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The apiary influence range: a new paradigm for managing the cohabitation of honey bees and wild bee communities

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Abstract

There is an emerging controversy among bee biologists, land managers and beekeepers about the legitimacy of high-density beekeeping in natural protected areas due to the risks of detrimental interactions with local wild bees. The conflicting needs of wild bee conservation and productive beekeeping requires the adoption of inclusive conservation measures. The distance-based beekeeping regulation is a relevant candidate approach in that respect. It consists in increasing spacings among neighbouring apiaries so as to reduce the proportion of land cover under detrimental competition for floral resources. This approach stems from the concept of Apiary Influence Range (AIR), i.e. the distance range around apiaries within which measurements of native plant-pollinators interactions are significantly altered. The seminal study on this topic reported AIRs spanning distances of 0.6–1.1 km around apiaries. The objective of this study is to provide conservation biologists and practitioners with a roadmap to manage the coexistence between productive beekeeping and wild bee conservation, along with a formalized terminology. We first

introduce the key theoretical ideas linked with the AIR. Then, we develop the associated calculation rationale to help land managers achieve their wild bee protection goals. Finally, we further provide original AIR values complementary to those available in recent literature. We believe the distance-based beekeeping regulation is in practice more tractable than setting maximal honey bee colony density rules. It may contribute to guide bee biologists and conservation practitioners towards successful inclusive bee conservation, providing the approach can be supported by a broader range of trials in various environmental contexts and using standardised terminology.

1. Introduction

As modern farming practices make agro-ecosystems less suitable environments for sustainable honey production, professional beekeepers periodically move large apiaries into natural areas, either to exploit temporary mass-flowering resources or to escape chemical hazards and seasonal food shortages (Odoux et al., 2014; Requier et al., 2017). But in recent years, conservation biologists have raised awareness about the risk of ecological interference between the massively introduced managed honey bee (*Apis mellifera*) and the diverse native wild bee fauna in protected natural areas. Expected interference mechanisms have been reviewed in recent studies and may include among others exploitation competition for nectar and pollen, behavioural and foraging time budget alteration, skewed sex ratio, fitness and offspring size reduction, alteration of pollination networks and spillover of shared pathogens and predators (Cane and Tepedino, 2017; Geslin *et al.*, 2017; Russo, 2016), though there is still some level of inconsistencies among studies assessing the honey bee induced competition (Wojcik *et al.*, 2018).

There is now in scientific literature an emerging controversy over excessively conservationist positions pleading for the complete ban of beekeeping out of protected areas

(Geldmann and González-Varo, 2018; González-Varo and Geldmann, 2018; Kleijn *et al.*, 2018; Saunders *et al.*, 2018). Bee biologists also recall the need to conserve the diversity of the honey bee in its native range, i.e. Africa, Europe and western Asia, in all its dimensions: genetic diversity, local adaptations, endangered subspecies as well as traditional beekeeping knowledge and practices (Alaux *et al.*, 2019; Requier *et al.*, 2019). This conservation beekeeping, aiming at preserving local honey bee genotypes, is another important component to consider in the debate alongside the more conventional beekeeping. From a social perspective, beekeepers are also now struggling to find suitable settlements because they do not own the land they exploit and are vulnerable to land management policies made by public and private owners (Durant, 2019).

These conflicting issues can only be conciliated with an inclusive conservation approach (Kleijn *et al.*, 2018), involving all the stakeholders for an overall enhanced effectiveness, social acceptability and sustainable results. To date, the recommendations found in scientific literature to inform inclusive conservation policies are scarce and plead for *density-based beekeeping regulation*, i.e. the introduction of *maximal colony density thresholds* that are recognized to have no observable adverse effect on the local pollinator fauna. For instance Steffan-Dewenter and Tscharntke (2000) suggested a precautionary principle based on the European-wide average density of 3.1 colonies/km^2. Later on, Torné-Noguera *et al.* (2016) reported empirically a threshold of 3.5 colonies/km^2. However, those recommended density thresholds are somehow difficult to apply in real-life situations. They appear too restrictive given the typical size of professional apiaries (100 to 200 colonies) and they do not state how colony numbers should be allocated among apiaries, nor distributed in space.

In a recent study (Henry and Rodet, 2018), we provided alternate guidance towards beekeeping regulation based on minimal distance thresholds between neighbouring apiaries. The field work was carried out in a protected Mediterranean rosemary scrubland covering

5,700 ha. During the spring rosemary bloom, professional beekeepers migrate numerous colonies into the area (up to 14 colonies/km^2). This activity triggers a foraging competition which depresses not only the occurrence and foraging success of local wild bees but also nectar and pollen harvesting by the honey bees themselves. We however noticed that competition was relaxed beyond a certain distance threshold away from apiaries, herein called the Apiary Influence Range (AIR). Practically, this means that the studied competition metrics were better accounted for by a two-step threshold effect model (closer-vs.-farther binary distance variable) rather than a progressive effect model (continuous distance variable). AIRs spanned distances of 0.6–1.1 km depending on the considered competition ecological metric. The concept of AIR has direct practical implications towards inclusive conservation. It may help land managers assessing land cover actually under the influence of honey bees (AIR cover) vs. land cover compatible with wild bee conservation at low competition levels.

We believe the AIR framework may contribute to guide bee biologists and conservation practitioners towards inclusive bee conservation. It provides a concrete criterion to reduce competition risks by setting a minimal distance threshold between neighbouring apiaries in order to ensure areas with relaxed competition. This distance-based beekeeping regulation (Henry and Rodet, 2018) appears more operational than any regulation based on colony density recommendations in protected areas. It is however necessary to further support these findings by carrying out more competition assessment studies in a range of protected areas from diverse biogeographical contexts.

The objective of this study is to establish a formalised terminology to facilitate future meta-analyses on that topic. We first demonstrate the basic theory and calculation in Material and Methods. We then present additional AIR data recomputed from the original study (Henry

and Rodet, 2018). Finally, we highlight perspectives and new challenges for the applicability of the AIR framework and distance-based beekeeping regulation in protected areas.

2. Material and Methods

We develop below the theory and calculation associated with the distance-based beekeeping regulation. All the terms we have coined hereafter are further defined in Table 1. The reasoning behind the distance-based beekeeping regulation is that exploitation competition between honey bees and wild bees, or among honey bees themselves, occurs within a determined distance range around apiaries, herein called the AIR and expressed in km (0.6 to 1.1 km in Henry and Rodet, 2018). For an enhanced applicability and effectiveness, we propose that any attempt to regulate beekeeping in a protected area may be based on minimum distance thresholds between neighbouring apiaries, rather than on maximal colony density thresholds. We however assume the AIR will be specific to the environmental context of interest and to the considered *competition metric*.

113 Table 1. Terminology and definitions associated with the concept of distance-based

114 beekeeping regulation in natural protected lands.

Terminology	Definitions
Exclusive wild bee conservation	Characterizes wild bee conservation policies based on the total ban (exclusion) of managed honey bees away from a focus protected land.
Inclusive wild bee conservation	Characterizes wild bee conservation policies aiming at reconciling the conflicting needs of wild bee conservation and productive beekeeping within a focus protected land. Inclusive conservation tolerates productive apiaries but organizes spaces or periods of moderate competition through beekeeping regulation measures. The density-based regulation imposes maximal colony density thresholds, while the distance-based regulation imposes minimal distance thresholds among neighbouring apiaries.
Competition metrics	Ecological response variables liable to reveal a competition for the exploitation of floral resources, either between honey bees and wild bees, or among honey bees themselves (respectively inter- or intra-specific competition). These metrics may relate to the individual foraging success, the reproductive success, the body condition, the population dynamics, the species community composition or the plant-pollinator interaction network sustainability (Table 2).
Apiary Influence Range (AIR)	Distance range around an apiary within which a given *competition metric* is significantly altered compared to its usual level observed beyond that distance. An apiary Influence Range can be defined as a distance threshold beyond which expected competition is relaxed (Fig. 1).
Land-cover protection goal	The amount of protected land (in %) managers are willing to dedicate to wild bee conservation *vs.* exploitation by productive beekeeping. A 100% protection goal in favour of wild bees is equivalent to an *exclusive wild bee conservation* policy. Inclusive conservation policies may target *conservative* (80%), *balanced* (50%) or *moderate* (20%) protection goals, depending on the local beekeeping history. The corresponding minimal distances requested among neighbouring apiaries may be derived from simple land cover formulas (Eqs. 1-4).
Spatially explicit distance-based regulation	Advanced version of the distance-based regulation of beekeeping whereby some specific parts of a focus protected land are identified as priority conservation areas that need to be explicitly located away from AIRs. These may be peculiar micro-refugia or sensitive habitats hosting threatened or emblematic plant or pollinator species. This option further constrains the spatial allocation of apiaries (Fig. 2).

115

116

117 *2.1. Competition metrics*

118 *Competition metrics* are the ecological response variables liable to reveal a competition for
119 the exploitation of floral resources. At the proximal level, it may involve assessments of
120 nectar or pollen availability in flowers, nectar or pollen foraging success in wild bees (inter-
121 specific competition), but also in the honey bee foragers themselves (intra-specific
122 competition). It may also comprise standardized assessments of wild bee fitness, body size
123 or abundance (flower visiting rate), though the latter metrics might reveal competition only
124 at the next generation if competition has eventually resulted in altered local wild bee fitness.

125

126 2.2. *The Apiary Influence Range* (AIR)

127 The AIR is the distance range around apiaries within which competition metrics are
128 significantly altered (Fig. 1). It may be readily delineated by threshold statistical models with
129 a moving function of distance. Simple threshold statistical models, such as generalized
130 fluctuation tests or breakpoint regressions (Zeileis et al., 2002), can easily locate the most
131 parsimonious thresholds for structural changes in univariate data patterns. Previous studies
132 (Henry and Rodet, 2018) have used generalized linear models and the Akaikee Information
133 Criterion framework to assess the probability that competition metrics are better accounted
134 for by a two-step threshold effect model (closer-vs.-farther binary distance variable) rather
135 than a progressive effect model (continuous distance variable). Results were in support of a
136 two-step distance threshold for most candidate competition metrics, which is the basic
137 assumption for the distance-based regulation of apiary influence we propose here. AIRs
138 shown in Fig. 1 range from 0.6 to 1.1 km, which is effectively comprised within the honey

139 bee median foraging range of 1–2 km usually reported in literature (Couvillon *et al.*, 2014;
140 Steffan-Dewenter and Kuhn, 2003; Visscher and Seeley, 1982).

141 The distance-based regulation of beekeeping lays on the AIR concept. It consists in
142 increasing the distance among neighbouring apiaries so as to provide wild bees with more
143 space outside the AIRs, i.e. more space under relaxed competition and therefore compatible
144 with wild bee conservation (Fig. 2a *vs.* 2b). As an interesting property, this approach gives
145 less importance to apiary size, and therefore to honey bee colony density. We still tentatively
146 recommend an upper limit of about 30 to 50 colonies per apiary in order to fit the actual
147 average apiary size observed in Henry and Rodet (2018), namely 30.1 ± 21.8 (sd) colonies.
148 The distance-based regulation can then be simply viewed as spacing out those apiaries with
149 respect to a minimal distance that should be a function of an overall wild bee *land cover*
150 *protection goal* decided by managers.
151

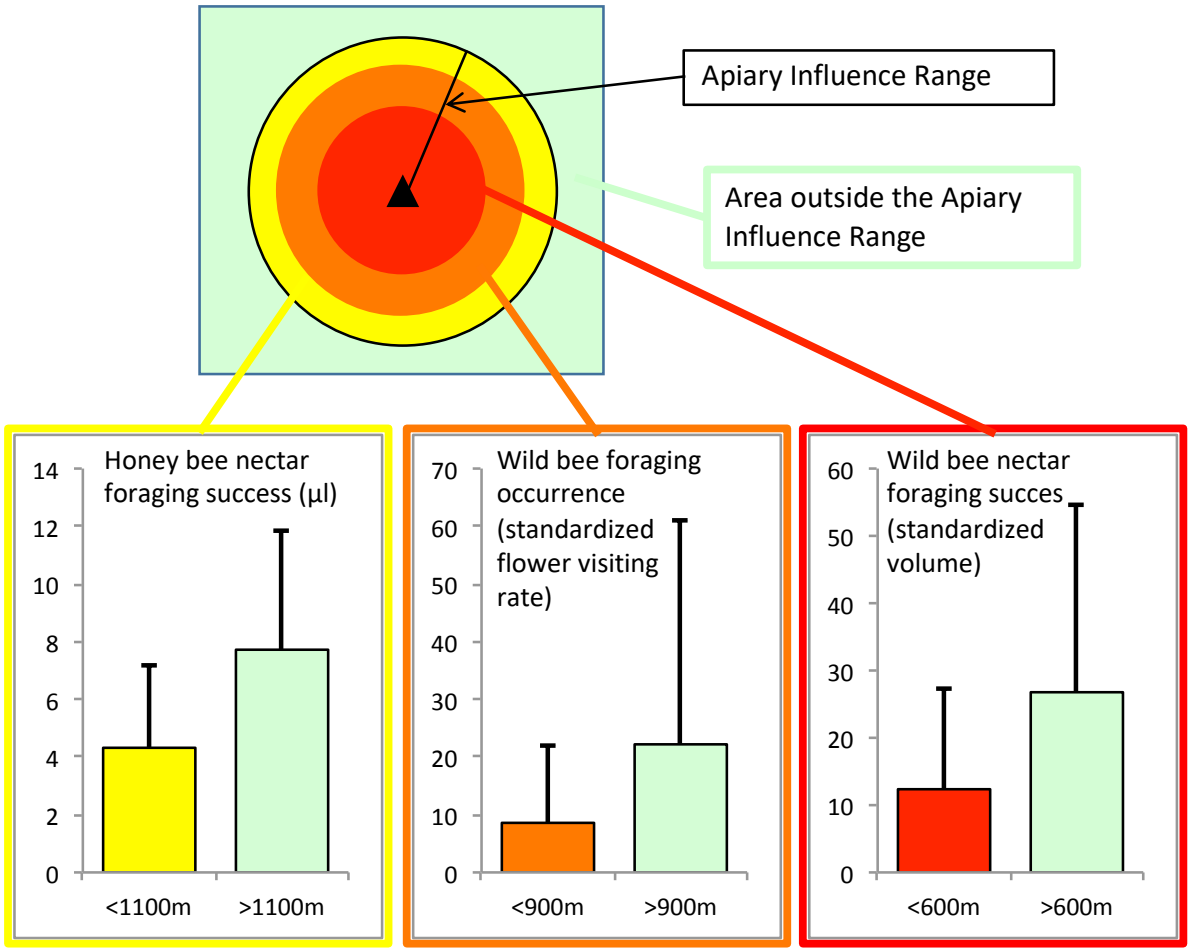

Fig. 1. Illustration of the Apiary Influence Range (AIR) applied to three competition metrics selected from Henry and Rodet (2018). Depending on the metric, AIRs expend from 0.6 to 1.1 km around apiaries (circles around the triangle), with significant differences between values from sampling sites located closer to (inside circles) *vs.* farther away (outside circles) from the nearest apiary. The AIR may be viewed as the most discriminatory distance threshold between closer and farther sites according to statistical threshold models. Examples stand for competition metrics measured in a rather homogeneous rosemary mass-flowering Mediterranean scrubland. Honey bee foraging success was assessed by nectar crop content measurements (µl). Wild bee foraging occurrence was expressed as a number of foraging individuals per 100 units of flowering rosemary volume. Wild bee nectar foraging success, initially assessed by

nectar crop content measurements (µl), was further standardised to the maximal expected field nectar crop content given each individual's body size.

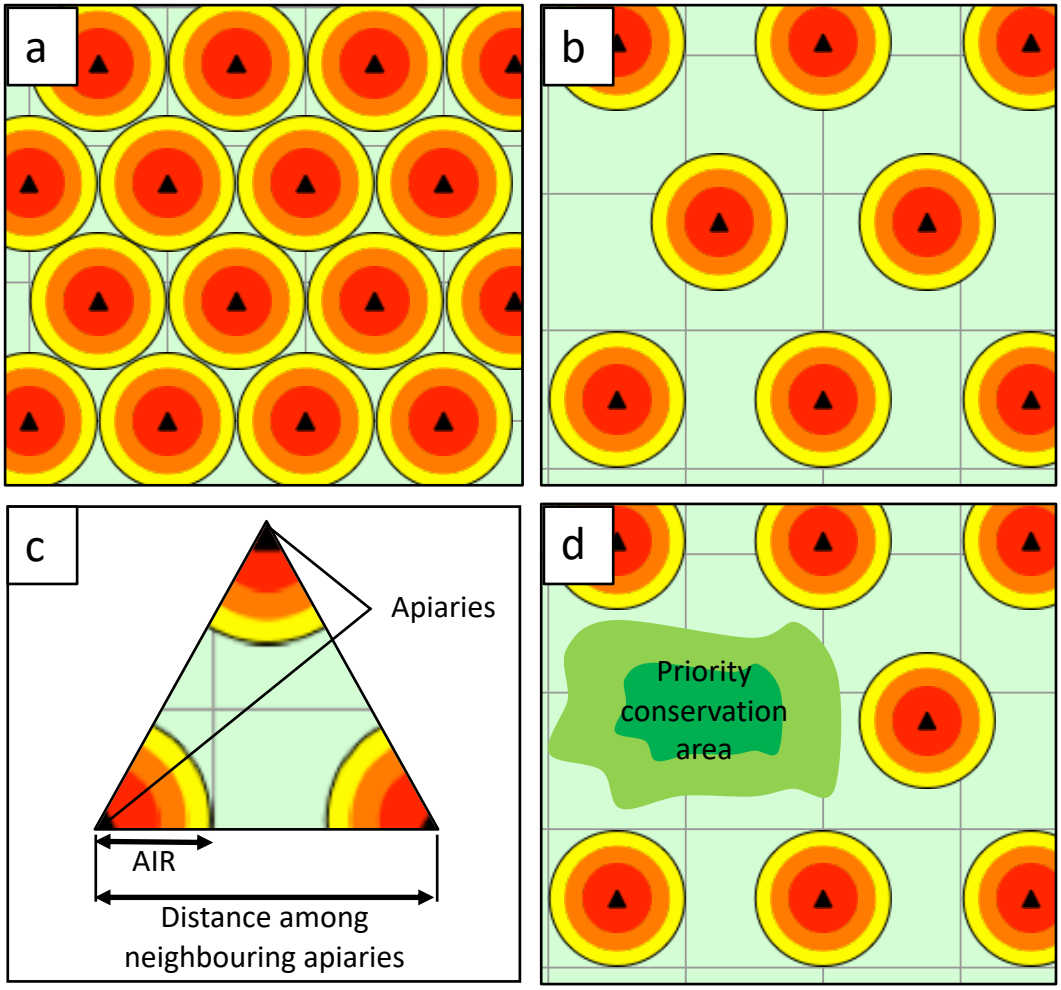

Fig. 2. Idealised representation of the distance-based beekeeping regulation in a natural protected area. (a) with no wild bee protection goal, apiaries may bee tightly clumped, with coalescent AIRs leaving few spaces with relaxed competition (here about 10% land cover). (b) increasing distances among neighbouring apiaries will provide more space under relaxed competition, compatible with wild bee conservation. (c) the idealised basis pattern may be used to compute the proportions of landscape covered by AIRs. (d) more advanced spatially explicit regulation approaches may include specific priority conservation areas based on peculiar local plant-pollinator interaction networks, and possibly including their own buffering area.

179

180 2.3. *The wild bee land cover protection goal*

181 The *land-cover protection goal* is the amount of protected land managers are willing to
182 dedicate to wild bee conservation vs. floral exploitation by beekeeping. In the absence of wild
183 bee protection goals, land managers may admit a tight network of apiaries, whose AIRs will
184 cover 100% of the land area. As AIRs become coalescent (apiary spacing equivalent to, or
185 shorter than, twice the AIRs, Fig. 2a), apiaries will theoretically impose a *saturating* influence
186 all over the protected area. At the opposite, an *exclusive* wild bee protection goal would
187 means the complete ban of beekeeping away from the protected area (0% AIRs land cover).
188 In the intermediate *inclusive conservation* strategy we propose here, managers may wish to
189 allocate a certain proportion of land cover to wild bee conservation vs. floral exploitation by
190 beekeeping. Depending on managers expertise and local beekeeping history, reasonable
191 wild bee protection goals may vary from a rather *balanced* 50% land protection goal to a
192 rather *conservative* 80% land protection goal in favour of wild bees. Managers of protected
193 lands with a longstanding beekeeping history at saturation level may rather target a
194 *moderate* 20% land protection goal as a first step towards honey bee regulation. It is
195 important to keep in mind that a 50% land protection goal does not mean that half the land
196 area is freed from forager honey bees. Rather, it states that half the area is under the
197 influence of apiaries, with potentially high levels of competition, while the second half allows
198 for the cohabitation of wild and managed bees at low competition levels. Conversely, we
199 believe that this protection goal framework should not be used as an argument to introduce
200 or intensify beekeeping in pristine areas, particularly those holding sensitive or endangered
201 plant or bee species, such as in small oceanic islands with high levels of endemism (e.g. Abe
202 et al., 2010; Kato et al., 1999).

203

204 2.4. *Land cover calculations*

205 To achieve their *wild bee land cover protection goal* strategy, managers may use a *land cover*
206 *formula* linking the minimal distance among neighbouring apiaries (d, km) with the Apiary
207 Influence Range (AIR, km). The formula may be derived from the basis pattern of the
208 idealised apiary spatial allocation (Fig. 2c). In this basis pattern, the three equidistant
209 neighbouring apiaries delineate a triangular landscape unit whose surface S_{unit} is given by:

210 $$S_{unit} = \frac{\sqrt{3}}{4} \times d^2 \qquad \text{(with } d \geq 2AIR\text{)} \qquad \text{(Eq. 1).}$$

211 Within the landscape unit S_{unit}, the three AIRs cover an influence surface S_{AIR} equivalent to:

212 $$S_{AIR} = \frac{1}{2} \times \pi \times AIR^2 \qquad \text{(with } AIR \leq \frac{1}{2}d\text{)} \qquad \text{(Eq. 2).}$$

213 In this configuration, the effective land cover protection goal, i.e. the proportion of low-
214 competition surface compatible with wild bee conservation, is given by the proportion of the
215 landscape unit surface S_{unit} *not* covered by apiary influence surfaces S_{AIR}, following:

216 $$Goal\ (\%) = 1 - \frac{S_{AIR}}{S_{unit}} = 1 - \left(\frac{2\pi}{\sqrt{3}} \times \frac{AIR^2}{d^2}\right) \quad \text{(with } Goal \text{ defined in [0.1, 1])} \qquad \text{(Eq. 3).}$$

217 Reciprocally, the spacing among neighbouring apiaries required to achieve a particular wild
218 bee land cover protection goal is given by:

219 $$d_{Goal} = \sqrt{\left(\frac{2\pi}{\sqrt{3}} \times \frac{AIR^2}{(1-Goal)}\right)} \qquad \text{(with } Goal \text{ defined in [0.1, 1])} \qquad \text{(Eq. 4).}$$

220 Importantly, Eqs. (1-4) only apply for distances d equal to or greater than twice the AIR,
221 which gives a wild bee protection goal >0.1 (or >10% land cover in favour of wild bee
222 conservation). Otherwise, AIRs overlap among neighbouring apiaries, and calculations
223 become a little bit more tricky just for targeting a whimsically low protection goal (<10%
224 land cover).

225

226

227 2.5. *Simple* vs. *Spatially explicit distance-based regulation*

228 We further distinguish between two mutually non-exclusive distance-based approaches,
229 namely the simple distance-based regulation (Fig. 2b) and the more advanced *spatially*
230 *explicit* one, which may be advisable in particular conservation contexts with specific
231 protection goals (Fig. 2d).

232 In the simple *distance-based regulation*, protected land managers will have no specific
233 protection goals other than optimising the proportions of land cover dedicated to
234 beekeeping *vs.* wild bee conservation, regardless of landscape heterogeneity. In other words,
235 they do not intend to target a specific location or habitat as being of priority conservation
236 concern. Instead, they assume the wild bee conservation issue is homogeneous throughout
237 the protected area.

238 Conversely, managers may want to target explicitly defined protection goals such as peculiar
239 micro-refugia or sensitive habitats hosting threatened or emblematic plant or pollinator
240 species. Once identified in the field, such priority conservation areas will constrain the
241 spatial allocation of apiaries in a manner that prevents overlap with AIR surfaces (Fig. 2d).
242 This spatial constraint will force managers to apply a spatially explicit allocation of apiaries.

243

244 2.6. *Computation of additional AIR values*

245 Figure 1 presents AIRs for three main competition metrics. For a more in-depth assessment
246 of possible values, additional AIRs were recomputed from raw data (Henry and Rodet, 2018).
247 We were especially interest in (i) the distance range of increased *honey bee foraging*
248 *occurrence* around apiaries (Cane and Tepedino, 2017) and (ii) the average *wild bee body*
249 *mass*. The former competition metric could be easily recomputed following the procedure

250 analogous to wild bee foraging occurrence. The latter competition metric, however,
251 consisted in converting the wild bee body length (mm) into dry body mass (mg), which is
252 arguably more informative when one is further concerned by consequences on the overall
253 wild bee community biomass (Torné-Noguera *et al.* 2016). Indeed, the wild bee body length
254 was on average 12% greater in bee surveys away from the AIR, as compared to samples
255 within the AIR. This effect size might however be viewed differently from a body mass
256 perspective, given that body mass increases exponentially with body length (Kendall et al.,
257 2019). To do so, we applied the allometric scaling law predicting dry body mass (mg) from
258 body length (mm) in Apidae (Kendall et al., 2019; Sabo et al., 2002), that we assumed to be a
259 model family liable to roughly depict scaling properties of wild bees as a whole:

260 $$\text{Dry body mass} = 0.006 \times \text{Body Length}^{3.407}$$

261 Doing so, the resulting AIR (distance threshold that best discriminates between wild bee
262 samples closer to vs. farther away from apiaries) will remain virtually unchanged. The
263 corresponding effect size of competition, however, is expected to increase due to the power
264 law.

265

266 **3. Results and discussion**

267 3.1. *Applying the wild bee protection goal formula to the Rosemary honey flow case-study*

268 In the context of the simple (implicit) distance-based regulation, Fig. 3 reports expected
269 apiary influence land covers (%) as a function of distances among neighbouring apiaries for
270 the Rosemary honey flow case-study (Henry and Rodet, 2018). It reveals that a balanced
271 protection goal, i.e. about 50% land sharing between productive beekeeping vs. wild bee
272 conservation at low competition levels, is achievable with about 2.5 km spacings among
273 apiaries. It further shows that highly conservative regulation schemes with a 80% wild bee

protection goal against 20% for beekeeping would require about 5-km apiary spacings, which admittedly exceeds the size of many small natural reserves or protected areas in Europe. Furthermore, the choice of one or another competition metric, leading to different AIRs, is critical. It substantially influences the distance recommendations for achieving a given protection goal. For instance, focusing on wild bee nectar foraging success (AIR = 0.6 km) or on honey bee foraging success (AIR = 1.1 km) returns 1.6-km and 3-km apiary spacings respectively.

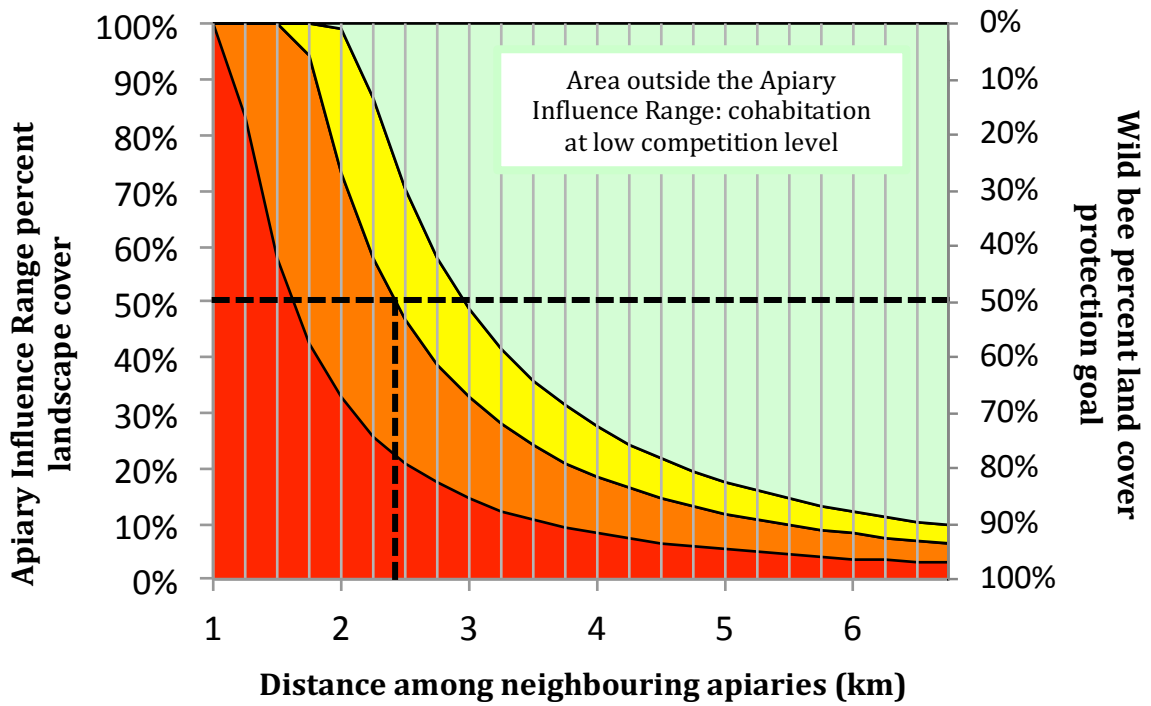

Fig. 3. Graphical Representation of the wild bee protection goal formula (Eq. 3) applied to the Rosemary case-study (Henry and Rodet, 2018). Curves show how distance among apiaries modulates the percent land cover under apiary competitive influence vs. land cover compatible with wild bee conservation at low competition level. Curves were computed with the AIRs of the three competition metrics shown in Fig. 1, with the same colour legends (AIRs = 0.6, 0.9 and 1.1 km for lower, medium

and upper curves, respectively). Dashed lines reveal that a balanced 50% land sharing between productive beekeeping vs. wild bee conservation is achievable with a ca. 2.5 km spacing among apiaries, considering the wild bee foraging occurrence as a competition metric (AIR = 0.9 km). Note the curves were corrected at low wild bee protection goals (<10% land cover) due to overlapping AIRs among neighbouring apiaries (see methods, section 2.6).

3.2. *Choice of the competition metric*

It appears critical to identify an appropriate competition metric in this context. Table 2 presents AIRs derived from several competition metrics in Henry and Rodet (2018). The honey bee foraging success shows the largest AIRs (nectar AIR = 1.1 km, pollen AIR > 1.2 km), and therefore would return the most conservative recommendations with large spacings among apiaries. On the one hand, those honey bee competition metrics may be relevant for beekeepers themselves because they reveal an intra-specific competition liable to affect honey yields. On the other hand, as discussed in Henry and Rodet (2018), the honey bee foraging success as measured here conveys information on both competition and a possible behavioural trade-off between distance and harvest. Indeed, foraging honey bees may collect more nectar and pollen when foraging farther away from their colony in order to balance the energetic and temporal costs of covering larger flight distances. This may also lead to increased foraging loads at larger distances from apiaries, independently from any intra-specific competition effect.

In an attempt to untangle the respective effects of competition and a possible behavioural trade-off with distance from apiaries in honey bees, we further compared nectar and pollen availabilities in rosemary flowers within *vs.* beyond the AIRs established for honey bee

313 foraging success. To do so, we used Linear Mixed Effect models (LME) as described in
314 Henry and Rodet (2018). In the original study, nectar and pollen availability data were both
315 significantly and negatively associated with honey bee foraging occurrence (also termed
316 foraging intensity), but not formally tested against distance to nearest apiaries. We first
317 found that nectar availability in rosemary flowers was indeed significantly lower within the
318 AIR corresponding to lower honey bee nectar foraging success, supporting the intra-
319 specific competition hypothesis (LME, n = 100 nectar measurements out of 26 sites, t =
320 2.87, P = 0.009, Fig. 4). Interestingly, the effect size of apiary proximity on honey bee nectar
321 foraging success and on nectar availability in flowers were similar (-44% and -41%,
322 respectively), supporting a possible link mediated by intra-specific competition. On the
323 other hand, we found no evidence that pollen availability in rosemary flowers varied with
324 distance from nearest apiaries (LME, n = 63 pollen measurements out of 26 sites, t = -0.43,
325 P = 0.67). Although pollen availability significantly decreased with higher honey bee
326 foraging occurrence (Henry and Rodet, 2018) further studies should investigate the
327 possible use of pollen availability and pollen foraging success as an effective competition
328 metric liable to reveal AIRs.

329

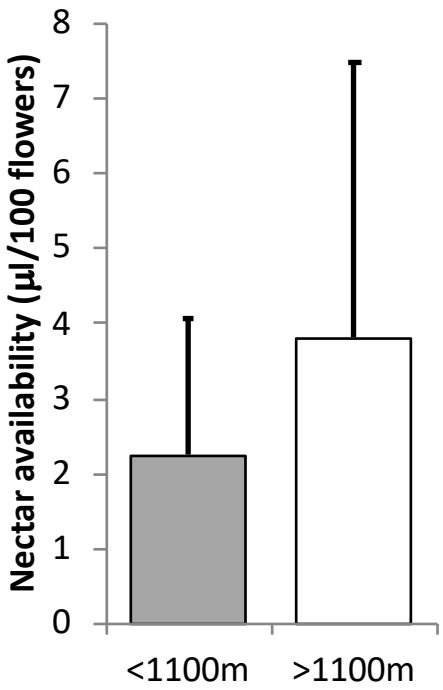

Fig. 4. Representation of the significant decrease in the rosemary nectar availability within the AIR defined by a lower honey bee nectar foraging success (<1.1 km from the nearest apiary), compared to areas beyond the AIR (>1.1 km). Mean nectar availability are 2.24 ± 1.81 (sd) and 3.81 ± 3.65 µl/100 flowers, respectively, leading to a 41% average decrease with apiary proximity.

The honey bee foraging occurrence might also be a relevant candidate metric to consider. When recomputed from raw data (Henry and Rodet, 2018), it returns an AIR of 0.8 km (Table 2), within which honey bee foragers are 58% more abundant than farther away (foraging occurrence index = 103.1 ± 92.2 (sd) vs. 65.0 ± 53.8, respectively). It seems that a 58% decrease in honey bee foraging occurrence might be sufficient to partly relax local competition, because wild bee occurrence presents a similar AIR (0.9 km, Table 2), with occurrence values varying in the opposite direction (Fig. 1). Still, further studies are needed to relate actual honey bee foraging occurrence with local wild bee foraging success. Some

345 managers may want to target the complete removal of honey bee foragers in wild bee
346 conservation areas. In a previous study, it was estimated that honey bee foraging occurrence
347 becomes marginal at ca. 7 km away from an apiary (Cane and Tepedino, 2017). Such a long-
348 distance AIR would translate into nearly 19-km spacings among apiaries for a 50%
349 protection goal (Eq. 4). This is definitely too far reaching for an operational conciliation of
350 beekeeping and wild bee conservation, and even hardly doable in most protected areas.
351

352 Finally, we found that converting wild bee body length into dry body mass (Table 2) could
353 greatly affect our perception of the competition effect on bee size. The mean individual
354 wild bee body length found in the surveys undertaken at different distances from apiaries
355 revealed a 12% decrease within a 0.65 km AIR (Henry and Rodet, 2018). Body size was
356 interpreted as a potential competition metric because the larger bee species are also more
357 mobile than smaller ones and can easily disperse away from apiaries to forage and nest in
358 low-competition areas. At first glance, a 12% difference, though significant, might appear
359 as a marginal effect. However, when converting body length into dry mass with an
360 appropriate allometric power law (Table 2), the 12% competition effect size translates into
361 a 33% decrease in mean individual wild bee dry body mass close to apiaries (mean
362 individual dry body mass = 24.77 vs. 36.95 mg, respectively). If one further combines this
363 33% mean wild bee body mass decrease with the 55% mean wild bee abundance decrease,
364 that would theoretically return an overall 69.8% decrease in wild bee dry biomass around
365 apiaries. This tentative biomass loss estimate appears excessively drastic. It should be re-
366 evaluated using thorough field biomass measurements, rather than extrapolated from
367 admittedly weak allometric models (herein based on n=10 data points only in Sabo et al.,
368 2002). Still, it reflects what has been found in previous studies, with significantly lower

369 wild bee biomass values close to apiaries as a result of reduced abundances of large (>70

370 mg fresh body mass) wild bees (Torné-Noguera *et al.*, 2016).

371

372

373 **Table 2 : Synthesis of the Apiary Influence Ranges (AIR) reported in Henry and Rodet**
374 **(2018), with significantly altered competition metrics. The competition effect size**
375 **refers to the relative difference between competition metrics closer to vs. farther**
376 **away from apiaries. The temporal lag indicates whether the effect was detected**
377 **during the season in progress or whether it was detected on the next-year generation**
378 **(particularly for competition metrics linked with reproductive success, and therefore**
379 **liable to become apparent at the next generation).**

380

Competition metrics	AIR (km)	Effect size	Temporal lag
Wild bee competition metrics			
Mean wild bee nectar foraging success	0.600 km	-50%[a]	Current season
Mean wild bee body length	0.650 km	-12%[a]	Current and Next season
Mean wild bee dry body mass	0.650 km	-33%[b]	Current and Next season
Wild bee foraging occurrence	0.900 km	-55%[a]	Next season
Honey bee competition metrics			
Honey bee foraging occurrence	0.800 km	+58%[c]	Current season
Mean honey bee nectar foraging success	1.100 km	-44%[a]	Current season
Mean honey bee pollen foraging success	>1.200 km[d]	-36%[a]	Current season

381 [a] Recovered from Supplementary Information in Henry and Rodet (2018)

382 [b] Estimated from raw data (Henry and Rodet, 2018) by converting body length (mm) into dry body
383 mass (mg) following the allometric scaling laws reviewed for pollinators (Kendall *et al.*, 2019), see
384 text.

385 [c] Recalculated from raw data in Henry and Rodet (2018), see text.

386 [d] No distance threshold detected. If existing, the AIR may extend beyond 1.2 km.

387

388 3.3. *Some perspectives and future directions*

389 As a first critical challenge, more studies should be undertaken on that topic to make better-
390 informed management decisions (Wojcik *et al.*, 2018), and in particular with the help of
391 rapid assessment methods (Cane and Tepedino, 2017) to appraise competition risks specific
392 to each locality of interest. It is necessary to test the AIR approach in a broad range of
393 environmental contexts, with varying floral resource availabilities and spatial distributions,
394 beekeeping managements, honey bee phenotypes, and peripheral agricultural practices.
395 Some issues are listed below.

396 *What happens with heterogenous resources?* The present AIR concept applies for apiary
397 migrations targeting mass flowering resources rather homogeneous in space. In most
398 natural contexts, however, floral resources tracked by beekeepers might be highly
399 heterogeneous in space, which is liable to modify the effective AIRs. The foraging habitat
400 fragmentation should therefore be implemented as a covariate into competition
401 assessments. Resources may also be heterogeneous in time, with food scarcity periods,
402 leading to different use of space by honey bee foragers (Couvillon *et al.*, 2014). In the absence
403 of mass-flowering resources, AIRs are likely to change drastically. They are even likely to
404 become less detectable or stable in space, therefore making the distance-based regulation
405 inoperative in practice. Conversely, the local floral diversity might become the main driver
406 of potential competition patterns. This remains to be investigated in greater detail.

407 *How shall we take apiary size into account?* The entire reasoning here is based on an average
408 empiric apiary size of 30.1 ± 21.8 (sd) colonies and lays on the assumption that AIRs are
409 independent from apiary size. In practice, some competition metrics are actually influenced
410 by colony density (Henry et Rodet, 2018), and may therefore respond to both the distance
411 and size of the nearest apiary. AIRs will most probably increase as apiaries will get much
412 larger. This should be explicitly tested with a broader range of realistic professional apiary

413 sizes (e.g. >150 colonies). Conversely, below a threshold that need be determined, small non-
414 professional apiaries may have virtually no influence and could be ignored in the process.

415 *Can periodic beekeeping break years help wild bee populations recovering?* Given the inter-
416 annual response delay in some of the observed competition metrics (Table 2), it has been
417 suggested that land managers could envision periodic break years to temporarily halt
418 competition disturbance regime and boost resilience in local wild bee populations (Henry
419 and Rodet, 2018). This is equivalent to a temporal regulation of beekeeping, and could
420 certainly be explored as a possible complementary wild bee protection measure. Long-term
421 studies would however be required to evaluate the actual effectiveness of such a practice.

422 *Do local honey bee phenotypes generate less competition?* Conventional beekeeping uses
423 selected phenotypes among others for their honey yield. Locally adapted subspecies or
424 phenotypes might be less productive and less prone to generating competition. That might
425 be studied as a part of an inclusive conservation strategy with the joint management of
426 conventional vs. conservation beekeeping (Requier *et al.*, 2019).

427 *Can bee-friendly practices help relax competition for floral resources?* Requier *et al.* (2019)
428 cleverly suggested to hold conservation beekeeping in (honey-) bee-friendly practice areas
429 around core protected areas to help organise apiary allocation between conservation and
430 conventional beekeeping. Likewise, promoting bee friendly practices in agrosystems around
431 or embedded in natural protected areas can contribute to segregate honey bee and wild bee
432 foragers (Rollin *et al.*, 2013) and reduce potential competition.

433 *What about non-bee flower-visiting insects?* Most of the studies on the interactions between
434 honey bees and other flower-visiting insects have focused on wild bees. There are however
435 a many other insect groups involved in plant-pollinator interactions including wasps,
436 syrphids, flies, beetles or butterflies (Rader et al., 2016). A broader taxonomic view of the
437 question would be welcome here.

Is the distance-based regulation economically sustainable for beekeepers? It appears critical that land managers involve beekeepers, as well as local farmers, whenever they intend to establish beekeeping regulation rules in their area. Some protection measures may become prohibitively constraining for professional beekeepers and generate counterproductive results. Human and social sciences have a central role to play here.

4. Conclusion

We developed in this study a distance-based beekeeping regulation paradigm to help land managers reconcile the conflicting needs of wild bee conservation and honey bee management in a context of intensifying agriculture. By combining empiric observations (Henry and Rodet, 2018) and theoretic calculations, we found that there is place for inclusive solutions liable to support both wild bee conservation and honey production (Kleijn *et al.*, 2018). As an handy conservation measure, the Apiary Influence Range principle is now envisioned by the French Coastal Protection agency, with a balanced (50%) land protection goal in the larger protected areas (>500 ha) and an exclusive conservation strategy in the smaller areas with no beekeeping history to date (Cavallin et al., 2019).

We however think that much work remains to be done to support the Apiary Influence Range and distance-based regulation paradigm, including replicated competition and distance threshold assessments in a broader range of situations, and testing the distance recommendation effectiveness in real world conditions. We provided here a roadmap to do so, as well as warnings against possible pitfalls on the way.

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Author contribution

All authors contributed to the conception of the study design, data collection and analysis, manuscript writing and revisions. MH developed the statistical rationale and released the first manuscript draft.

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