

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

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

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36 **Authors' contributions:** All authors conceived ideas and planned data collection and
37 analysis. DAM, AW, and KO coordinated the data collection; TR led
38 the field team; DAM analysed and visualized the data; DAM led the
39 writing of the manuscript. All authors contributed to the writing
40 and gave final approval for publication.

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52 **Manuscript highlights:** - Shade-trees in agroforests are commonly cut due to trade-offs
53 between shade and yields

54 - Across a chronosequence with 209 vanilla agroforests, we do not
55 find such trade-offs

56 - The lack of this trade-off offers an opportunity for yield-neutral
57 tree rehabilitation

58 **Keywords:** agroecology, agroforestry, canopy cover, ecosystem services, land-
59 use history, Madagascar, rehabilitation, restoration, vanilla, yield
60

61 **Abstract**

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

83 Introduction

84 Rehabilitation of historically forested open land is widely advocated to re-establish
85 connectivity and increase ecosystem functions in tropical rainforest landscapes (Bastin and
86 others, 2019; Chazdon, 2003). To date, governments and institutions have pledged to restore
87 140 million hectares of land in the tropics (Brancalion and others, 2019). However, realizing
88 those pledges could jeopardize food security if tree cover restoration replaces cropland,
89 questioning how feasible (Eitelberg and others, 2016) and indeed desirable (Holl &
90 Brancalion, 2020) their fulfilment is. In this light, agroforests may provide an opportunity to
91 combine trees with agricultural production on the same land (De Beenhouwer and others,
92 2016; FAO, 2017). Agroforests that are established on historically forested open-land hold a
93 particularly large potential, because open-land-derived agroforests rehabilitate selected
94 ecosystem functions like erosion control or carbon storage on open land (Martin, Osen, and
95 others, 2020). To describe this process, we specifically use the word ‘tree rehabilitation’ based
96 on Chazdon and others (2016), as the focus lies on the rehabilitation of ecosystem functions,
97 without necessarily restoring ecological integrity. In contrast to this, agroforests planted
98 under the canopy of existing forests typically contribute to forest degradation (Martin, Osen,
99 and others, 2020), thus hampering ecosystem functioning and ecological integrity (Coe and
100 others, 2013; McDowell and others, 2020).

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

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

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

123 In north-eastern Madagascar, vanilla is the main cash crop for smallholder farmers (Hänke
124 and others, 2018) who farm the bulk of Madagascar's 40% share on the world market (FAO,
125 2020). Here, vanilla is almost exclusively produced in rather extensively managed agroforestry
126 systems without the application of fertilizers, herbicides and pesticides. This is partly in
127 contrast to other production areas, such as La Réunion or Mexico, where artificial shade
128 houses are common (Havkin-Frenkel & Belanger, 2018). These extensively managed vanilla
129 agroforests also have value for biodiversity: various endemic lemur species live in diverse

130 agroforests (Hending and others, 2018). Vanilla agroforests also have a more diverse avifauna
131 than open land uses (Martin, Andriafanomezantsoa, and others, 2020). Other prominent land
132 uses in the Malagasy vanilla region include remnant forest fragments, irrigated rice paddies
133 and hill rice fields with the associated herbaceous and woody fallows, that form part of the
134 shifting cultivation cycle, locally known as *tavy* (Martin, Andriafanomezantsoa, and others,
135 2020; Styger and others, 2007). The first cycle of shifting cultivation, where fire is used to
136 convert forest into hill rice fields, is the main reason for forest loss in the region (Schüßler and
137 others, 2020; Zaehring and others, 2015). This dynamic is consistent with trends across
138 most of Africa, but contrasts with trends in the remaining tropics (Curtis and others, 2018;
139 van Vliet and others, 2012).

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

154 endemism (Goodman & Benstead, 2005) and high deforestation rates (Vieilledent and others,
155 2018) and qualifies as a biodiversity hotspot (Myers and others, 2000). This exacerbates the
156 need for both effective biodiversity conservation within the existing protected areas as well
157 as restoration within the agricultural landscape.



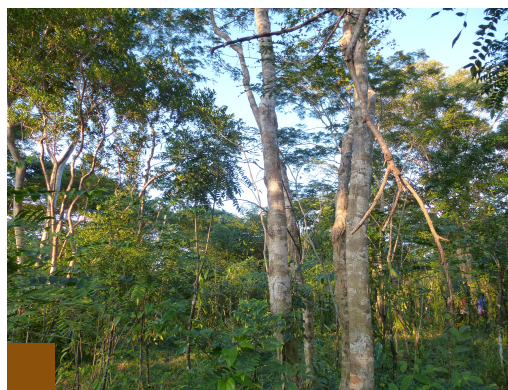
Tropical forest fragment



Forest-derived vanilla agroforest



Open land (Woody fallow)



Open-land-derived vanilla agroforest



Vanilla *pied* (unit of vanilla vine and support tree), flower and green pods



Agricultural landscape in north-eastern Madagascar

158

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

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

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

181 **Methods**

182 **Study region**

183 The SAVA region (25 518 km² / Latitude: 14° 16' S, Longitude: 50° 10' E) of north-eastern
184 Madagascar is the historic (Correll, 1953) and current (Hänke and others, 2018) center of

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

191 **Selection of vanilla agroforests**

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

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

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

208 forest- and open-land-derived agroforests in the final sample. In those four villages, we visited
209 65 households included in Hänke and others (2018). Those households owned 86 additional
210 accessible agroforests (7 open-land-derived, 79 forest-derived). This led to a total sample of
211 115 forest-derived and 94 open-land-derived agroforests (209 in total) owned by 152
212 households across 14 villages. SM Figure 2 shows all 14 villages with field data and the 60
213 villages from the initial sample.

214 **Data collection in agroforests**

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

230 slope-corrected agroforest size and number of *pieds*, we calculated planting density [*pieds*
231 ha⁻¹].

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

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

247 **Data extraction from raster layers**

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

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

257 **Analysis of vanilla yields, canopy cover and canopy height**

258 We used three linear mixed-effects models to analyse variation in vanilla yields, canopy cover
259 and canopy height, with 'household' (owner of agroforest, N= 152) and 'village' (N=14) as
260 random effects in all models. We fitted all models using the R-Package *lme4* version 1.1.21
261 (Bates, 2014) and scaled all explanatory and response variables to zero mean and unit
262 variance, allowing for direct comparison of effect sizes within and across models (Harrison
263 and others, 2018). We used an alpha level of 0.05 and calculated marginal and conditional R²-
264 values for all models (Nakagawa & Schielzeth, 2013). We used QQ-plots to assess normality
265 of model residuals and tested for variable inflation; none of the models had significant
266 deviations in the QQ-plots or variable inflation values above 1.5.

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

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

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

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

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

299 **Analysis of canopy cover dynamics in the agricultural landscape**

300 We used remotely sensed canopy cover data to explore how observed tree rehabilitation
301 within agroforests translated to the landscape scale. We obtained canopy cover data for the
302 year 2000 and 2010 from a Landsat-derived product of continuous canopy cover values with
303 30 m resolution (Hansen and others, 2013). Using the *raster* R-package version 3.0.12
304 (Hijmans and others, 2019), we subtracted the 2000 layer from the 2010 layer to obtain a new
305 raster layer with tree cover gains and losses, respectively (change of canopy cover between
306 2000 and 2010 [%]). We restricted both layers to an area of 2 km around the centers of 60
307 focal villages (excluding any offshore areas), for which we knew that vanilla farming was
308 common and from which we selected the villages for the plot-based part of this study (Village
309 selection described in Hänke and others, 2018). We chose 2 km because agroforests in this
310 range will typically belong to the focal village (*personal observation*). We then fitted a
311 generalized additive mixed model (GAMM) using the R-package *mgcv* version 1.8-28 (Wood,
312 2012) to evaluate how the dependent variable ‘initial canopy cover in the year 2000’
313 determined the independent variable ‘change in canopy cover from 2000 to 2010’. We
314 included ‘village’ as a random effect and also included longitude and latitude of each raster
315 cell as random effects to control for spatial autocorrelation. Therefore, the model read:
316 $\text{change in canopy cover} \sim \text{initial canopy cover} + (1 \mid \text{village}) + (1 \mid \text{longitude}) + (1 \mid \text{latitude})$.
317 We further ran the model on the basis dimension $k = 8$. We checked model assumptions using
318 the *gam.check* function of the *mgcv* R-package which demonstrated $k=8$ to be adequate and
319 a near-normal distribution of residuals.

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

322 Results

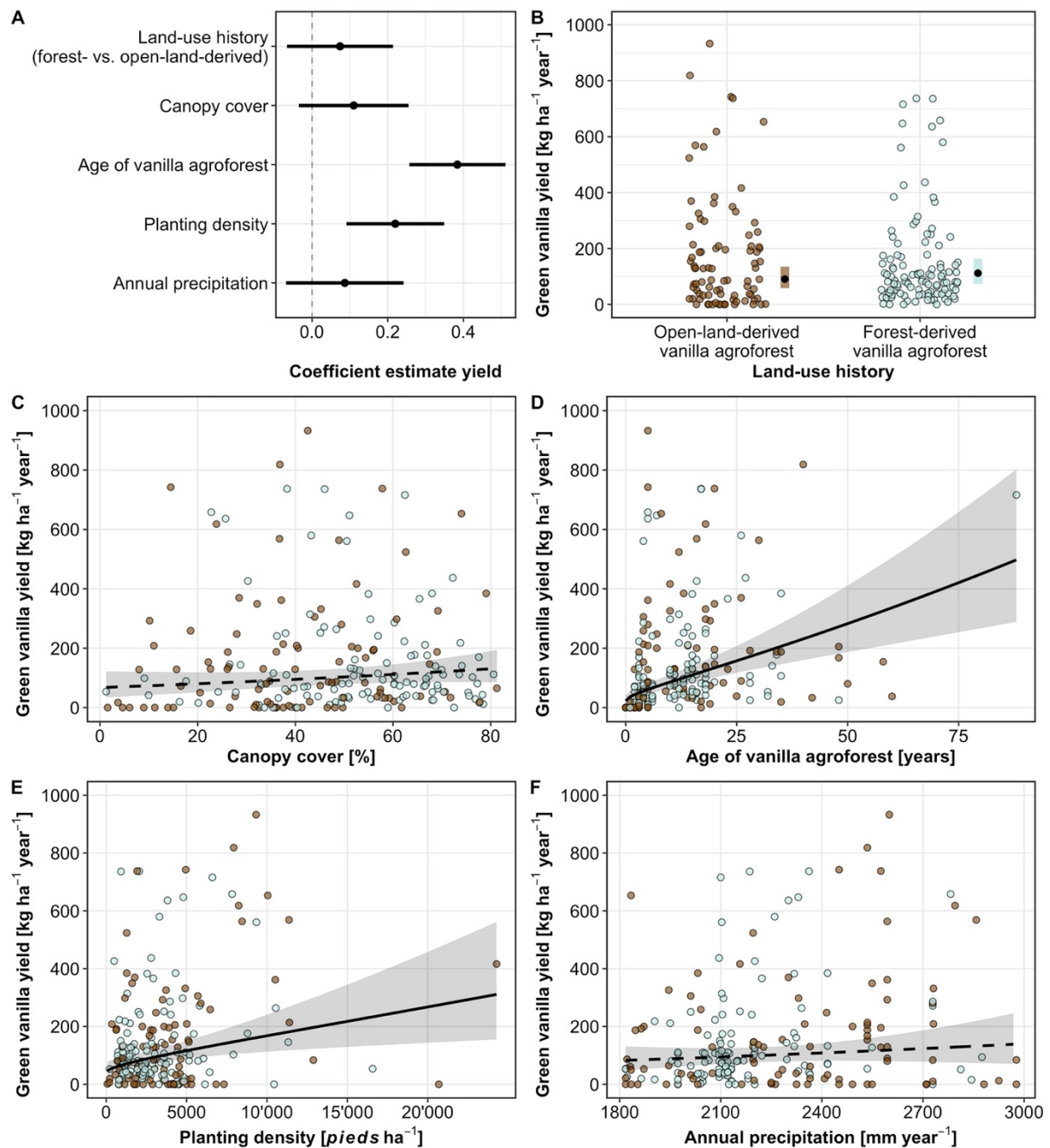
323 Determinants of vanilla yields

324 Green vanilla yield per *ped* varied strongly and ranged from 0 – 860 g *ped*⁻¹ year⁻¹ with an
325 average of 69.9 g *ped*⁻¹ year⁻¹ (*SD* = 112.3; N = 209 agroforests; mean from 2017 and 2018).

326 Note that this estimate includes *pieds* without any yield as it is calculated by dividing the total
327 yield by the number of *pieds* in each agroforest. Similarly, green vanilla yields differed strongly
328 across agroforests, ranging from 0 - 932.7 kg ha⁻¹ year⁻¹ with an average of 154.6 kg ha⁻¹ year⁻¹
329 (*SD* = 186.9; N= 209 agroforests; mean of 2017 and 2018). Using farmgate vanilla prices for
330 the year 2017 (Hänke and others, 2018), this average yield translates into gross earnings of
331 4684 € ha⁻¹. However, a household in this dataset only farmed 0.46 ha (*SD* = 0.42; N=152) of
332 accessible vanilla agroforests in average. The difference in green vanilla yield per ha between
333 the two years was small (2017: 158.8 kg ha⁻¹ (*SD* = 200.1); 2018: 150.2 kg ha⁻¹ (*SD* = 202.6))
334 and a Wilcoxon rank sum test revealed no significant differences between years (*W* = 21267,
335 *p* = 0.642, N = 209 agroforests). Farmers reported green vanilla theft in 26 agroforests (12.4%)
336 for 2017 and in 25 agroforests (12.0%) for 2018. Farmers who reported theft, stated that they
337 lost on average 9.15 kg (*SD* = 15.3) green vanilla per agroforest in 2017 and 8.72 kg (*SD* = 8.7)
338 per agroforest in 2018.

339 Our yield model (**Figure 2**, SM Table 1) revealed that vanilla yields varied independently of
340 land-use history, i.e. whether an agroforest was forest- or open-land-derived. Yields were
341 furthermore not significantly related to canopy cover and annual precipitation. Yields rose
342 with increasing agroforest age and planting density. Overall, the marginal R²-value of the
343 model was 0.216 while the conditional R²-value was 0.450. The difference between the two
344 values was mainly driven by the random intercept variance for the random effect 'household'

345 ($\tau_{00} = 0.26$); the random intercept variance for the random effect 'village' was negligible ($\tau_{00} =$
 346 0.03)



347

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

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

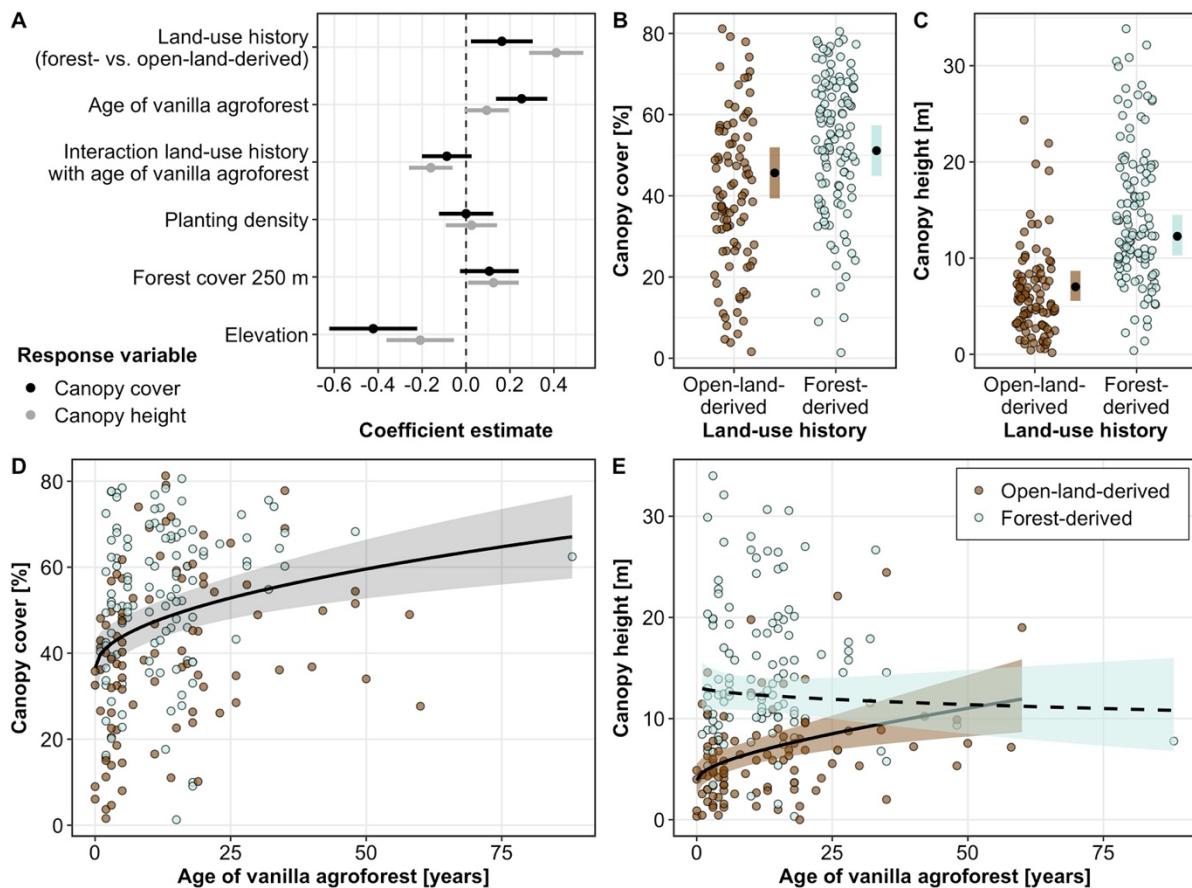
359 **Determinants of canopy cover and canopy height**

360 Canopy cover was 12.8% (estimated marginal means 6.3%) higher in forest-derived vanilla
361 agroforests (mean = 52.9%, $SD = 17.2$) compared to open-land-derived agroforests (mean =
362 40.1%, $SD = 19.0$; Figure 3, SM Table 2). The age of the agroforests differed along the
363 chronosequence between 1 and 88 years in forest-derived agroforests and between 0 and 60
364 years in open-land-derived agroforests. Age positively related to canopy cover, in both forest-
365 and open-land derived agroforestry: canopy cover increased by 39.5% (CI 34.5 – 44.6%) over
366 88 years.

367 Similarly, canopy height was 8.2 m (estimated marginal means 5.2 m) higher in forest-derived
368 agroforests (mean = 14.5 m, $SD = 7.3$) compared to open-land-derived agroforests (mean =
369 6.3 m, $SD = 4.6$; Figure 4, SM Table 3). The age of the agroforest positively affected canopy
370 height in open-land-derived agroforests where canopy height increased on average by 8 m
371 (CI 6.1 – 10.3 m) over 60 years. Canopy height in forest-derived agroforests was relatively
372 stable (mean decrease of 1.7 m (CI -2.7 – -0.4) over 60 years and a mean decrease of 2.1 m
373 (CI -3.9 – +0.4) over 88 years).

374 Vanilla planting density did not correlate with canopy cover or height (Figure 3 & 4, SM Table
375 2 & 3). Furthermore, agroforests with more surrounding forest cover had taller trees and
376 greater canopy cover, but confidence intervals overlapped zero for the latter (Figure 3 A).
377 Elevation was negatively associated with both tree height and canopy cover (Figure 3 A). The
378 canopy cover model (Figure 3, SM Table 2) had a marginal R^2 -value of 0.34 and a conditional
379 R^2 -value of 0.56, while the canopy height (Figure 4, SM Table 3) model had a marginal R^2 -

380 value of 0.35 and a conditional R^2 -value of 0.74. The substantial difference between
 381 conditional and marginal R^2 -values stemmed from the strong explanatory power of the
 382 random effect 'household' (canopy cover model: $\tau_{00} = 0.16$ / canopy height model: $\tau_{00} = 0.37$);
 383 the random intercept variance for the random effect 'village' was small (canopy cover model:
 384 $\tau_{00} = 0.07$ / canopy height model: $\tau_{00} = 0.02$).



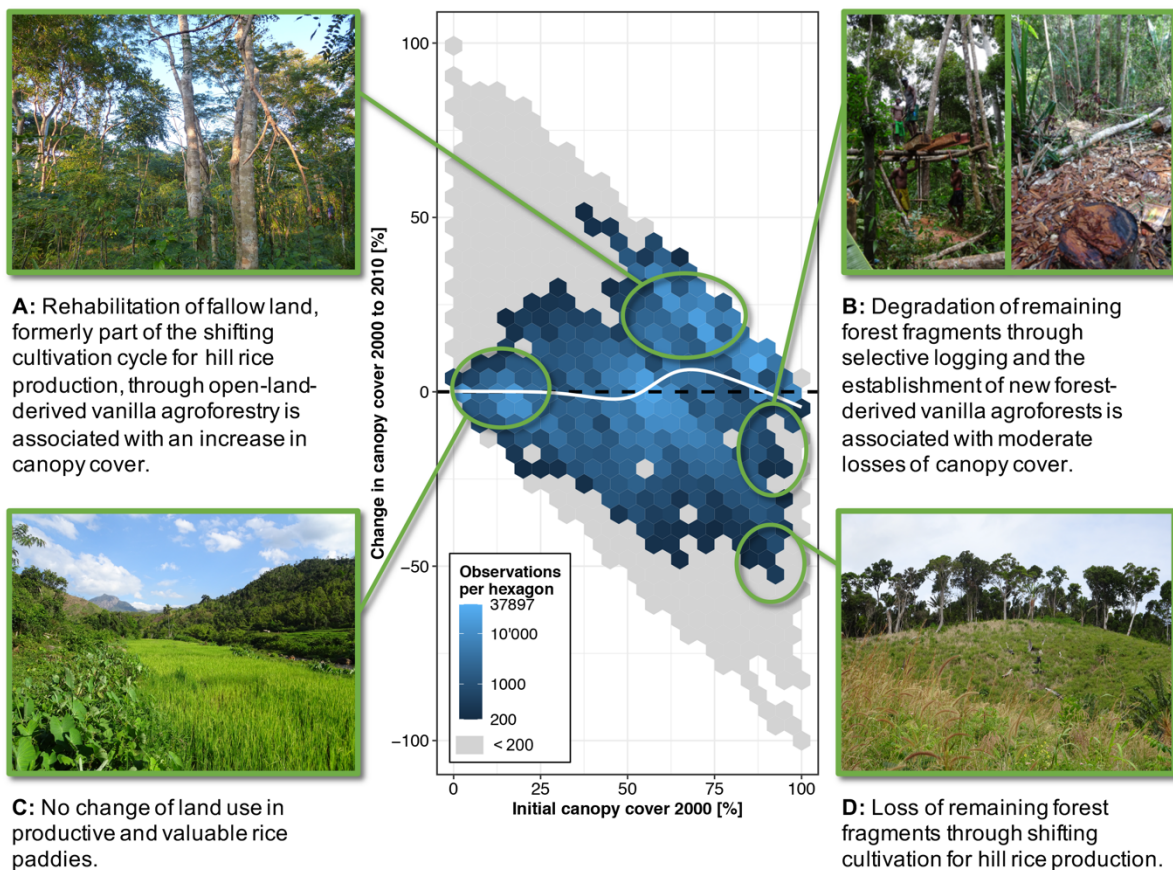
385

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

398

399 Canopy cover dynamics in the agricultural landscape

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



407

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

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

418 **Discussion**

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

425 **Determinants of vanilla yields**

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

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

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

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

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

469 **Increasing vanilla yields without impairing canopy cover**

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

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

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

491 **Limitations of yield data**

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

502 **Increasing canopy cover and tree height over time**

503 Tree rehabilitation in agroforestry systems is a global priority (FAO, 2017). However, many
504 tropical agroforests of key cash crops like cacao or coffee are forest-derived, thus typically
505 contributing to forest degradation rather than tree rehabilitation (Martin, Osen, and others,
506 2020). Open-land derived agroforests, on the other hand, may contribute to tree

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

519 In contrast to open-land-derived agroforests, canopy cover in forest-derived agroforests will
520 likely only recover after an initial drop at the time of establishment (Martin, Osen, and others,
521 2020), which is not covered here as our chronosequence does not include forest fragments.

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

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

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

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

533 We used remotely sensed canopy cover data to explore how observed plot-scale tree
534 rehabilitation translates to the landscape-scale. Comparing canopy cover changes between
535 2000 and 2010, we found that areas with lowest initial canopy cover, probably mostly rice
536 paddies, had stable canopy cover (**Figure 24**, SM Table 4). This is to be expected, given the
537 high productivity of irrigated rice and its local importance for food security (Hänke and others,
538 2018; Laney & Turner, 2015), which make a conversion of rice paddies to other land uses
539 unlikely. Areas with very high canopy cover, i.e. forest fragments around villages, lost canopy
540 cover over time. Here, small losses may represent forest degradation through selective
541 logging for timber or through the establishment of new forest-derived vanilla agroforests.
542 Some of these areas also showed large losses, likely reflecting shifting cultivation, where
543 forest is cut and burned for hill rice cultivation (**Figure 4**).

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

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

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

566 **Conclusion**

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

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589 **Literature cited**

590 Andriatsitohaina, R. N. N., Celio, E., Llopis, J. C., Rabemananjara, Z. H., Ramamonjisoa, B. S.,
591 & Grêt-Regamey, A. (2020). Participatory Bayesian network modeling to understand
592 driving factors of land-use change decisions: Insights from two case studies in
593 northeast Madagascar. *Journal of Land Use Science*, 0(0), 1–22.
594 <https://doi.org/10.1080/1747423X.2020.1742810>
595 Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., &
596 Crowther, T. W. (2019). The global tree restoration potential. *Science*, 365(6448),
597 76–79. <https://doi.org/10.1126/science.aax0848>

598 Bates, D. M. (2014). *lme4: Mixed-effects modeling with R* (Version 1.1-21) [R-Package].

599 Bianchi, S., Cahalan, C., Hale, S., & Gibbons, J. M. (2017). Rapid assessment of forest canopy
600 and light regime using smartphone hemispherical photography. *Ecology and*
601 *Evolution*, 7(24), 10556–10566. <https://doi.org/10.1002/ece3.3567>

602 Blaser, W. J., Opong, J., Hart, S. P., Landolt, J., Yeboah, E., & Six, J. (2018). Climate-smart
603 sustainable agriculture in low-to-intermediate shade agroforests. *Nature*
604 *Sustainability*, 1(5), 234–239. <https://doi.org/10.1038/s41893-018-0062-8>

605 Box, G. E., & Cox, D. R. (1964). An analysis of transformations. *Journal of the Royal Statistical*
606 *Society: Series B (Methodological)*, 26(2), 211–243. [https://doi.org/10.1111/j.2517-](https://doi.org/10.1111/j.2517-6161.1964.tb00553.x)
607 [6161.1964.tb00553.x](https://doi.org/10.1111/j.2517-6161.1964.tb00553.x)

608 Brancalion, P. H. S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F. S. M., Zambrano, A.
609 M. A., Baccini, A., Aronson, J., Goetz, S., Reid, J. L., Strassburg, B. B. N., Wilson, S., &
610 Chazdon, R. L. (2019). Global restoration opportunities in tropical rainforest
611 landscapes. *Science Advances*, 5(7), eaav3223.
612 <https://doi.org/10.1126/sciadv.aav3223>

613 Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural
614 disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1), 51–71.
615 <https://doi.org/10.1078/1433-8319-00042>

616 Chazdon, R. L., Brancalion, P. H. S., Laestadius, L., Bennett-Curry, A., Buckingham, K., Kumar,
617 C., Moll-Rocek, J., Vieira, I. C. G., & Wilson, S. J. (2016). When is a forest a forest?
618 Forest concepts and definitions in the era of forest and landscape restoration.
619 *Ambio*, 45(5), 538–550. <https://doi.org/10.1007/s13280-016-0772-y>

620 Clough, Y., Barkmann, J., Jührbandt, J., Kessler, M., Wanger, T. C., Anshary, A., Buchori, D.,
621 Cicuzza, D., Darras, K., Putra, D. D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C.

622 H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., ... Tschardtke, T.
623 (2011). Combining high biodiversity with high yields in tropical agroforests.
624 *Proceedings of the National Academy of Sciences*, 108(20), 8311–8316.
625 <https://doi.org/10.1073/pnas.1016799108>

626 Clough, Y., Faust, H., & Tschardtke, T. (2009). Cacao boom and bust: Sustainability of
627 agroforests and opportunities for biodiversity conservation. *Conservation Letters*,
628 2(5), 197–205. <https://doi.org/10.1111/j.1755-263X.2009.00072.x>

629 Coe, M. T., Marthens, T. R., Costa, M. H., Galbraith, D. R., Greenglass, N. L., Imbuzeiro, H. M.
630 A., Levine, N. M., Malhi, Y., Moorcroft, P. R., Muza, M. N., Powell, T. L., Saleska, S. R.,
631 Solorzano, L. A., & Wang, J. (2013). Deforestation and climate feedbacks threaten
632 the ecological integrity of south–southeastern Amazonia. *Philosophical Transactions*
633 *of the Royal Society B: Biological Sciences*, 368(1619), 20120155.
634 <https://doi.org/10.1098/rstb.2012.0155>

635 Correll, D. S. (1953). Vanilla-its botany, history, cultivation and economic import. *Economic*
636 *Botany*, 7(4), 291–358. <https://doi.org/10.1007/BF02930810>

637 Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying
638 drivers of global forest loss. *Science*, 361(6407), 1108–1111.
639 <https://doi.org/10.1126/science.aau3445>

640 De Beenhouwer, M., Aerts, R., & Honnay, O. (2013). A global meta-analysis of the
641 biodiversity and ecosystem service benefits of coffee and cacao agroforestry.
642 *Agriculture, Ecosystems & Environment*, 175, 1–7.
643 <https://doi.org/10.1016/j.agee.2013.05.003>

644 De Beenhouwer, M., Geeraert, L., Mertens, J., Van Geel, M., Aerts, R., Vanderhaegen, K., &
645 Honnay, O. (2016). Biodiversity and carbon storage co-benefits of coffee

646 agroforestry across a gradient of increasing management intensity in the SW
647 Ethiopian highlands. *Agriculture, Ecosystems & Environment*, 222, 193–199.
648 <https://doi.org/10.1016/j.agee.2016.02.017>

649 Diaz, G. M., & Lencinas, J. D. (2015). Enhanced Gap Fraction Extraction From Hemispherical
650 Photography. *IEEE Geoscience and Remote Sensing Letters*, 12(8), 1785–1789.
651 <https://doi.org/10.1109/LGRS.2015.2425931>

652 Díez, M. C., Moreno, F., & Gantiva, E. (2017). Effects of light intensity on the morphology
653 and CAM photosynthesis of *Vanilla planifolia* Andrews. *Revista Facultad Nacional de*
654 *Agronomía*, 70(1), 8023–8033. <https://doi.org/10.15446/rfna.v70n1.61736>

655 Eitelberg, D. A., van Vliet, J., Doelman, J. C., Stehfest, E., & Verburg, P. H. (2016). Demand for
656 biodiversity protection and carbon storage as drivers of global land change
657 scenarios. *Global Environmental Change*, 40, 101–111.
658 <https://doi.org/10.1016/j.gloenvcha.2016.06.014>

659 FAO (2017). *Agroforestry for landscape restoration—Exploring the potential of agroforestry*
660 *to enhance the sustainability and resilience of degraded landscapes* (p. 28).
661 <http://www.fao.org/3/b-i7374e.pdf>

662 FAO (2020). *FAOSTAT*. Food and Agriculture Organisation of the United Nations.
663 <http://www.fao.org/faostat/en/#home>

664 Ferreira Arruda, T. (2018). *Spatial-temporal patterns of deforestation in Northeast*
665 *Madagascar* [MSc Thesis]. University of Goettingen.

666 Fouché, J. G., & Jouve, L. (1999). *Vanilla planifolia*: History, botany and culture in Reunion
667 island. *Agronomie*, 19(8), 689–703. <https://doi.org/10.1051/agro:19990804>

668 Goodman, S. M., & Benstead, J. P. (2005). Updated estimates of biotic diversity and
669 endemism for Madagascar. *Oryx*, 39(01).
670 <https://doi.org/10.1017/S0030605305000128>

671 Hänke, H., Barkmann, J., Blum, L., Franke, Y., Martin, D. A., Niens, J., Osen, K., Uruena, V.,
672 Witherspoon, S. A., & Wurz, A. (2018). *Socio-economic, land use and value chain*
673 *perspectives on vanilla farming in the SAVA Region (north-eastern Madagascar): The*
674 *Diversity Turn Baseline Study (DTBS). July 2019 Edition.* [https://doi.org/DOI:](https://doi.org/DOI:10.13140/RG.2.2.22059.80163)
675 [10.13140/RG.2.2.22059.80163](https://doi.org/DOI:10.13140/RG.2.2.22059.80163)

676 Hänke, H., & Fairtrade International. (2019). *Living Income Reference Price for Vanilla from*
677 *Uganda and Madagascar.* Fairtrade International.

678 Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A.,
679 Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., & others. (2013). High-
680 resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–
681 853. <https://doi.org/10.1126/science.1244693>

682 Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D.,
683 Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed
684 effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794.
685 <https://doi.org/10.7717/peerj.4794>

686 Havkin-Frenkel, D., & Belanger, F. C. (Eds.). (2018). *Handbook of vanilla science and*
687 *technology* (Second edition). Wiley.

688 Hending, D., Andrianiana, A., Rakotomalala, Z., & Cotton, S. (2018). The Use of Vanilla
689 Plantations by Lemurs: Encouraging Findings for both Lemur Conservation and
690 Sustainable Agroforestry in the Sava Region, Northeast Madagascar. *International*
691 *Journal of Primatology*, 39(1), 141–153. <https://doi.org/10.1007/s10764-018-0022-1>

692 Hijmans, R. J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A.,
693 Lamigueiro, O. P., Bevan, A., Racine, E. B., & Shortridge, A. (2019). *Package ‘raster’*
694 (Version 3.0-7) [R-Package].

695 Holl, K. D., & Brancalion, P. H. S. (2020). Tree planting is not a simple solution. *Science*,
696 368(6491), 580–581. <https://doi.org/10.1126/science.aba8232>

697 Holloway, L. (2004). Ecosystem Restoration and Rehabilitation in Madagascar. *Ecological*
698 *Restoration*, 22(2), 113–119. <https://doi.org/10.3368/er.22.2.113>

699 Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S.
700 M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, M. J., Rakotondravony, D.,
701 Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L., & Ganzhorn, J. U. (2010).
702 Patterns of species change in anthropogenically disturbed forests of Madagascar.
703 *Biological Conservation*, 143(10), 2351–2362.
704 <https://doi.org/10.1016/j.biocon.2010.01.023>

705 Japan Aerospace Exploration Agency. (2018). *ALOS Global Digital Surface Model «ALOS*
706 *World 3D - 30m (AW3D30)*. <http://www.eorc.jaxa.jp/ALOS/en/aw3d30/>

707 Jezeer, R. E., Verweij, P. A., Santos, M. J., & Boot, R. G. A. (2017). Shaded Coffee and Cocoa –
708 Double Dividend for Biodiversity and Small-scale Farmers. *Ecological Economics*, 140,
709 136–145. <https://doi.org/10.1016/j.ecolecon.2017.04.019>

710 Karger, D. N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann,
711 N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the
712 earth’s land surface areas. *Scientific Data*, 4(1), 1–20.
713 <https://doi.org/10.1038/sdata.2017.122>

714 Laney, R., & Turner, B. L. (2015). The Persistence of Self-Provisioning Among Smallholder
715 Farmers in Northeast Madagascar. *Human Ecology*, 43(6), 811–826.
716 <https://doi.org/10.1007/s10745-015-9791-8>

717 Leakey, R. R. B. (2014). The Role of Trees in Agroecology and Sustainable Agriculture in the
718 Tropics. *Annual Review of Phytopathology*, 52(1), 113–133.
719 <https://doi.org/10.1146/annurev-phyto-102313-045838>

720 Length, R., Singmann, H., & Love, J. (2018). *Emmeans: Estimated marginal means, aka least-*
721 *squares means* (Version 1.4.5) [R-Package].

722 Llopis, J. C., Harimalala, P. C., Bär, R., Heinemann, A., Rabemananjara, Z. H., & Zaehring, J.
723 G. (2019). Effects of protected area establishment and cash crop price dynamics on
724 land use transitions 1990–2017 in north-eastern Madagascar. *Journal of Land Use*
725 *Science*, 0(0), 1–29. <https://doi.org/10.1080/1747423X.2019.1625979>

726 Lobell, D. B., Cassman, K. G., & Field, C. B. (2009). Crop Yield Gaps: Their Importance,
727 Magnitudes, and Causes. *Annual Review of Environment and Resources*, 34(1), 179–
728 204. <https://doi.org/10.1146/annurev.enviro.041008.093740>

729 Martin, D. A., Andriafanomezantsoa, R., Dröge, S., Osen, K., Rakotomalala, E., Wurz, A.,
730 Andrianarimisa, A., & Kreft, H. (2020). Bird diversity and endemism along a land-use
731 gradient in Madagascar: The conservation value of vanilla agroforests. *Biotropica*. In
732 press. <https://doi.org/10.1111/BTP.12859>

733 Martin, D. A., Osen, K., Grass, I., Hölscher, D., Tschardt, T., Wurz, A., & Kreft, H. (2020).
734 Land-use history determines ecosystem services and conservation value in tropical
735 agroforestry. *Conservation Letters*. <https://doi.org/10.1111/conl.12740>

736 McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B.,
737 Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C.,

738 Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh,
739 T. A. M., Seidl, R., ... Xu, C. (2020). Pervasive shifts in forest dynamics in a changing
740 world. *Science*, 368(6494), eaaz9463. <https://doi.org/10.1126/science.aaz9463>

741 Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000).
742 Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858.
743 <https://doi.org/10.1038/35002501>

744 Nair, P. K. R., Kumar, B. M., & Nair, V. D. (2009). Agroforestry as a strategy for carbon
745 sequestration. *Journal of Plant Nutrition and Soil Science*, 172(1), 10–23.
746 <https://doi.org/10.1002/jpln.200800030>

747 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from
748 generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2),
749 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>

750 Neimark, B., Osterhoudt, S., Blum, L., & Healy, T. (2019). Mob justice and ‘The civilized
751 commodity.’ *The Journal of Peasant Studies*, 1–20.
752 <https://doi.org/10.1080/03066150.2019.1680543>

753 Nijmeijer, A., Lauri, P.-E., Harmand, J.-M., Freschet, G. T., Essobo Nieboukaho, J.-D., Fogang,
754 P. K., Enock, S., & Saj, S. (2019). Long-term dynamics of cocoa agroforestry systems
755 established on lands previously occupied by savannah or forests. *Agriculture,
756 Ecosystems & Environment*, 275, 100–111.
757 <https://doi.org/10.1016/j.agee.2019.02.004>

758 Perfecto, I., Vandermeer, J., Mas, A., & Pinto, L. S. (2005). Biodiversity, yield, and shade
759 coffee certification. *Ecological Economics*, 54(4), 435–446.
760 <https://doi.org/10.1016/j.ecolecon.2004.10.009>

761 R Core Team. (2019). *R: A language and environment for statistical computing* (Version
762 3.6.0) [R].

763 Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B.
764 (2013). *Package 'mass'* (Version 7.3.51.4) [R-Package].

765 Santosa, E., Sugiyama, N., Nakata, M., & Kawabata, S. (2005). Profitability of Vanilla
766 Intercropping in Pine Forests in West Java, Indonesia. *Japanese Journal of Tropical*
767 *Agriculture*, 49(3), 207–214. <https://doi.org/10.11248/jsta1957.49.207>

768 Schüßler, D., Mantilla-Contreras, J., Stadtmann, R., Ratsimbazafy, J. H., & Radespiel, U.
769 (2020). Identification of crucial stepping stone habitats for biodiversity conservation
770 in northeastern Madagascar using remote sensing and comparative predictive
771 modeling. *Biodiversity and Conservation*. [https://doi.org/10.1007/s10531-020-](https://doi.org/10.1007/s10531-020-01965-z)
772 01965-z

773 Schwab, D., Wurz, A., Grass, I., Rakotomalala, A. A. N. A., Osen, K., Soazafy, M. R., Martin, D.
774 A., & Tschardtke, T. (2020). Decreasing predation rates and shifting predator
775 compositions along a land-use gradient in Madagascar's vanilla landscapes. *Journal*
776 *of Applied Ecology*. In press. <https://doi.org/10.1111/1365-2664.13766>

777 Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M. M., Buchori, D., Erasmi, S., Faust, H.,
778 Gerold, G., Glenk, K., Gradstein, S. R., Guhardja, E., Harteveld, M., Hertel, D., Hohn,
779 P., Kappas, M., Kohler, S., Leuschner, C., Maertens, M., Marggraf, R., ... Tschardtke, T.
780 (2007). Tradeoffs between income, biodiversity, and ecosystem functioning during
781 tropical rainforest conversion and agroforestry intensification. *Proceedings of the*
782 *National Academy of Sciences*, 104(12), 4973–4978.
783 <https://doi.org/10.1073/pnas.0608409104>

784 Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M., & Bates, D. M. (2007).
785 Influence of slash-and-burn farming practices on fallow succession and land
786 degradation in the rainforest region of Madagascar. *Agriculture, Ecosystems &*
787 *Environment*, 119(3–4), 257–269. <https://doi.org/10.1016/j.agee.2006.07.012>

788 Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken
789 with a smartphone. *Journal of Vegetation Science*, 27(2), 427–435.
790 <https://doi.org/10.1111/jvs.12350>

791 Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable
792 intensification of agriculture. *Proceedings of the National Academy of Sciences*,
793 108(50), 20260–20264. <https://doi.org/10.1073/pnas.1116437108>

794 Tscharntke, T., Clough, Y., Bhagwat, S. A., Buchori, D., Faust, H., Hertel, D., Hölscher, D.,
795 Juhbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., &
796 Wanger, T. C. (2011). Multifunctional shade-tree management in tropical
797 agroforestry landscapes—A review. *Journal of Applied Ecology*, 48(3), 619–629.
798 <https://doi.org/10.1111/j.1365-2664.2010.01939.x>

799 Tscharntke, T., Milder, J. C., Rice, R., & Ghazoul, J. (2014). Conserving biodiversity through
800 certification of tropical agroforestry crops at local and landscape scales.
801 *Conservation Letters*, 8(1), 14–23. <https://doi.org/10.1111/conl.12110>

802 van Vliet, N., Mertz, O., Heinimann, A., Langanke, T., Pascual, U., Schmook, B., Adams, C.,
803 Schmidt-Vogt, D., Messerli, P., Leisz, S., Castella, J.-C., Jørgensen, L., Birch-Thomsen,
804 T., Hett, C., Bech-Bruun, T., Ickowitz, A., Vu, K. C., Yasuyuki, K., Fox, J., ... Ziegler, A. D.
805 (2012). Trends, drivers and impacts of changes in swidden cultivation in tropical
806 forest-agriculture frontiers: A global assessment. *Global Environmental Change*,
807 22(2), 418–429. <https://doi.org/10.1016/j.gloenvcha.2011.10.009>

808 Vieilledent, G., Gardi, O., Grinand, C., Burren, C., Andriamanjato, M., Camara, C., Gardner, C.
809 J., Glass, L., Rasolohery, A., Rakoto Ratsimba, H., Gond, V., & Rakotoarijaona, J.-R.
810 (2016). Bioclimatic envelope models predict a decrease in tropical forest carbon
811 stocks with climate change in Madagascar. *Journal of Ecology*, *104*(3), 703–715.
812 <https://doi.org/10.1111/1365-2745.12548>

813 Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R.,
814 Allnutt, T. F., & Achard, F. (2018). Combining global tree cover loss data with
815 historical national forest cover maps to look at six decades of deforestation and
816 forest fragmentation in Madagascar. *Biological Conservation*, *222*, 189–197.
817 <https://doi.org/10.1016/j.biocon.2018.04.008>

818 Wood, S. (2012). *mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness*
819 *estimation* (Version 1.8-28) [R-Package].

820 Zaehring, J., Eckert, S., & Messerli, P. (2015). Revealing Regional Deforestation Dynamics
821 in North-Eastern Madagascar—Insights from Multi-Temporal Land Cover Change
822 Analysis. *Land*, *4*(2), 454–474. <https://doi.org/10.3390/land4020454>

823 Zomer, R. J., Neufeldt, H., Xu, J., Ahrends, A., Bossio, D., Trabucco, A., van Noordwijk, M., &
824 Wang, M. (2016). Global Tree Cover and Biomass Carbon on Agricultural Land: The
825 contribution of agroforestry to global and national carbon budgets. *Scientific*
826 *Reports*, *6*(1). <https://doi.org/10.1038/srep29987>

827