intervals. Points are raw data separated in forest-*  
363 *derived (blue) and open-land-derived (brown) agroforests. A table with model results can be*  
364 *found in the Supplementary Materials (SM Table 1).*

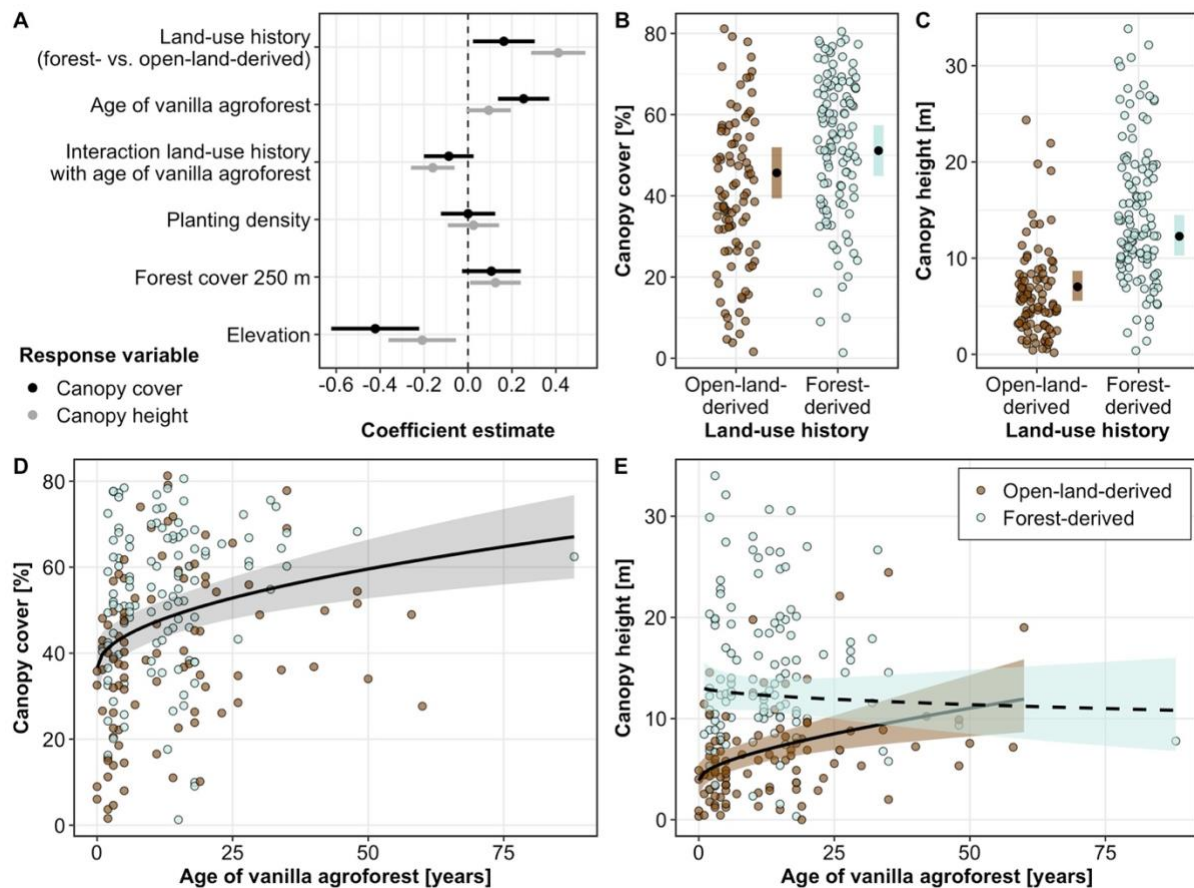
### 365 **Determinants of canopy cover and canopy height**

366 Canopy cover was 12.8% (estimated marginal means 6.3%) higher in forest-derived vanilla  
367 agroforests (mean = 52.9%,  $SD = 17.2$ ) compared to open-land-derived agroforests (mean =  
368 40.1%,  $SD = 19.0$ ; Figure 3, SM Table 2). The age of the agroforests differed along the  
369 chronosequence between 1 and 88 years in forest-derived agroforests and between 0 and 60  
370 years in open-land-derived agroforests. Age positively related to canopy cover, in both forest-  
371 and open-land derived agroforestry: canopy cover increased by 39.5% (CI 34.5 – 44.6%) over  
372 88 years.

373 Similarly, canopy height was 8.2 m (estimated marginal means 5.2 m) higher in forest-derived  
374 agroforests (mean = 14.5 m,  $SD = 7.3$ ) compared to open-land-derived agroforests (mean =  
375 6.3 m,  $SD = 4.6$ ; Figure 4, SM Table 3). The age of the agroforest positively affected canopy  
376 height in open-land-derived agroforests where canopy height increased on average by 8 m  
377 (CI 6.1 – 10.3 m) over 60 years. Canopy height in forest-derived agroforests was relatively  
378 stable (mean decrease of 1.7 m (CI -2.7 – -0.4) over 60 years and a mean decrease of 2.1 m  
379 (CI -3.9 – +0.4) over 88 years).

380 Vanilla planting density did not correlate with canopy cover or height (Figure 3 & 4, SM Table  
381 2 & 3). Furthermore, agroforests with more surrounding forest cover had taller trees and  
382 greater canopy cover, but confidence intervals overlapped zero for the latter (Figure 3 A).  
383 Elevation was negatively associated with both tree height and canopy cover (Figure 3 A). The  
384 canopy cover model (Figure 3, SM Table 2) had a marginal  $R^2$ -value of 0.34 and a conditional  
385  $R^2$ -value of 0.56, while the canopy height (Figure 4, SM Table 3) model had a marginal  $R^2$ -

386 value of 0.35 and a conditional  $R^2$ -value of 0.74. The substantial difference between  
 387 conditional and marginal  $R^2$ -values stemmed from the strong explanatory power of the  
 388 random effect 'household' (canopy cover model:  $\tau_{00} = 0.16$  / canopy height model:  $\tau_{00} = 0.37$ );  
 389 the random intercept variance for the random effect 'village' was small (canopy cover model:  
 390  $\tau_{00} = 0.07$  / canopy height model:  $\tau_{00} = 0.02$ ).



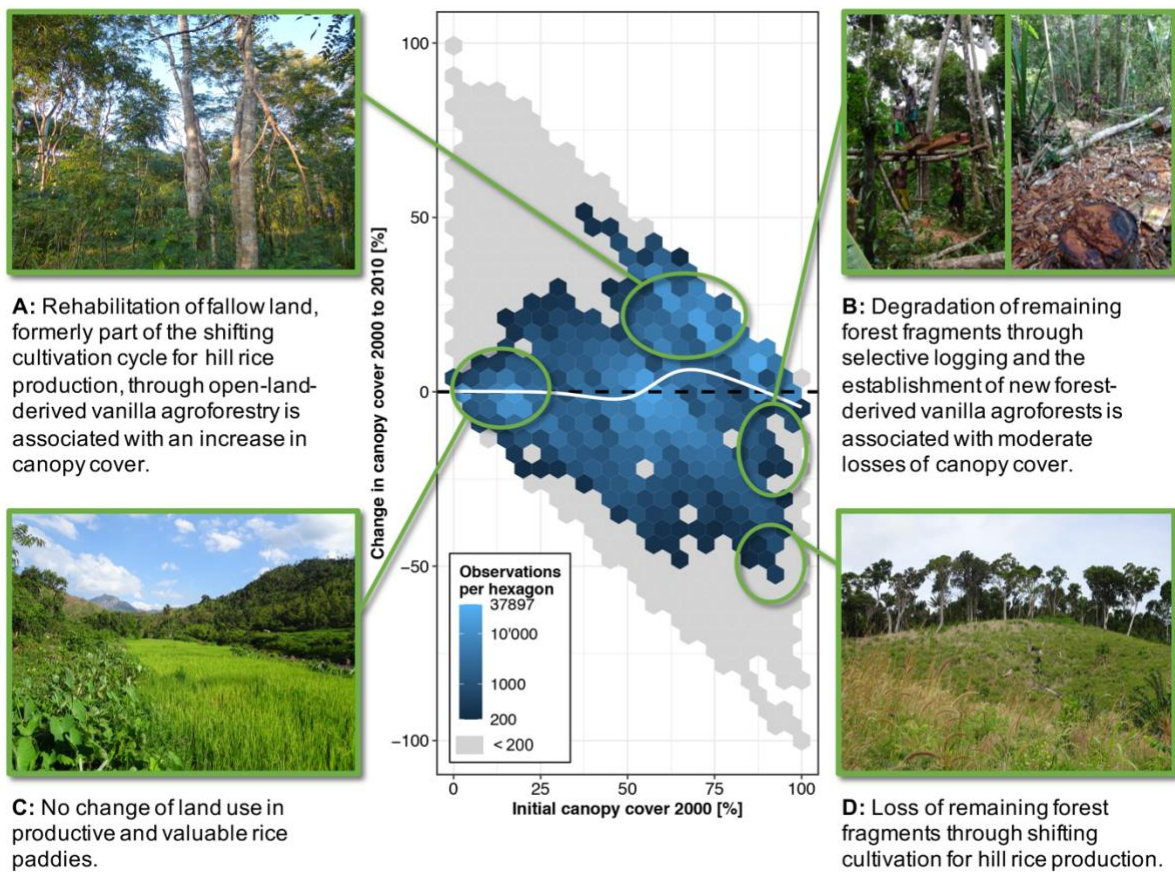
391

392 **Figure 3:** Results of two linear mixed effect models explaining canopy cover [%] and canopy  
 393 height [m] across 209 vanilla agroforests. **A:** Scaled effect plot of the reduced canopy cover  
 394 model (black) and the reduced canopy height model (grey) for all five predictors, including the  
 395 interaction between land-use history and age [years] in the canopy height model. **B & C:**  
 396 Forest-derived agroforests (blue) had both higher canopy height and higher canopy cover  
 397 compared to open-land-derived agroforests (brown). **D:** Older forest- and open-land-derived  
 398 agroforests had higher canopy cover. **E:** Older agroforests also had higher canopies, but only  
 399 if open-land-derived. Lines and black dots respectively show back-transformed estimated  
 400 marginal means based on linear mixed-effect models and shaded areas depict 95% confidence  
 401 intervals. Points are raw data separated in forest-derived (blue) and open-land-derived  
 402 (brown) agroforests. Tables with the results of both models can be found in the supplementary  
 403 materials (SM Table 2 and 3).

404

405 **Canopy cover dynamics in the agricultural landscape**

406 Areas within the agricultural landscape around villages that had low initial canopy cover in  
407 the year 2000 experienced little change from 2000 to 2010 (**Figure 4 C**, SM Table 4). Areas  
408 with medium to high initial canopy cover experienced an increase in canopy cover, reaching  
409 the maximum increase of 6.4% at 68.3% initial canopy cover (**Figure 4 A**). Areas with very high  
410 initial canopy cover lost in average 4.4% of canopy cover (**Figure 4 B & D**). Overall, canopy  
411 cover increased by 2.7%. The general additive model explained 8.0% of the variation in the  
412 data.



413

414 **Figure 4:** Canopy cover dynamics in the agricultural landscape in a 2 km circle around centres  
415 of 60 focal villages between 2000 and 2010 using canopy cover raster data with 30 m  
416 resolution (Hansen and others, 2013). Canopy cover increased overall by 2.7%, driven by  
417 canopy cover increase in areas with medium to high initial canopy cover (e.g. vanilla

418 *agroforests; A). Canopy cover did, however, decrease in areas with very high initial canopy*  
419 *cover (e.g. forest; B, D) and was stable in areas with little initial canopy cover (e.g. rice paddies;*  
420 *C). The central plot shows hexagon bins of bin-width 5% which are coloured according to the*  
421 *number of 30x30 m raster cells (i.e. observations) within each hexagon bin. Hexagon bins with*  
422 *less than 200 observations are grey. The white line depicts predicted outcomes of a general*  
423 *additive model explaining change in canopy cover (SM Table 4). All photos by the authors.*

## 424 **Discussion**

425 Across an 88-year chronosequence of 209 agroforests in the SAVA region of north-eastern  
426 Madagascar, we found vanilla yields to vary widely and to be positively affected by planting  
427 density and agroforest age, while land-use history, canopy cover, and precipitation had no  
428 effects on yields. Older vanilla agroforests had higher canopy cover, and, if open-land-derived,  
429 also greater canopy height. On the landscape-scale, areas within the agricultural landscape  
430 with medium canopy cover gained canopy cover between the years 2000 and 2010.

### 431 **Determinants of vanilla yields**

432 We found vanilla yields to be hugely variable across agroforests, ranging from 0 - 932.7 kg  
433 green vanilla per hectare. This variability was driven by variable yields per *piéd* (unit of  
434 support tree and vanilla vine) and planting densities. Such variability is typical for smallholder  
435 agroforests in tropical countries (Clough and others, 2011) and points towards large yield gaps  
436 caused by sub-optimal management practices (Lobell and others, 2009). This also suggests a  
437 large intensification potential in existing agroforests and opportunities for sustainable  
438 intensification (Tilman and others, 2011). Our mean yield estimate of 154.6 kg ha<sup>-1</sup> is lower  
439 than most other vanilla yield estimates, but published studies cover a large range of rather  
440 intensive systems, including plantations with artificial shade (Supplementary Material Table  
441 1), potentially explaining lower yields in rather extensively managed Malagasy agroforests.  
442 Our mean yield estimate of 154.6 kg ha<sup>-1</sup> translates into gross earnings of annually 4684 € ha<sup>-1</sup>

443 <sup>1</sup>, exhibiting the exceptional income opportunity vanilla provides under the high prices of the  
444 year 2017 (Hänke and others, 2018). However, an average rural household in the study region  
445 only sells 51.6 kg of green vanilla per year (Hänke and others 2018; also including households  
446 which did not sell any vanilla) and labour demands for the crop are high (Correll, 1953).  
447 Furthermore, high vanilla prices have led to a surge in local living costs, which are estimated  
448 at 5751 € per household and year (Hänke & Fairtrade International, 2019), and vanilla theft is  
449 commonplace (Neimark and others, 2019), further impairing the situation for farmers.

450 In contrast to other studies (Havkin-Frenkel & Belanger, 2018; Santosa and others, 2005), we  
451 do not see yield declines after a certain plantation age (**Figure 2**, SM Table 1). The explanation  
452 for this is twofold: farmers constantly establish new *pieds*, resulting in old agroforests that  
453 still contain vanilla vines of young and medium age (*DAM personal observation*). Furthermore,  
454 constant ‘looping’ of vines on the same *piéd* is common: hereby, vanilla vines are guided back  
455 down to the soil where new roots establish (Fouché & Jouve, 1999). The originally planted  
456 part of the vine may die at some point, but the vanilla plant can survive due to the water and  
457 soil access that the additional roots provide. Given that new *pieds* are also propagated by  
458 vine-cuttings (Fouché & Jouve, 1999; Havkin-Frenkel & Belanger, 2018), planting of new *pieds*  
459 and looping are comparable processes. In combination with the relatively short time to first  
460 produce (circa three years; Havkin-Frenkel and Belanger 2018), the looping of vanilla vines  
461 may lead to stable yields over time and could thus avoid boom and bust cycles. Such cycles  
462 are a common occurrence in other agroforestry crops like cacao (Clough and others, 2009)  
463 and refer to farmers realising short-term increases in yields through shade tree removal at  
464 the expense of associated biodiversity and ecosystem functions (Tscharntke and others,  
465 2011). The resulting yield increase may be followed by a decrease, caused by elevated pest  
466 pressure and dwindling soil fertility (Clough and others, 2009). Falling yields prompt the

467 abandoning of plantations and further forest conversion to agroforestry elsewhere (Clough  
468 and others, 2009). The likely absence of these busts in vanilla agroforests does hence point  
469 towards the long-term sustainability of these agroforestry systems.

470 We also found no link between precipitation and vanilla yields using down-scaled climate data  
471 (**Figure 2**, SM Table 1), suggesting that all villages where this data was collected have suitable  
472 general growing conditions. Nonetheless, the data is not year- or season-specific and can thus  
473 only represent general differences in precipitation between sites, possibly hiding effects  
474 caused by exceptionally dry or wet years or seasons.

#### 475 **Increasing vanilla yields without impairing canopy cover**

476 We show that vanilla yields vary independently of canopy cover suggesting that no trade-offs  
477 exist between yields and maintaining or restoring trees (**Figure 2**, SM Table 1), much in  
478 contrast to comparable crops, where yields typically decline above 40% canopy cover, for  
479 example in cacao (Blaser and others, 2018; Clough and others, 2011) or coffee (Jezeer and  
480 others, 2017; Perfecto and others, 2005). The here-shown independence of yields and canopy  
481 cover enables farmers to maintain remnant forest trees, which are highly beneficial for  
482 ecosystem services and biodiversity (Tscharntke and others, 2011), in forest-derived  
483 agroforests, at no direct cost. Furthermore, tree and canopy cover rehabilitation in open-  
484 land-derived agroforests is also possible without compromising on yields. The independence  
485 of vanilla yields and shade is supported by plant-physiological experiments which show that  
486 vanilla performs well under various light regimes (Díez and others, 2017).

487 Interestingly, vanilla planting density was independent of canopy cover and canopy height  
488 (**Figure 23**, SM Table 2). This suggests that closing yield gaps is possible by planting vanilla  
489 *pieds* more densely and that doing so does not *per se* impair canopy cover or height within

490 the currently existing planting density range. Maintaining or promoting trees will likely have  
491 positive effects on biodiversity and ecosystem functions (Leakey, 2014; Tschardtke and  
492 others, 2011). For example, predation rates rise with increasing stem density in vanilla  
493 agroforests of north-eastern Madagascar (Schwab and others, 2020), indicating that trees  
494 promote pest control. In sum, the possibility to plant vanilla more densely without impairing  
495 canopy cover further strengthens the case for sustainable intensification opportunities in  
496 vanilla agroforestry.

#### 497 **Limitations of yield data**

498 Despite methodological improvements over, to our knowledge, all previous studies (SM Table  
499 1), this study lacks detail on many potential drivers of vanilla yields. This is highlighted by the  
500 strong random intercept variance. The random effect 'household' might reflect differences in  
501 management practices between households (Hänke and others, 2018), while 'village' might  
502 represent biotic or abiotic village-level effects, such as different soil properties. We also  
503 acknowledge that the estimation of the weight of stolen vanilla pods, which we had to factor  
504 in for ~12% of agroforests, brings in additional uncertainty. Lastly, our study cannot draw  
505 conclusions beyond the range of the data examined, for example the effects of shade on  
506 vanilla yields in highly intensified systems. We thus call for more research on vanilla yield  
507 determinants that may generate more applicable management advice for farmers.

#### 508 **Increasing canopy cover and tree height over time**

509 Tree rehabilitation in agroforestry systems is a global priority (FAO, 2017). However, many  
510 tropical agroforests of key cash crops like cacao or coffee are forest-derived, thus typically  
511 contributing to forest degradation rather than tree rehabilitation (Martin, Osen, and others,  
512 2020). Open-land derived agroforests, on the other hand, may contribute to tree



513 rehabilitation, but empirical chronosequences that document tree recovery in open-land  
514 derived agroforests are rare (but see Nijmeijer and others (2019)). Here we show that canopy  
515 cover is higher in older forest- and open-land-derived agroforests than in younger ones  
516 (**Figure 2**, SM Table 2). Furthermore, trees were taller in older open-land-derived agroforests,  
517 but not in older forest-derived agroforest (**Figure 2**, SM Table 3). This suggests that open-  
518 land-derived agroforests can play a key role in tree rehabilitation, given that they originate  
519 from open fallow land. They could thus contribute to increased carbon storage (Nair and  
520 others, 2009) and the restoration of ecosystem services (De Beenhouwer and others, 2013)  
521 while providing new habitat for tree-dependent taxa (Clough and others, 2011). To what  
522 extent this will be the case also depends on the tree species that farmers allow to regenerate  
523 or plant. Here, native trees will be necessary for many biodiversity benefits while introduced  
524 fruit and timber trees could provide benefits to farmers (Tscharntke and others, 2011).

525 In contrast to open-land-derived agroforests, canopy cover in forest-derived agroforests will  
526 likely only recover after an initial drop at the time of establishment (Martin, Osen, and others,  
527 2020), which is not covered here as our chronosequence does not include forest fragments.

528 The stable tree height is in line with this interpretation, as the removal of single trees at time  
529 of establishment may not reduce mean tree height at the plot level. Alternatively, the  
530 resulting chronosequence could also stem from a change of practices over time, resulting in  
531 recently established forest-derived agroforests with low canopy cover in the  
532 chronosequence.

533 Taken together, our results show that forest-derived vanilla agroforests may have relatively  
534 stable canopy cover over time and highlight the potential of open-land-derived agroforests  
535 to restore ecosystem functions in cultivated landscapes. The transformation of land under

536 shifting cultivation into cash cropping systems is furthermore in line with regional  
537 (Andriatsitohaina and others, 2020) and global trends (van Vliet and others, 2012).

### 538 **Canopy cover dynamics in the agricultural landscape**

539 We used remotely sensed canopy cover data to explore how observed plot-scale tree  
540 rehabilitation translates to the landscape-scale. Comparing canopy cover changes between  
541 2000 and 2010, we found that areas with lowest initial canopy cover, probably mostly rice  
542 paddies, had stable canopy cover (**Figure 24**, SM Table 4). This is to be expected, given the  
543 high productivity of irrigated rice and its local importance for food security (Hänke and others,  
544 2018; Laney & Turner, 2015), which make a conversion of rice paddies to other land uses  
545 unlikely. Areas with very high canopy cover, i.e. forest fragments around villages, lost canopy  
546 cover over time. Here, small losses may represent forest degradation through selective  
547 logging for timber or through the establishment of new forest-derived vanilla agroforests.  
548 Some of these areas also showed large losses, likely reflecting shifting cultivation, where  
549 forest is cut and burned for hill rice cultivation (**Figure 4**).

550 Areas with medium to high initial canopy cover showed increases in canopy cover, most likely  
551 representing fallows that were transformed to open-land-derived vanilla agroforests. Here,  
552 the cessation of repeated burning for shifting cultivation, that comes with the establishment  
553 of permanent agroforestry, may have enabled tree rehabilitation on the land, as observed  
554 inside the plots.

555 Overall, these dynamics resulted in a net increase in canopy cover on the landscape scale, as  
556 observed for agricultural landscapes across Madagascar (Zomer and others, 2016). The  
557 combination of canopy cover gains and losses may be positive for species and ecosystem  
558 services that can be provided by areas with medium canopy cover, such as the provision of

559 fruit or firewood. Forest-dependent species and ecosystem services that depend on high  
560 canopy cover, as found in forest, will suffer. Conservation of remaining forests is thus  
561 necessary to conserve the large share of Malagasy biodiversity that cannot persist outside  
562 forest (Irwin and others, 2010). Furthermore, the forests of north-eastern Madagascar have  
563 some of the highest carbon stocks of all Malagasy forest (Vieilledent and others, 2016),  
564 underlining the importance of forest conservation also in light of climate change mitigation.  
565 Importantly, these findings are limited to the agricultural landscape around 60 focal villages  
566 that are predominantly not at the deforestation frontier. Canopy cover dynamics might be  
567 different around villages closer to large connecting forest blocks, where an overall increase in  
568 canopy cover seems unlikely given the ongoing deforestation trend in north-eastern  
569 Madagascar (Vieilledent and others, 2018). Further research elucidating the differences in  
570 canopy cover dynamics between villages close and far away from the forest frontier will hence  
571 be highly relevant.

## 572 **Conclusion**

573 Our main finding, that yields and canopy cover in vanilla agroforests of north-eastern  
574 Madagascar varied independently, suggests the possibility to combine high vanilla yields with  
575 a high tree cover. This has potential benefits for ecosystem services and biodiversity in a  
576 globally important biodiversity hotspot. Our finding contrasts with other agroforestry crops  
577 for which higher canopy cover typically impairs yields. Furthermore, the higher canopy cover  
578 in older compared to younger vanilla agroforests suggests opportunities to rehabilitate  
579 landscapes by enhancing tree cover in open-land-derived agroforests. If coupled with  
580 effective protection of remaining forests, yield-neutral tree recovery in agroforestry systems  
581 could contribute to a multifunctional and biodiversity-friendly agricultural landscape.

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