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**The assembly and importance of a novel ecosystem: the ant community of coffee farms in
Puerto Rico**

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Running Head: Novel ant assembly in Puerto Rican coffee farms

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ABSTRACT

Agricultural ecosystems are, by their very nature novel and by definition the more general biodiversity associated with them must likewise constitute a novel community. Here we examine the community of arboreally foraging ants in the coffee agroecosystem of Puerto Rico. We surveyed 20 coffee plants in 25 farms three times in a period of one year. We also conducted a more spatially explicit sampling in two of the farms and conducted a species interaction study between the two most abundant species, *Wasmannia auropunctata* and *Solenopsis invicta* in the laboratory. We find that the majority of the most common species are well-known invasive ants and that there is a highly variable pattern of dominance that varies considerably over the main coffee producing region of Puerto Rico, suggesting an unusual modality of community structure. The distribution pattern of the two most common species, *W. auropunctata* and *S. invicta*, suggests strong competitive exclusion. However, they also have opposite relationships with the percent of shade cover, with *W. auropunctata* showing a positive relationship with shade, while *S. invicta* has a negative relationship. The spatial distribution of these two dominant species in the two more intensively studied farms suggests that young colonies of *S. invicta* can displace *W. auropunctata*. Laboratory experiments confirm this. In addition to the elaboration of the nature and extent of this novel ant community, we speculate on the possibilities of its active inclusion as part of a biological control system dealing with several coffee pests, including one of the ants itself, *W. auropunctata*.

Key Words: biological control, coexistence, community structure, dominance, invasive species, *Solenopsis invicta*, *Wasmannia auropunctata*

RESUMEN

Los ecosistemas agrícolas son, por su propia naturaleza, novedosos y, por definición, la biodiversidad más general asociada con ellos también debe constituir una comunidad novedosa. Aquí examinamos la comunidad de hormigas arborícolas en el agroecosistema cafetalero de Puerto Rico. Muestreamos 20 plantas de café en 25 fincas tres veces en un período de un año.

61 También realizamos un muestreo espacialmente más explícito en dos de las fincas y realizamos
62 un estudio de interacción de especies entre las dos especies más abundantes, *Wasmannia*
63 *auropunctata* y *Solenopsis invicta* en el laboratorio. Encontramos que la mayoría de las especies
64 más comunes son hormigas invasoras bien conocidas y que existe un patrón de dominio muy
65 variable que varía considerablemente en la principal región productora de café de Puerto Rico, lo
66 que sugiere una modalidad inusual de estructura comunitaria. El patrón de distribución de las dos
67 especies más comunes, *W. auropunctata* y *S. invicta*, sugiere una fuerte exclusión competitiva.
68 Sin embargo, también tienen relaciones opuestas con el porcentaje de cobertura de sombra, con
69 *W. auropunctata* mostrando una relación positiva con la sombra, mientras que *S. invicta* tiene
70 una relación negativa. La distribución espacial de estas dos especies dominantes en las dos fincas
71 estudiadas más intensamente sugiere que las colonias jóvenes de *S. invicta* pueden desplazar a *W.*
72 *auropunctata*. Los experimentos de laboratorio confirman esto. Además de la elaboración de la
73 naturaleza y el alcance de esta nueva comunidad de hormigas, especulamos sobre las
74 posibilidades de su inclusión activa como parte de un sistema de control biológico que se ocupa
75 de varias plagas de café, incluida una de las hormigas, *W. auropunctata*.

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79 **Introduction**

80 Novel ecosystems present an opportunity that has been common yet rarely recognized in
81 the field of ecology; the opportunity to study how “not-necessarily-coevolved” organisms come
82 together and structure an ecological community (Hobbs et al., 2006; Hobbs, Higgs, & Harris,
83 2009; Perfecto & Vandermeer, 2015; Evers et al., 2018; Godoy, 2019). Our ability to understand
84 these new systems is a test of the extent to which we understand the natural laws that determine
85 community and ecosystem structure (Perfecto & Vandermeer, 2015). Ants represent an
86 interesting case in that they form novel communities that are consistent both taxonomically (all
87 species in the same clade) and ecologically (all species live in similar ecological niches). There
88 are some functional and phylogenetically distinguishable categories, to be sure. For example, the
89 division into carbohydrate-dependent species versus protein-dependent species (Davidson, 1997)
90 imperfectly but sensibly partitions species according to a niche trait, and the four subfamilies,
91 Myrmecinae, Pseudomyrmecinae, Formicinae, and Dolichodorinae make phylogenetic sense of a

92 plethora of species with a similar range of ecological niches. Although the Poneriniiformes
93 present both ecological and phylogenetic problems (Ward ,2007), and the Dorylinae combine
94 monophylogeny with the obvious ecological niche of predator with special behavior, the four
95 main subfamilies contain species whose niches are relatively consistent. Here we are mainly
96 concerned with these more generalized four omnivore subfamilies, which include most of the
97 world’s most infamous invasive ant species.

98 Community structure is a complicated subject even when restricted to a small guild
99 operating on a single trophic level, as is the case here. Yet the very novelty of the system
100 provides a unique view of how the various components fit together. For example, while
101 competitive exclusion is expected to permit only minimal niche overlap amongst coexisting
102 species, such an expectation is not palpable in the novel ecosystem context since the tacit
103 assumption of equilibrium is rarely justified. Habitat specialization at various scales is
104 frequently thought to account for many coexistence patterns, certainly a key factor in ant
105 communities. Migration and extinction patterns represent a distinct level of explanatory
106 phenomena, undoubtedly of potential importance in a spatially distributed system which is the
107 case in the present study. The important issue of “invasion meltdown” (Simberloff, 2006), in
108 which non-native species facilitate one another’s invasion, is frequently cited in warnings of the
109 impact of invasive species. In contrast, the eventual reduction of the impact of a key invasive
110 species, almost the inverse of the invasion meltdown idea, is frequently noted (Lach & Hoopper
111 Bui, 2010; Braga, Gomez-Aparicio, Hegger, Vitule, & Jeschke, 2018). Both invasion meltdown
112 and impact reduction strongly suggest that transient phenomena rather than equilibria are
113 dominant, in terms of all elements of community dynamics, including population densities,
114 species compositions, and species interactions.

115 In a series of important studies, Torres (1984 a, b) summarized much of the knowledge
116 obtainable from the distribution of ants on the island of Puerto Rico, concentrating on ecological
117 observables such as food type, habitat occurrence, island isolation, and microhabitat factors.
118 Here we effectively restrict our analysis to one particular habitat type, the coffee agroecosystem,
119 with its community of mainly non-native ants, clearly within the general category of a novel
120 ecosystem (Perfecto & Vandermeer, 2015). It is worth noting that ants present a particularly
121 interesting problem from a practical point of view. On the one hand they are most frequently
122 generalist predators (Torres & Snelling, 1997; Perfecto & Castiñeiras, 1998; Eubanks, 2001;

123 Philpott & Armbrrecht, 2006; Philpott, Perfecto, Armbrrecht, & Parr, 2010; Offenberg, 2015) and
124 thus of potential importance in providing the ecosystem service of pest control. On the other
125 hand, some species are regarded as noxious pests themselves, with leaf cutting ants reducing
126 photosynthetic area, mutualists protecting hemipteran herbivores, or fire ants stinging farmers
127 and farm workers (Febres & Brown, 1978; Haines & Haines, 1978; Reimer, Beardsley, & Jahn,
128 1990; Jetter, Hamilton, & Klotz, 2002). Understanding how the overall community of ants is
129 structured thus has important practical implications, in addition to the more theoretical
130 justification of understanding community structure through the lens of the novel ecosystem.

131 In this study we take the opportunity to study how “not-necessarily-coevolved”
132 organisms come together to form an ecological community, using the “novel ecosystem” of ants
133 on coffee farms as a focal system. The background habitat is easily recognized as “the coffee
134 system” which presents an environmental background that has both consistency (all sites are
135 coffee farms, and all are in the central mountain range of Puerto Rico) and variability
136 (management styles vary from farm to farm). The consistency is more notable than the
137 variability under casual observation, and we can presume that the general population and
138 community dynamics of the organisms making up the novel ecosystem are the main drivers of
139 community assembly. What that assembly looks like, qualitatively, is the underlying goal of this
140 study.

141 In focusing on this particular community, we find unsurprisingly, that there is an unequal
142 distribution among species, more rare species than common ones at a given site. Most evident in
143 this situation is the occurrence of two particular species, *Solenopsis invicta* and *Wasmannia*
144 *auropunctata*, both of which are non-native and happen to be regarded as pests by local farmers.
145 Given the commonness of these two species, and given the obvious observation that they rarely
146 occurred together as common occupants on any given farm, it was most natural to focus on them
147 as an important dynamic component of the overall community structure. Thus, much of this
148 study focuses on these two species as an important element of the overall community dynamics.

149

150 **Methods**

151 From a survey of 85 coffee farms throughout the coffee growing region of Puerto Rico
152 (effectively from the municipality of Orocovis to Las Marias) we chose 25 as representative of
153 the habitat types, based on shade cover and geographic position. That is, we chose the farms to

154 study based on an intention to sample the whole range of coffee farms on the island. The
155 position of all farms studied is shown in figure 1, and the basic geographic information (latitude,
156 longitude and elevation) and percent canopy cover can be found in table S1 in the supplementary
157 material. Farms were separated from each other by a minimum distance of one kilometer, but
158 most farms were separated by more than 5 kilometers. Since the area is relatively small, climatic
159 conditions vary little across the farms, with the ones located further south (subtropical moist
160 forest: 1000-2000 ml annual precipitation) being slightly drier than the ones further north
161 (subtropical wet forest: 2000-4000 ml annual precipitation), and the northern ones being closer to
162 the massive limestone formations (known locally as mogotes) on the north west side of the island
163 (Miller and Lugo, 2009). It is unlikely that any of these geographic conditions affect the ant
164 communities, and our results offer no hint that such could be the case.

165 The study farms were located over the whole range of the coffee-growing area and
166 included farms that ranged from very sunny (low shade cover) to highly shaded (Table S1).
167 Preliminary analysis of these habitat factors demonstrated no relationship between management
168 type or geographic position and the ant community, so these variables are not pursued further in
169 this study.

170

171 *Figure 1 here*

172

173 During the months of December 2018 and January, 2019 we visited each of the farms and
174 placed 5 tuna fish baits directly on the stem (or stems) of each of 20 coffee plants (baits stuck
175 easily on the bark of the plant), chosen randomly from a 10 x 10m plot, which, in turn was
176 chosen to reflect the basic management style of the farm. Thus, we placed a total of 100 arboreal
177 baits in a representative area of 100 m² on each of 25 farms, waited for 40 minutes and checked
178 each bait for ants, recording presence (no counts of numbers of foragers) at each bait. Since the
179 number of foragers on a bait is more an indication of the activity of a nearby nest and has very
180 little to do with the abundance of the species itself, it is wise to reject any notion of counting
181 workers as some sensible indication of population density or abundance. More relevant is simply
182 the number of baits occupied, in the present case the number of baits occupied on a given tree
183 ranged from 0 to 5, meaning that our estimates of abundance on a given tree always ranges from
184 0 to 5. Most species were identified in the field, and specimens collected and examined in the lab

185 only for those cases when the identity was not obvious. On each farm, the species that occupied
186 the most coffee trees was called the dominant species. It was almost always the case that one
187 species was clearly dominant in this sense, although in a few cases two or three species were
188 almost equally represented with respect to number of trees occupied and, in a few cases, there
189 was no clear dominance. Subdominant is defined as occurrence on less than 10 observations over
190 the course of the study, on a particular farm. All farms were revisited in July of 2019 and January
191 of 2020 and the sampling was repeated using the same methodology. Based on the work of
192 Tschinkel (1988) we noted that it was almost always possible to distinguish two basic forms of
193 swarms of the red imported fire ant, *Solenopsis invicta* on the baits, one form with almost all
194 individuals of small or “minor” proportions and the other form with a few to many very large or
195 “major” forms, especially noted for a very large gaster. Based on Tschinkel’s results we
196 interpreted these two forms as “young” colonies versus “old” colonies, since it seems that in
197 younger colonies the queens produce only minor workers and only when they reach an older age
198 do they begin producing what seems to be a totally different cast of individuals, the majors. We
199 also noticed that the characteristic sting of *S. invicta* with the formation of an evident pustule on
200 the skin at the site of the sting seems to be caused only by these major workers. Furthermore, the
201 most common phorid fly parasitoid observed in all our *S. invicta* samples seemed to strongly
202 prefer attacking the major workers, as has been reported elsewhere (Williams & Banks, 1987).
203 The information on worker size was used to help interpret some of our findings as reported in the
204 results.

205 It is evident from our 25 farm surveys, that the most dominant ants are also the ones
206 frequently cited by farmers as undesirable because of their potent stings, *Wasmannia*
207 *auropunctata* and *S. invicta*, although these two species are also potentially important as
208 providers of the ecosystem service of pest control (Eubanks, 2001; Morris & Perfecto, 2016;
209 Morris, Jimenez-Soto, Philpott, & Perfecto, 2018). Especially important is the locally named
210 *abyarde* (electric fire ant), *W. auropunctata*, which occurs in large patches on the farms and is
211 such a nuisance to workers during the harvest that efficiency of harvest is dramatically reduced
212 since workers tend to skip areas that have concentrations of this species (I. P. personal
213 communication with farmers in Puerto Rico). Two farms were chosen for more detailed study of
214 these two species (codes for all farms are listed in table S1 in the supplementary material, also
215 see caption to table 2), *W. auropunctata* and *S. invicta*, at a larger scale, UTUA 2 (Finca Gran

216 Batey) and UTUA 20 (Finca Cítricos, Inc), the first dominated by *W. auropunctata* and the
217 second by *S. invicta* in the 10 x 10m plots located on those farms. On those two farms, we
218 geolocated all coffee bushes (550 bushes in UTUA2 and 479 on UTUA 20) on an area of 2500
219 m² in UTUA 2 and on an area of 1950 m² in UTUA 20, placed 5 baits on each coffee plants, let
220 the baits set for 40 minutes and then recorded the ant species on each of them. We sampled on
221 these two farms once in December/January of 2018/2019, once in July of 2019 and once in
222 January of 2020, effectively covering a twelve month period. Sampling of the larger areas was
223 limited by roads, fences and other limitations of the section of the farm we sampled.

224 As described in the results, our third sampling time in the UTUA 2 farm revealed what
225 appeared to be an invasion of the area previously dominated by *W. auropunctata* by swarms of
226 young *S. invicta*. From many natural history observations, we understand that some of the
227 competitive interactions between these two species take place on the ground. Recognizing that
228 part of the expected competitive interactions of these two species occurs not only on coffee
229 bushes but also on the ground and in the citrus trees above the coffee, we sampled these two
230 venues as well in January of 2020. Placing five tuna baits on each of the citrus trees within a
231 25X25 m² area we examined each bait for the occurrence of all ants after a 40 minute waiting
232 period. Within the same 25 X 25 m² plot we set up a 4 X 4 m grid on the ground and placed baits
233 to sample ants on the ground. This plot was located in a section of the area where we discovered
234 the apparent local invasion of *S. invicta*.

235 Finally, we performed six interaction trials between *S. invicta* and *W. auropunctata* in the
236 laboratory. Fractions of nests of *S. invicta* and *W. auropunctata* containing workers and brood,
237 were introduced into nesting boxes (15X15X15cm plastic containers), augmented with water and
238 honey. After 5 days, nesting boxes were connected with pipe cleaners, and behavioral
239 observations made. A week later all nests were harvested, and number of workers estimated in
240 all 12 containers (six interspecific comparisons).

241

242 **Results**

243 *10X10 m² surveys in 25 farms: species richness and dominance*

244 A total of 21 species (and/or morphospecies) of ants were recorded in the study (Table 1).
245 Eight were dominant on one or more (but never all) of the farms, while others were very active
246 but only rarely dominant (Table 2). Collating all the species together from all sites over all three

247 years, the pattern of number of species versus rank abundance follows the typical power law,
248 known in ecology since at least the 1940s (Fisher, Colbert, & Williams, 1943) (Fig. 2). This
249 regularity is frequently interrogated from the point of view of underlying mechanism (e.g.,
250 Hubbell, 2001), a research program reflected in our unaggregated data, as presented in table 1
251 and further explored below. The linear relationship between the natural log of species abundance
252 (number of bushes on which the species occurred) and the rank of the species (most abundant
253 first, least abundance last), has been argued to be one of the most important fundamental tools in
254 community ecology due to the universality of the pattern produced and the insights it provides
255 about how communities are organized (MacArthur, 1957; McGill et al., 2007).

256

257 *Figure 2 here*

258

259 Over our whole sampling region (which was designed to sample the entire background
260 habitat in which the dominant understory species is coffee), temporal consistency of the
261 dominant ant species was variable (Table 2). Of the 25 farms, 13 were consistent with the same
262 dominant species on all three sampling dates. Of the 12 farms that experienced a change in the
263 dominant species, two of them had major activity by two invasive species, *Tetramorium*
264 *bicarinatum* and *Nylanderia fulva*, neither species of which was encountered on any of the farms
265 on the first sampling date, nor any other farms on the second sampling date, but were extremely
266 common on the farms where they occurred.

267

268 *Table 1 here*

269

270 *Table 2 here*

271

272 It is notable that, from our 25 farm surveys we find that two of the most dominant ants are also
273 the ones frequently cited by farmers as undesirable because of their potent stings (*W.*
274 *auropunctata* and *S. invicta*), as mentioned above. It is also evident that these two species are the
275 most common species (Table 1), although some farms had very low activity of either.
276 Eliminating those site visits that had fewer than 10 individuals of either/or *W. auropunctata* or *S.*
277 *invicta*, the abundance of the two is plotted in figure 3. There is, for the most part, a dominance

278 of one or the other of these two species. In all 75 farm surveys (25 farms surveyed three times),
279 in only 11 surveys did we fail to find one or the other, and in the remaining 64 surveys, one or
280 the other was clearly sub dominant (observed less than 10 times) in all but five surveys. Thus, in
281 consideration of these two species only, in almost 80% of the cases there was clear dominance of
282 one or the other (Fig. 3), a pattern consistent with a strong competitive exclusion of one by the
283 other, not necessarily in one direction or the other. Of course, such data are also consistent with
284 a hypothesis of some underlying habitat factor that might be causing the pattern, especially the
285 amount of shade in the system, a factor well-known to influence ant abundance in the coffee
286 system (Philpott et al., 2010; Pardee & Philpott, 2011; Teodoro et al., 2010; Armbrrecht &
287 Gallego, 2007). While there is no geographical pattern associated with dominance of either of
288 these two species, and in three of the farms there was a change in the dominance of one to the
289 other, there was a clear relationship between the average canopy cover and abundance (number
290 of baits occupied), for both *W. auropunctata* and *S. invicta* (Fig. 4).

291

292 *Figure 3 here*

293

294 *Figure 4 here*

295

296 *Spatial distribution of the two dominant species in two farms*

297 In figures 5 and 6, we display the results of the larger areas sampled on farms UTUA 2
298 and UTUA 20 for the two dominant species, *W. auropunctata* and *S. invicta*. There are clear
299 patterns on these two farms over the 12 month interval. In UTUA 2, the dominance of *W.*
300 *auropunctata* increased between January 2019 and July 2019, but there was also an expansion of
301 *S. invicta* into the area where *W. auropunctata* had been rare (the right side of the sampling
302 area), although *W. auropunctata* had increased there also (Fig. 5). That expansion of *W.*
303 *auropunctata* continued on the right section of the plot between July 2019 and January 2020, but,
304 notably, there also appeared a cluster of coffee bushes that were dominated by *S. invicta*.
305 Interestingly, these new *S. invicta* bushes were all classified as from young colonies (based on
306 the absence of very large workers, as explained in the methods section). For closer examination
307 of the region in which these young swarms were evident, we set ground tuna baits at 4m intervals
308 on a 20x20m grid and found that the “incursion” of *S. invicta* into the region formerly dominated

309 by *W. auropunctata*, was considerably larger than evidenced in the observations strictly on
310 coffee bushes, suggesting that this new “incursion” of *S. invicta* into the area previously
311 dominated by *W. auropunctata* was driven by terrestrial (ground) dynamics involving these two
312 species (Fig. 5). The pattern might suggest that the presence of *S. invicta* is limiting the further
313 expansion of *W. auropunctata*, although the mechanism driving this limitation remains obscure
314 (as discussed further below). All but one of the 12 citrus trees sampled were dominated by *W.*
315 *auropunctata*, suggesting that the displacement of this species by *S. invicta* starts with the
316 establishment of *S. invicta* on the ground followed by foraging on coffee bushes, but not on the
317 citrus trees.

318

319 *Figure 5 here*

320

321 On UTUA 20, there was also significant change over the three sampling times, but here
322 there was an evident contraction in the special positions occupied by *W. auropunctata* (Fig 6).
323 Most interesting, there seems to be a relationship between the “young” colonies of *S. invicta* and
324 the contraction of the *W. auropunctata*, especially between 2018 and 2019. In contrast, the
325 change from July 2019 to January 2020 appears to have allowed *W. auropunctata* to reoccupy
326 some of the space it seems to have lost to young *S. invicta* colonies the previous 6 months,
327 perhaps suggesting a seasonal effect influencing the basic competitive interactions. Also notable
328 is the reduction in occupation of old *S. invicta* colonies in the lower part of the plot over the 12
329 month period. In table 3 we display the number of coffee bushes in UTUA 20 for each category
330 of occurrence or co-occurrence. It is clear that *W. auropunctata* co-occurs much more frequently
331 with young colonies of *S. invicta* (51 and 59%) than with old ones (0.5 and 3%), consistent with
332 the hypothesis that *S. invicta* replaces *W. auropunctata*, at least temporarily. This replacement is
333 hindered by the attacks of phorids, some species of which clearly prefer the megaworkers of *S.*
334 *invicta*, which are abundant only in the older colonies. Thus, the young colonies of *S. invicta*
335 (with few or no megaworkers) can dominate in competition with *W. auropunctata*, but as they
336 become old (i.e., begin producing more megaworkers), the phorids become more active and
337 abundant, thus detracting from the competitive dominance, and potentially reversing it to favor
338 *W. auropunctata*.

339

340 *Figure 6 here*

341

342 *Table 3 here*

343

344 *Laboratory nest box trials of interactions between W. auropunctata and S. invicta*

345 In the laboratory nest box trials, after connecting the nests, it became evident within
346 hours that the *W. auropunctata* were severely affected by the foraging *S. invicta* workers. The
347 inside walls of the nest boxes contained hundreds of *W. auropunctata* workers apparently trying
348 to escape, and *S. invicta* workers were actively foraging in areas that had been occupied by *W.*
349 *auropunctata*. Much of the *W. auropunctata* nesting material was woody stems with entrance
350 holes small enough that *S. invicta* workers could not likely penetrate, so initial observations
351 could not determine if the *W. auropunctata* workers were within those stems or not. A week
352 after initiation of trials all *W. auropunctata* workers had disappeared and nest boxes that had
353 contained *W. auropunctata* were now occupied with *S. invicta* workers. Opening all woody
354 stems that had been in the *W. auropunctata* nest boxes revealed a complete lack of *W.*
355 *auropunctata* workers.

356

357 **Discussion**

358 The ant assembly of this arboreally foraging ant community in this study is a dramatic
359 example of a novel ecosystem in which we might expect clear ecological modalities to emerge
360 (Perfecto & Vandermeer, 2015). Perhaps adding extra novelty is the fact that the most common
361 of the species in the system are well-known invasive species. If the expected modality forged by
362 an “invasive” is the practical exclusion of other species, as is commonly thought, what emerges
363 when the collection is mainly composed of such species? Perhaps the novelty here is simply
364 alternative states of single species dominance in a large area, perhaps generating an unusual form
365 of a metacommunity at a very large scale. We see some farms that, at least for a 12 month
366 period, retain the dominance of a single one of these invasive species, while the change from one
367 farm to another suggests that the permanent monospecific dominance is necessarily temporary, at
368 least at a local level.

369 At a macro scale (25 farms across the entire coffee-growing region of Puerto Rico; Fig
370 1), there is a great deal of variability in this novel community (Table 1). Although the majority

371 of farms retained the main species dominance over the 12 month sampling period, several had
372 major transformations, including five cases in which the site contained a species that had not
373 been there on the previous sampling date (Table 2). We suspect that a 10 x 10m² sampling plot
374 did not really sample the biodiversity on the farm as a whole, as evidenced by the more extensive
375 sampling on the two intensively sampled farms (Figs. 5 and 6). While the classification of
376 UTUA 2 as a *W. auropunctata* farm was accurate, the classification of UTUA 20 as a *S. invicta*
377 farm was completely misleading (Fig. 6).

378 Regarding *S. invicta*, the notable difference between the swarms identified as coming
379 from young colonies and those coming from older colonies and the relationship thereof with *W.*
380 *auropunctata* (Table 3) defies any direct and obvious interpretation. The pattern could be related
381 to the abundant phorid fly parasitoids (*Pseudacteon* spp.) which we regularly observe on swarms
382 of *S. invicta* on the ground (rarely on the arboreal baits). It is well-established that phorids have a
383 dramatic effect on the ecology of *S. invicta* (e.g., Morrison, 1999; Morrison & Porter, 2005;
384 Chirino, Gilbert & Folgarait, 2009; Puckett & Harris, 2010; Reed, Puckett, & Gold, 2015). It is
385 evident that at least the most commonly observed phorid species has a very strong preference for
386 the larger majors in a swarm of old *S. invicta*. We hypothesize that the harassment from these
387 flies interferes with the foraging ability of workers from the older colonies more than the
388 younger ones, and makes the older colonies less competitive with *W. auropunctata*. Studies of
389 the effect of phorid flies on size ratios of *S. invicta* foragers, document an increase of small
390 foragers in the presence of phorid flies in both native and introduced habitats of *S. invicta*
391 (Chirino, Gilbert, & Folgarait, 2009; Puckett & Harris, 2010; Reed, Puckett, & Gold, 2015). The
392 harassment effect of the phorid flies can also affect competitive interactions between species
393 (Morrison, 1999). In our study, non-systematic but extensive observations on the behavior of the
394 phorid flies suggest they may have a very large effect. For example, in one case a single phorid
395 was seen to attack at least 10 and perhaps as many as 20 workers in a one minute observation
396 period. Multiplying that number by the number of hours available for phorid attack, and the
397 potential effect on workers could be substantial. However, we should also note that in laboratory
398 experiments as well as an extensive three-year field study of the effect of an introduced phorid
399 species on *S. invicta* in Florida, the authors failed to find an effect of parasitism pressure on
400 density or activity of *S. invicta* (Mottern et al. 2004; Morrison and Porter 2005). Whatever the
401 mechanism, it is evident that there is a significant change in the pattern of occurrence across the

402 12 month sampling period on UTUA 2 and UTUA 20 with respect to *S. invicta* and *W.*
403 *auropunctata* (Figs. 5 and 6).

404 On farm UTUA2, there are two qualitative patterns that stand out (Fig. 5). In January
405 2019 *W. auropunctata* clearly dominated most of the area, but was relatively rare on the right
406 hand part of the sampling area. By July 2019, *S. invicta* had increased its activity significantly
407 on the right part of the plot, with coffee bushes mainly harboring old colonies, presumably
408 excellent targets for the phorids. In January 2020, there were two evident events that emerged.
409 First, the concentration of older colonies that had been on the right part of the plot in July 2019,
410 disappeared almost entirely, perhaps due to large-scale attack from phorids. Second, a group of
411 coffee bushes were recorded to be occupied by foraging swarms from young colonies of *S.*
412 *invicta* in the middle of the area formerly dominated by *W. auropunctata*. Furthermore, activity
413 on the ground of *S. invicta* was considerably more extensive than the activity on the bushes
414 themselves, suggesting that we are witnessing a local “invasion” of *S. invicta*, perhaps a single
415 colony. In searching the ground for surface mounds, only a single very small mound was
416 encountered immediately at the edge of the area that *S. invicta* was invading.

417 On farm UTUA 20, from January to July 2019, there was a dramatic increase in the
418 number and extent of *S. invicta* foragers from young colonies, accompanied by a reduction in
419 bushes occupied by *W. auropunctata* (Fig. 6 and Table 3). Furthermore, the pattern of occurrence
420 on the farm was clearly not random, with the distribution of *W. auropunctata* seemingly
421 restricted from both above and below by the incursion of *S. invicta*. This pattern was slightly
422 reversed between 2019 and 2020, perhaps reflecting a seasonal component of the dynamics.
423 Also, the concentration of *S. invicta* old colonies near the lower right of the plot was dramatically
424 reduced by July 2019, consistent with the idea of a phorid effect on older colonies. Casual
425 observations regularly observed phorids attacking *S. invicta* in this area.

426 Given these general spatial and temporal patterns, combined with the abundant literature
427 documenting the importance of phorid flies on *Solenopsis* species (Feener & Brown 1992;
428 Porter, Meer, Pesquero, Campiolo, & Foeler, 1995; Porter, 1998; Puckett & Harris, 2010; Chen
429 & Fadamiro, 2018; Oi et al., 2019), it is possible to suggest a narrative of how *S. invicta* and *W.*
430 *auropunctata* interact in the coffee-growing region of Puerto Rico. When a colony enters an
431 “empty” space, either from a founding queen or a queen moving with some of her workers and
432 brood, it persists there when normal resources are available. Eventually a colony from the other

433 species co-occupies the space, challenging the first species for available resources. Notably both
434 species actively tend scale insects and other hemipterans on coffee trees, prey on other insects,
435 and scavenge for organic detritus both on the trees and on the ground below, and thus are likely
436 to compete, at least over the long term (Torres, 1984b). When the occupying colony is *S. invicta*,
437 its foraging advantage begins the process of competitively excluding *W. auropunctata* from the
438 site. As *S. invicta* spreads locally to nearby coffee bushes, its population builds up to the point
439 that it begins producing the mega-workers so characteristic of older colonies (Tschinkel, 1988).
440 As the numbers of mega-workers continues increasing, the local phorid population begins to
441 increase. Eventually the phorids become so common that the *S. invicta* colony either dies or
442 moves to a site considerably removed from the local concentration of phorids. This narrative is
443 illustrated qualitatively in figure 7. This sort of dynamic process of competition is both spatial
444 and temporal and is a narrative that concords well with observations on both of the intensively
445 studied farms as well as the more spatially extensive observations of this novel community over
446 the entire coffee production area.

447
448 *Figure 7 here*

449
450 It is important to note that the process of competition suggested here is speculative since
451 we do not have direct evidence of the competition between these two species. Although
452 laboratory trials did demonstrate strong aggressive behavior of *S. invicta* workers against *W.*
453 *auropunctata*, this type of antagonistic behavior between a pair of species does not necessarily
454 imply interspecific competition, because competition is a population level process not and
455 individual level process. Aggressive behavior is a component of competition in ants, to be sure,
456 but as have been noted elsewhere (Perfecto, 1994), competitive outcomes can easily be the
457 reverse of what aggressive encounters might imply. Additionally, we cannot infer competition
458 from species distribution data alone since abiotic conditions, like nesting sites or food
459 availability could be the structuring mechanisms (Parr & Gibb, 2010). However, the data that we
460 accumulated does fit with the narrative in Fig. 7. It will take more detailed and controlled
461 experiments to test the proposed process that we speculate based on descriptive data and field
462 observations.

463 These results are of practical significance since *W. auropunctata* is regarded as one of the
464 most important “pests” in the coffee system due to its effect on harvesting efficiency (informal
465 interviews with multiple coffee farmers). Yet, it has potential to be a major natural enemy of at
466 least two of the major pests in coffee, the coffee leaf miner, *Leucoptera coffeella* (Perfecto &
467 Vandermeer, unpublished data) and the coffee berry borer *Hypothenemus hampei* (Morris,
468 Jimenez-Soto, Philpott, & Perfecto, 2018). Elsewhere we report on the complicated antagonistic
469 relationship between *W. auropunctata* and lizards of the genus *Anolis* (Perfecto & Vandermeer,
470 2020; Perfecto & Vandermeer, in review), the latter of which appear to be significant natural
471 enemies of both the coffee berry borer (Monahan, Morris, Davis Rabosky, Perfecto &
472 Vandermeer, 2017) and the miner (Perfecto, Hajian-Forooshani, White, & Vandermeer, 2020).
473 The end result may be that the potential biological control effect of *W. auropunctata* is countered
474 by its negative effect on the more efficient controlling agents, the anoline lizards. Understanding
475 the effect of other ant species on this noxious ant may aid in developing strategies to limit its
476 presence. In this study, *W. auropunctata* dominated only six of the 25 farms surveyed,
477 suggesting that its notoriety as one of the most important pests in the system is hardly ubiquitous.
478 However, in the farms where it is present, it is certainly a problem for farmers, particularly
479 during the harvest period. Understanding the forces that make it dominant on some farms while
480 virtually absent on others, may lead to strategies for managing it.

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Table 1. List of species encountered and basic distributional statistics.

Ant Species	Number of times/farms dominant	Total abundance	Number of times/farms occurrence	Presumed origin
<i>Wasmannia auropunctata</i>	25	1776	48	American Tropics (not PR)
<i>Solenopsis invicta</i>	14	919	65	South America
<i>Monomorium floricola</i>	13	917	41	South Asia
<i>Tapinoma melanocephala</i>	7	619	38	Old World Tropics
<i>Brachymyrmex heeri</i>	0	205	42	Native
<i>Linepithema iniquum</i>	3	187	13	Native

<i>Monomorium ebenium</i>	1	171	13	Native
<i>Tetramorium bicarinatum</i>	2	98	2	Southeast Asia
<i>Nylanderia pubens</i>	0	89	16	Native
<i>Pheidole megacephala</i>	0	88	20	Africa
<i>Nylanderia fulva</i>	0	69	3	South America
<i>Brachymyrmex obscurior</i>	0	59	19	Native
<i>Cardiocondyla emeryi</i>	1	43	3	Native
<i>Myrmelachista remulorum</i>	0	29	5	Native
<i>Paratrachina longicornis</i>	0	23	6	Native
<i>Pheidole moerens</i>	0	16	5	Native
<i>Pheidole exigua</i>	0	10	2	Native
<i>Pheidole sculptior</i>	0	5	2	Native
<i>Solenopsis</i> sp. 1	0	3	2	?
<i>Solenopsis</i> sp. 2	0	3	3	?
<i>Cardiocondyla venustula</i>	0	2	2	Africa

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699 Table 2. Farms and dominant species on all three sampling dates (January 2019 [covering a
700 sampling period from Dec2018 to Jan2019], July 2019 and January 2020). Farm code indicates

701 municipality and farm number code within the municipality (code numbers stem from previous

702 larger sample of coffee farms). UTUA = Utuado, ADJU = Adjuntas, MARI = Maricao, LASM =

703 Las Marias, OROC = Orocovis, YAUC = Yauco, JUAN = Juana Días, JAYU = Jayuya.

Site Code	Jan-19	Jul-19	Jan-20	Species Identification
UTUA16	W	W	W	W = <i>Wasmannia auropunctata</i>
UTUA 2	W	W	W	S = <i>Solenopsis invicta</i>
MARI3	W	W	W	Tm = <i>Tapinoma melanocephala</i>
LASM3	W	W	W	Mf = <i>Monomorium floricola</i>
LASM1	W	W	W	L = <i>Linepithema iniquum</i>
OROC1	W	W	W	N = <i>Nylanderia fulva</i>
UTUA10	Tm	Tm	Tm	Tb = <i>Tetramorium bicarinatum</i>
UTUA20	S	S	S	C = <i>Cardiocondyla emeryi</i>
YAUC3	S	S	S	Me = <i>Monomorium ebenium</i>

UTUA30	Mf	Mf	Mf	ND = No Dominance
ADJU7	Mf	Mf	Mf	
JUAN7	Mf	Mf	Mf	
UTUA18	L	L	L	
MARI2	W	W	C	
JUAN1	W	Tm	Tm	
PONC1	W	S	S	
MARI18	W	N	W	
JAYU3	Tm	Mf/Tm	Mf	
UTUA17	Tm	Mf	Mf	
UTUA5	S	W/Mf/Tm	W/Mf/Tm	
ADJU8	S	S	Mf	
LASM2	S	Me	W	
UTUA13	S	Mf	S	
JAYU2	ND	Tb	Tb	
YAUC4	ND	ND	ND	

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718 Table 3. Co-occurrence of *W. auropunctata* with *S. invicta* on the UTUA 20 farm on the three
 719 sampling dates (January 2019 (covering a sampling period from Dec 2918 to January 2020),
 720 July 2019, and Jan 2020). Young swarms (i.e., presumably coming from young nests) are
 721 defined as those having few or no large majors while old swarms (i.e., presumably coming from
 722 older nests) are defined as those having significant numbers of large majors. Numbers are the
 723 number of coffee plants with the indicated ant presence.

Species	Jan-19	Jul-19	Jan-20	Total
<i>Wasmannia auropunctata</i>	149	70	219	438
<i>Solenopsis invicta</i> (young nest)	111	170	149	430
<i>Solenopsis invicta</i> (old nest)	81	53	52	186
<i>S. invicta</i> (young nest) and <i>W. auropunctata</i>	67	109	78	254
<i>S. invicta</i> (old nest) and <i>W. auropunctata</i>	1	5	6	12

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734 **Figure Legends**

735 Figure 1. Positions of the 25 farms in the sample. Image from Google Earth.

736 Figure 2. Power function relationship between species abundance and species rank. Complete
 737 collection consists of all point with a subset of the intermediate ranks in red. The four most
 738 abundance species seem somewhat out of the general pattern for the intermediate ones (in red
 739 with the shallower slope).

740 Figure 3. Abundance at a site of the two most common species by visit (black closed circles) or
741 by average of three visits at a site (open red circles). Note the strong tendency of one or the
742 other being dominant, with only four visits exhibiting more than 20 (out of 100) bait occupancies
743 of both species.

744 Figure 4. Relationship between the two most common species and average percent of shade
745 cover.

746 Figure 5. A 12 month record of the spatial dynamics of two of the most dominant species on
747 farm UTUA 2 (grid is 5 X 5 m²). Size of the symbol proportional to activity at that site (largest =
748 5 baits occupied, smallest = 1 bait occupied, small dots are bushes that had no individuals of the
749 three species on any of the five baits). Dashed outline square in January 2020(dry) frame
750 indicates the position of area baited with ground baits and presented on the right. All ground
751 baits with *S. invicta*, where apparently from young colonies.

752 Figure 6 . A 12 month record of the spatial dynamics of two of the most dominant species on
753 farm UTUA 20.

754 Figure 7. Diagrammatic picture of the hypothetical spatio/temporal competitive process between
755 *S. invicta* and *W. auropunctata*. Dashed connections indicate the negative effect that *S. invicta*
756 colonies are hypothesized to have on the establishment and/or survival of *W. auropunctata* nests.

757 **Data Availability Statement**

758 Data for this study is available in Dryad under "Data Base for novel ant ecosystems"

759 doi:10.5061/dryad.8sf7m0ck5

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762 **Competing Interest Statement**

763 The authors declare no competing interests.

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765 **Author's Contributions**

766 IP and JV participated in the design, data gathering, data analyses, manuscript writing and
767 editing of this manuscript.

768

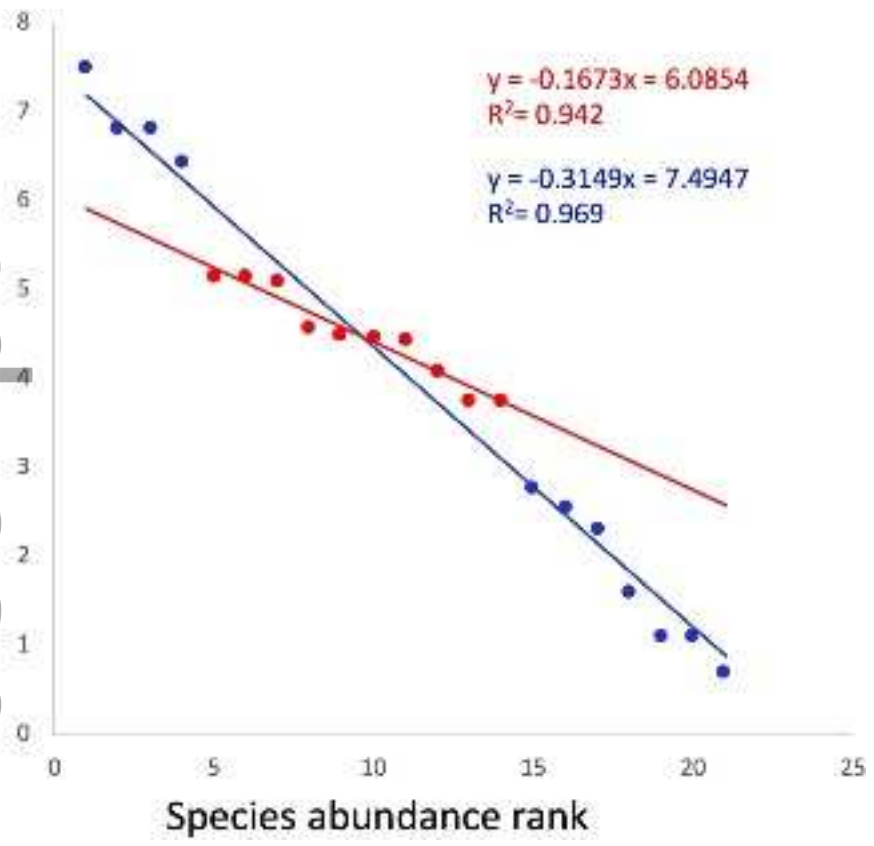
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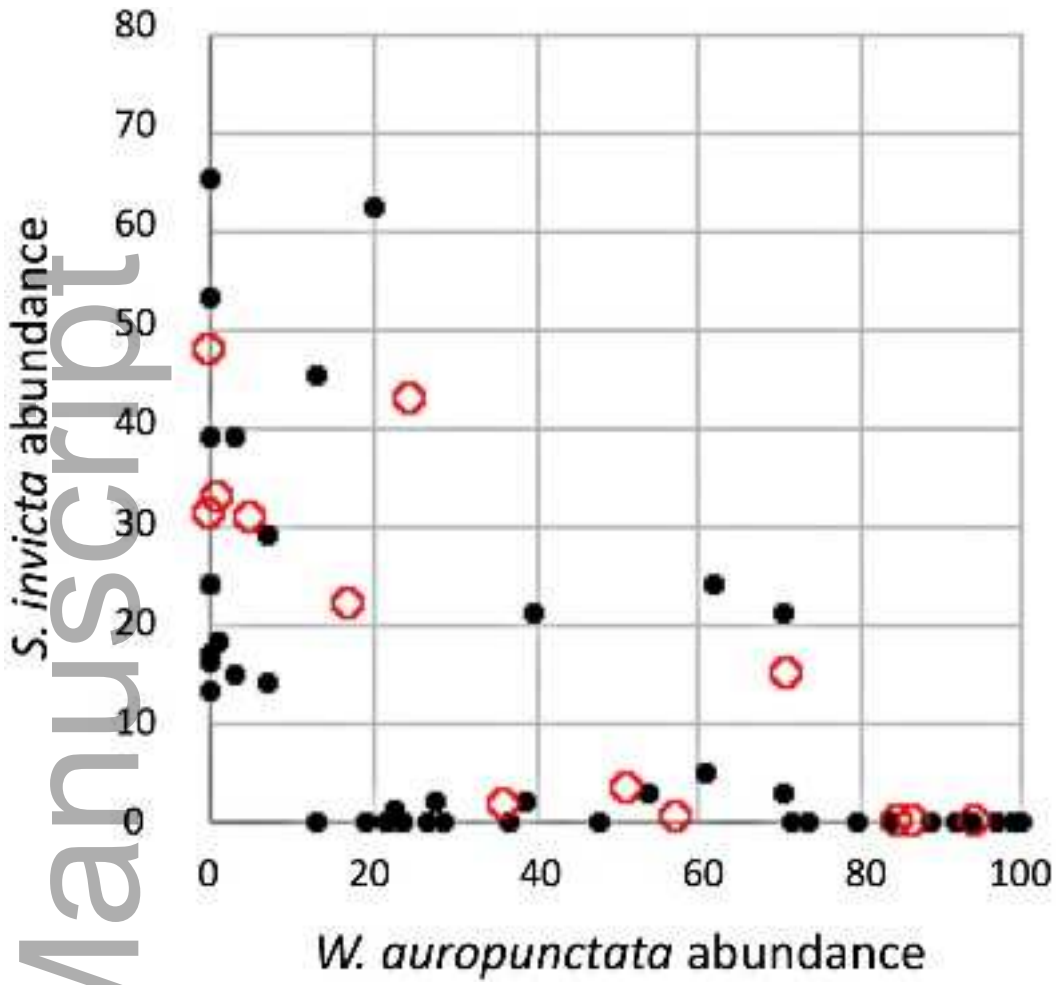
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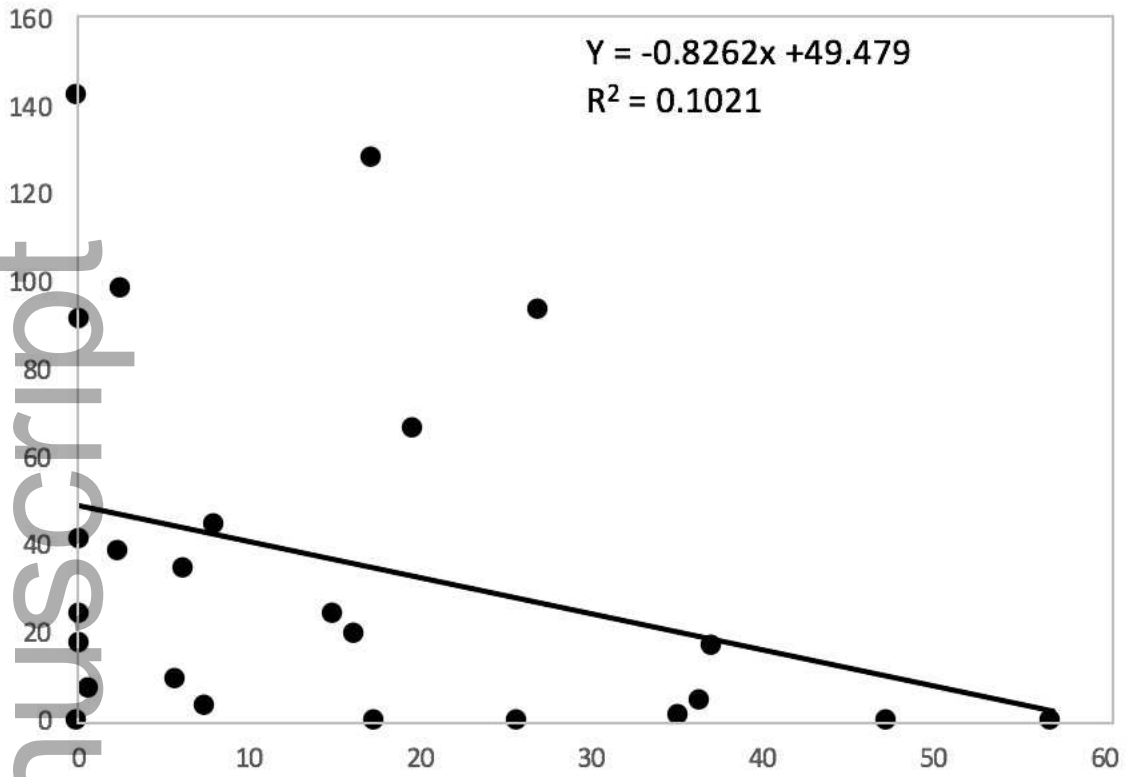


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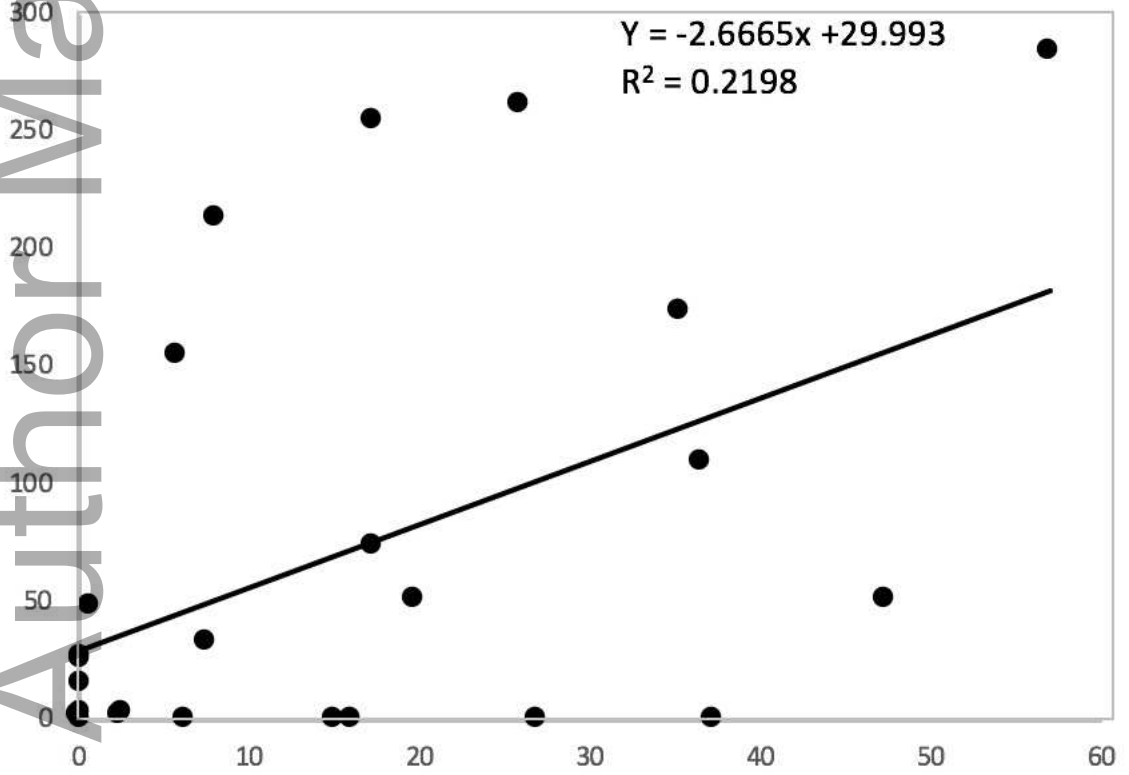


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Abundance of *S. invicta*

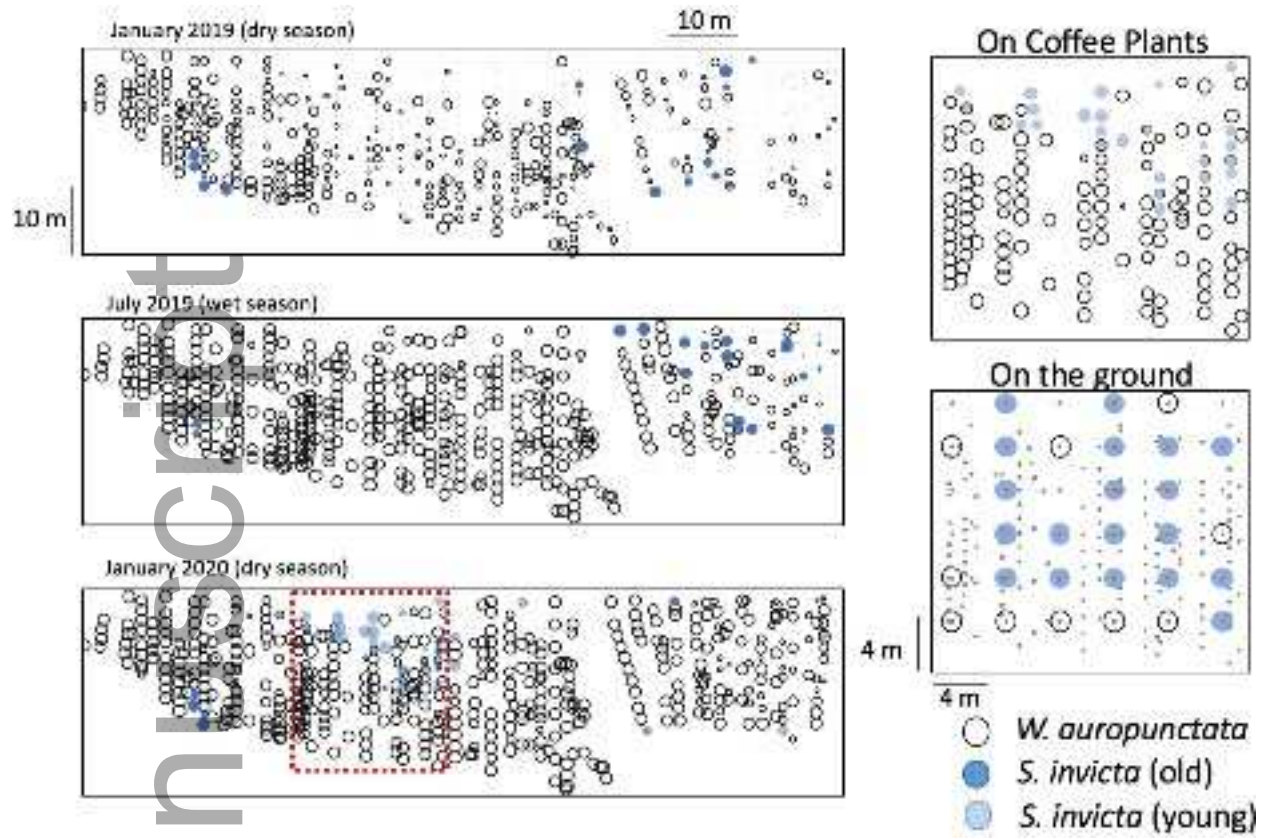


Abundance of *W. auropunctata*

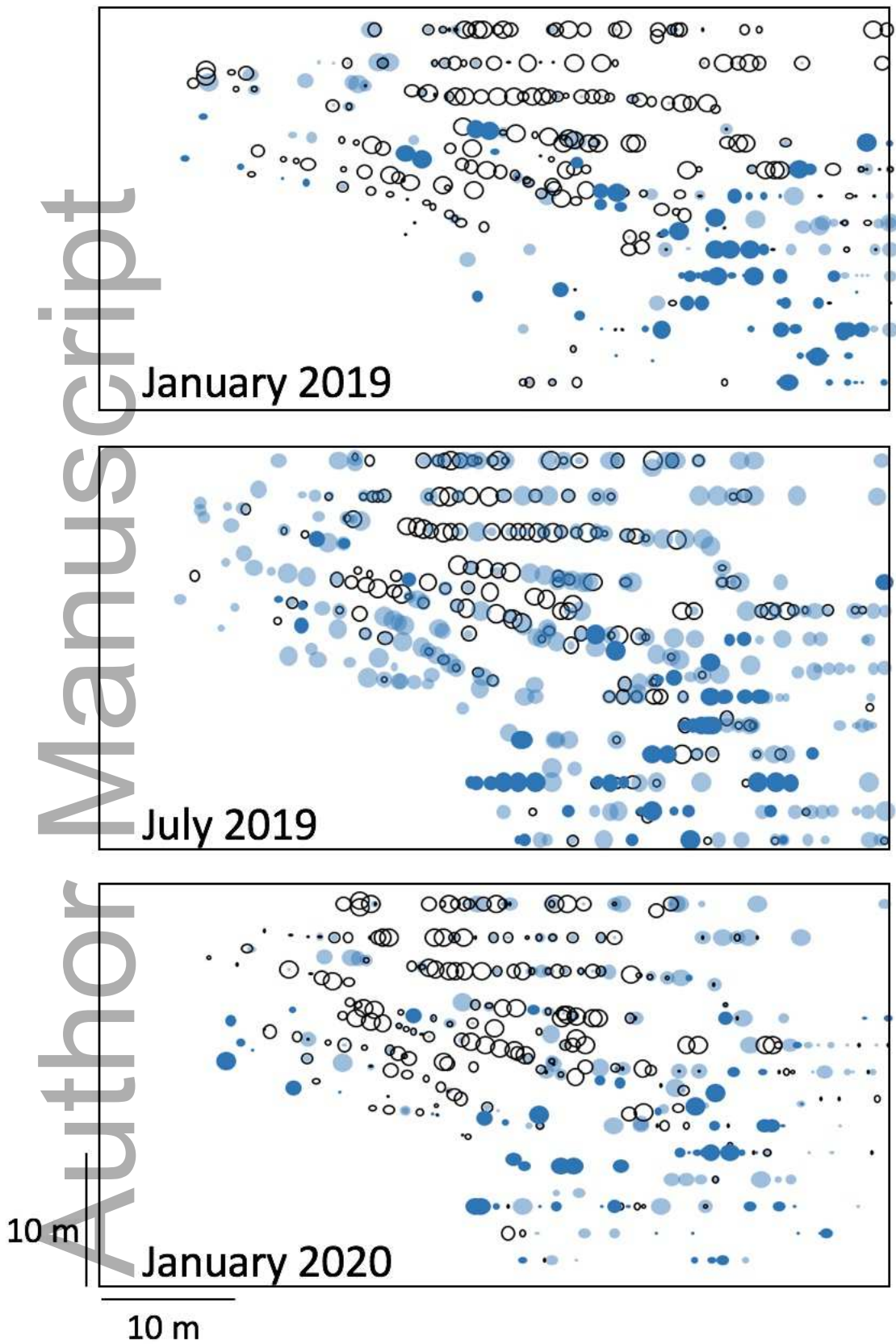


Average % canopy cover

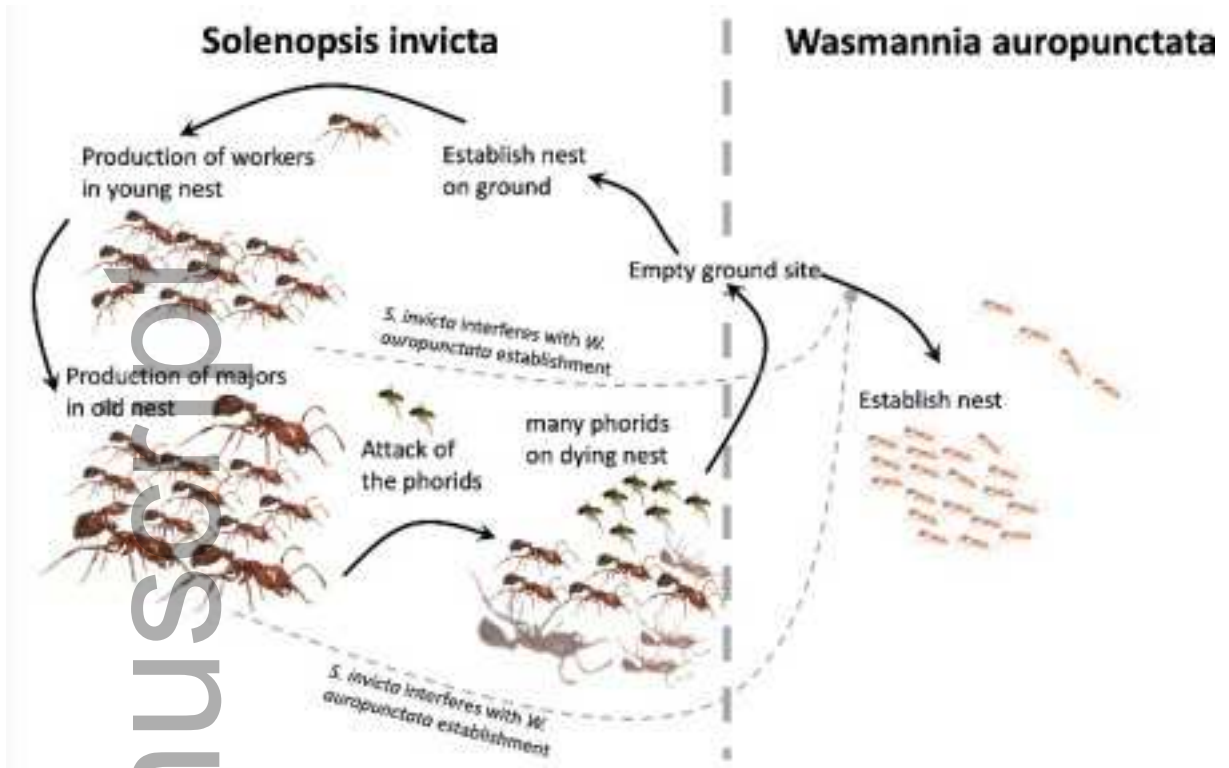
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