# 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*.

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

*2.1. Competition metrics*

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

2.2. *The Apiary Influence Range* (AIR)

The AIR is the distance range around apiaries within which competition metrics are significantly altered (Fig. 1). It may be readily delineated by threshold statistical models with a moving function of distance. Simple threshold statistical models, such as generalized fluctuation tests or breakpoint regressions (Zeileis et al., 2002), can easily locate the most parsimonious thresholds for structural changes in univariate data patterns. Previous studies (Henry and Rodet, 2018) have used generalized linear models and the Akaikee Information Criterion framework to assess the probability that competition metrics are 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). Results were in support of a two-step distance threshold for most candidate competition metrics, which is the basic assumption for the distance-based regulation of apiary influence we propose here. AIRs shown in Fig. 1 range from 0.6 to 1.1 km, which is effectively comprised within the honey bee median foraging range of 1–2 km usually reported in literature (Couvillon *et al.*, 2014; Steffan-Dewenter and Kuhn, 2003; Visscher and Seeley, 1982).

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

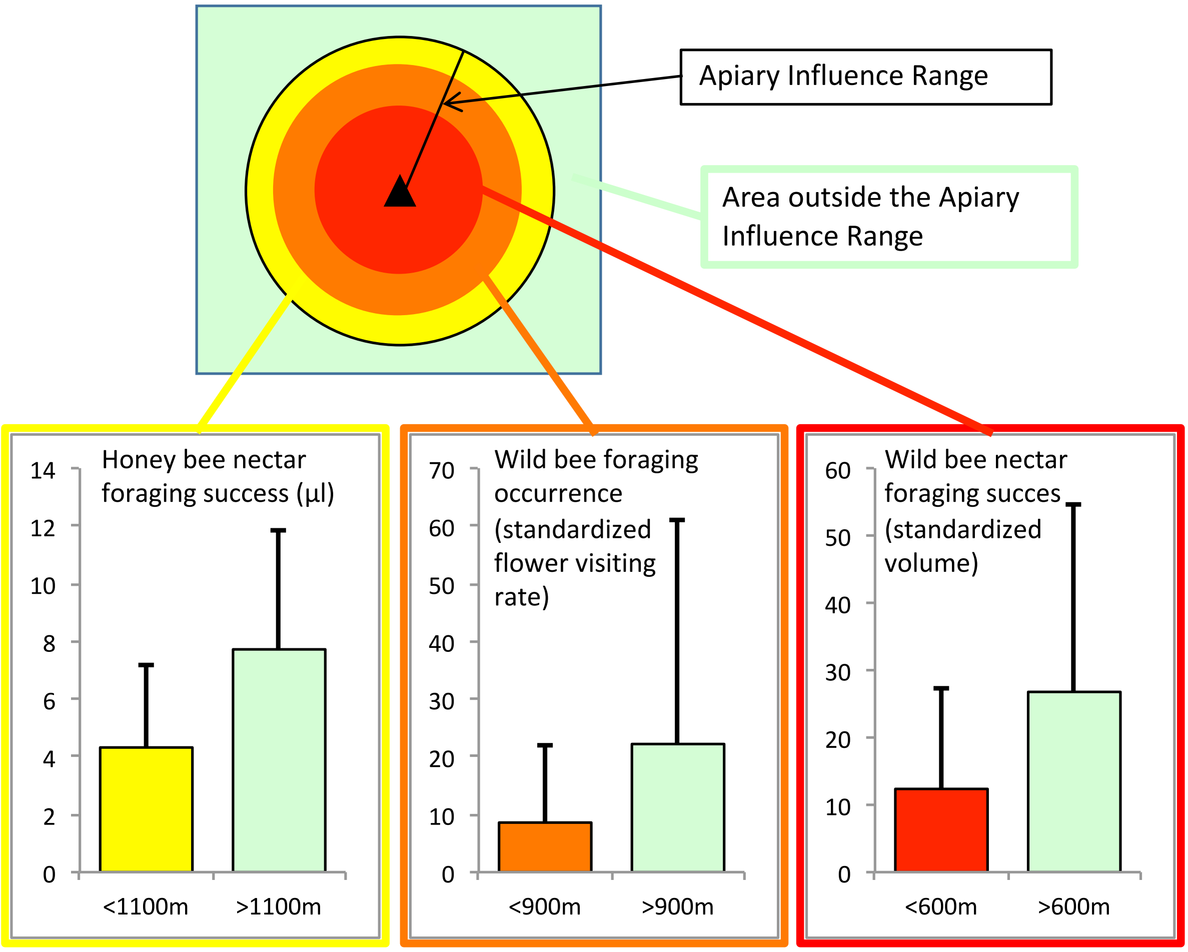


**Fig. 1. Illustration of the Apiary Influence Range (AIR) applied to three competition metrics selected from Henry and Rodet (2018). Depending on the metric, AIRs expend from 0.6 to 1.1 km around apiaries (circles around the triangle), with significant differences between values from sampling sites 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.**

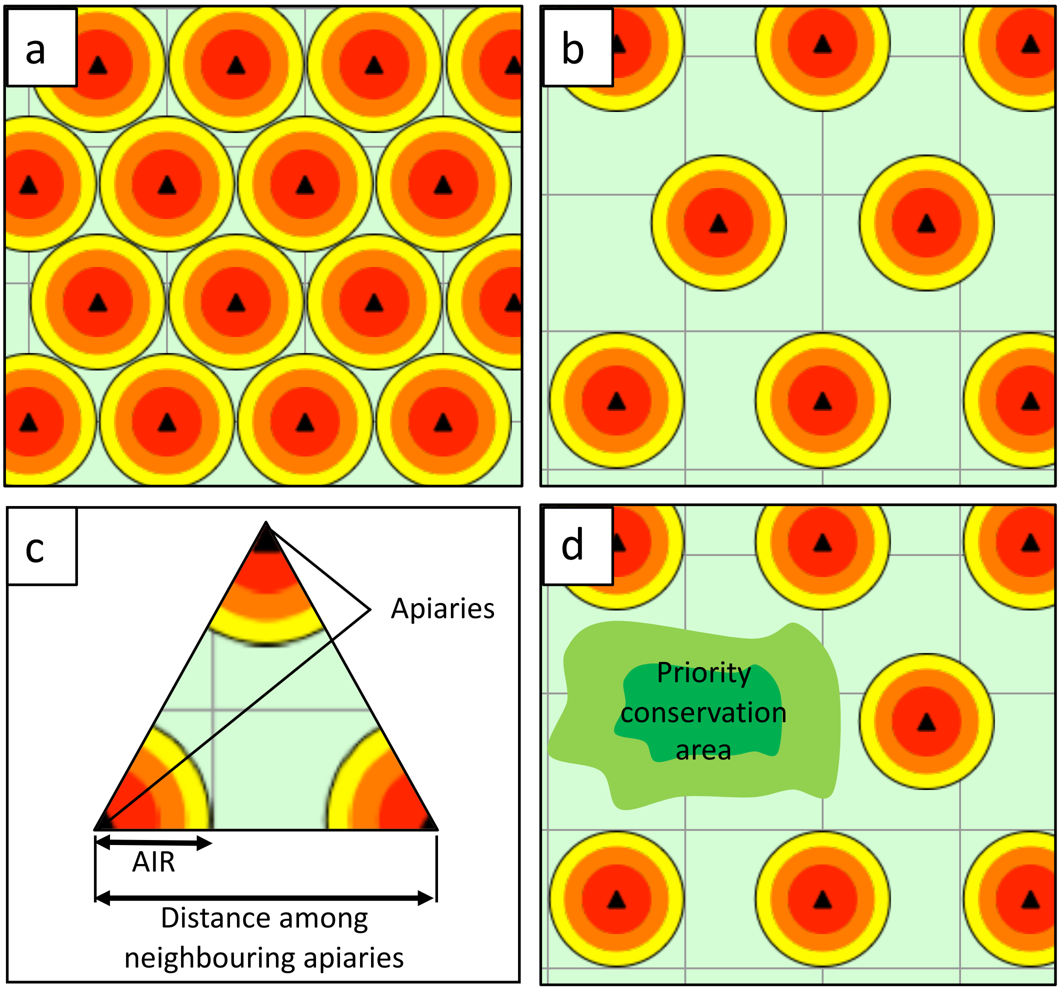


**Fig. 2. Idealised representation of the distance-based beekeeping regulation in a natural protected area. (a) with no wild bee protection goal, apiaries may bee tightly clumped, with coalescent AIRs leaving few spaces with relaxed competition (here about 10% land cover). (b) increasing distances among 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.**

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

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

## 2.4. *Land cover calculations*

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

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

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

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

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

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

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

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

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

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

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

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

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

## 2.6. *Computation of additional AIR values*

Figure 1 presents AIRs for three main competition metrics. For a more in-depth assessment of possible values, additional AIRs were recomputed from raw data (Henry and Rodet, 2018). We were especially interest in (i) the distance range of increased *honey bee foraging occurrence* around apiaries (Cane and Tepedino, 2017) and (ii) the average *wild bee body mass*. The former competition metric could be easily recomputed following the procedure analogous to wild bee foraging occurrence. The latter competition metric, however, consisted in converting the wild bee body length (mm) into dry body mass (mg), which is arguably more informative when one is further concerned by consequences on the overall wild bee community biomass (Torné-Noguera *et al.* 2016). Indeed, the wild bee body length was on average 12% greater in bee surveys away from the AIR, as compared to samples within the AIR. This effect size might however be viewed differently from a body mass perspective, given that body mass increases exponentially with body length (Kendall et al., 2019). To do so, we applied the allometric scaling law predicting dry body mass (mg) from body length (mm) in Apidae (Kendall et al., 2019; Sabo et al., 2002), that we assumed to be a model family liable to roughly depict scaling properties of wild bees as a whole:

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

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

## 3. Results and discussion

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

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

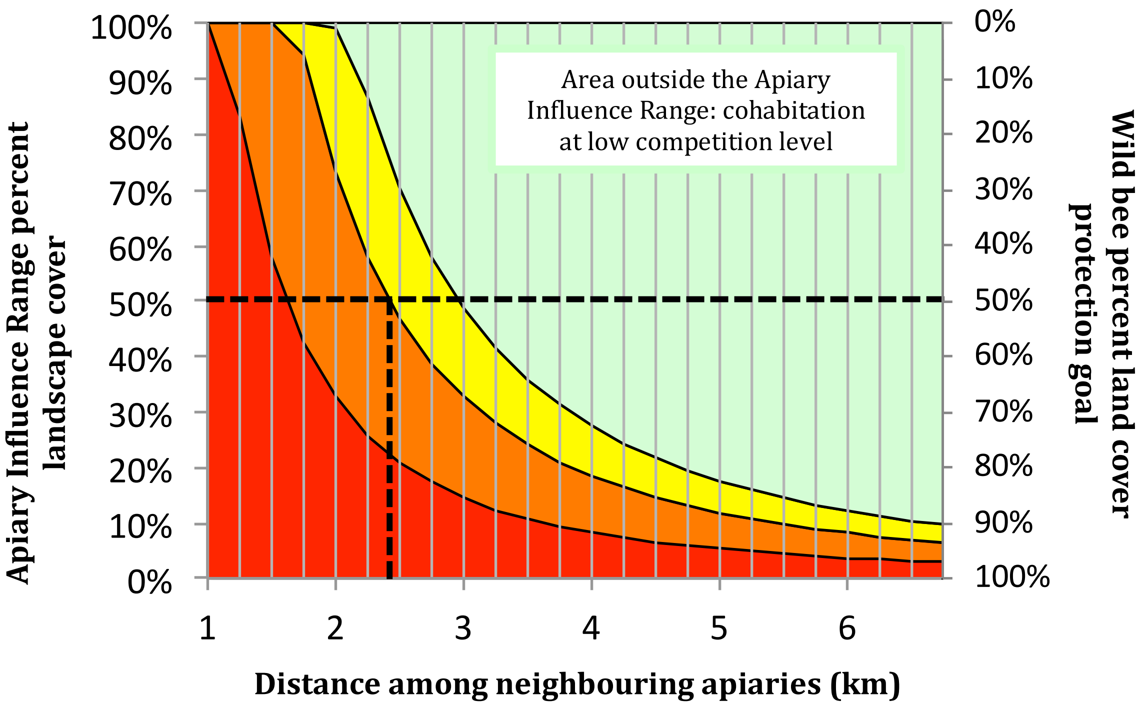


**Fig. 3. Graphical Representation of the wild bee protection goal formula (Eq. 3) applied to the Rosemary case-study (Henry and Rodet, 2018). Curves show how distance among apiaries modulates the percent land cover under apiary competitive influence vs. land cover compatible with wild bee conservation 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 foraging success. To do so, we used Linear Mixed Effect models (LME) as described in Henry and Rodet (2018). In the original study, nectar and pollen availability data were both significantly and negatively associated with honey bee foraging occurrence (also termed foraging intensity), but not formally tested against distance to nearest apiaries. We first found that nectar availability in rosemary flowers was indeed significantly lower within the AIR corresponding to lower honey bee nectar foraging success, supporting the intra-specific competition hypothesis (LME, n = 100 nectar measurements out of 26 sites, $t$ = 2.87, $P$ = 0.009, Fig. 4). Interestingly, the effect size of apiary proximity on honey bee nectar foraging success and on nectar availability in flowers were similar (-44% and -41%, respectively), supporting a possible link mediated by intra-specific competition. On the other hand, we found no evidence that pollen availability in rosemary flowers varied with distance from nearest apiaries (LME, n = 63 pollen measurements out of 26 sites, $t$ = -0.43, $P$ = 0.67). Although pollen availability significantly decreased with higher honey bee foraging occurrence (Henry and Rodet, 2018) further studies should investigate the possible use of pollen availability and pollen foraging success as an effective competition metric liable to reveal AIRs.

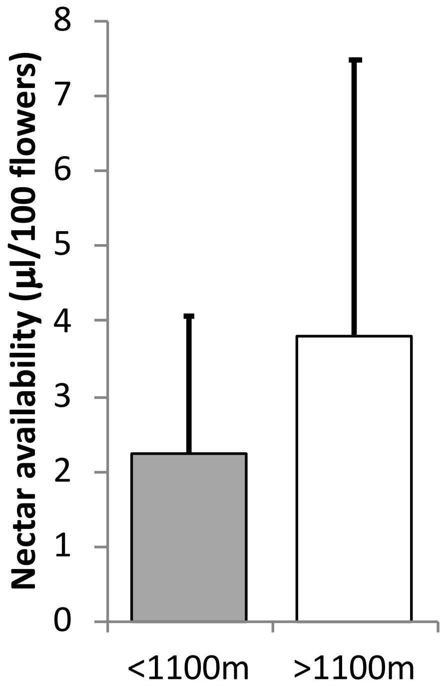


**Fig. 4. Representation of the significant decrease in the rosemary nectar availability within the AIR defined by a lower honey bee nectar foraging success (<1.1 km from the nearest apiary), compared to areas beyond the AIR (>1.1 km). Mean nectar availability are 2.24 ± 1.81 (sd) and 3.81 ± 3.65 µl/100 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 managers may want to target the complete removal of honey bee foragers in wild bee conservation areas. In a previous study, it was estimated that honey bee foraging occurrence becomes marginal at ca. 7 km away from an apiary (Cane and Tepedino, 2017). Such a long-distance AIR would translate into nearly 19-km spacings among apiaries for a 50% protection goal (Eq. 4). This is definitely too far reaching for an operational conciliation of beekeeping and wild bee conservation, and even hardly doable in most protected areas.

Finally, we found that converting wild bee body length into dry body mass (Table 2) could greatly affect our perception of the competition effect on bee size. The mean individual wild bee body length found in the surveys undertaken at different distances from apiaries revealed a 12% decrease within a 0.65 km AIR (Henry and Rodet, 2018). Body size was interpreted as a potential competition metric because the larger bee species are also more mobile than smaller ones and can easily disperse away from apiaries to forage and nest in low-competition areas. At first glance, a 12% difference, though significant, might appear as a marginal effect. However, when converting body length into dry mass with an appropriate allometric power law (Table 2), the 12% competition effect size translates into a 33% decrease in mean individual wild bee dry body mass close to apiaries (mean individual dry body mass = 24.77 vs. 36.95 mg, respectively). If one further combines this 33% mean wild bee body mass decrease with the 55% mean wild bee abundance decrease, that would theoretically return an overall 69.8% decrease in wild bee dry biomass around apiaries. This tentative biomass loss estimate appears excessively drastic. It should be re-evaluated using thorough field biomass measurements, rather than extrapolated from admittedly weak allometric models (herein based on n=10 data points only in Sabo et al., 2002). Still, it reflects what has been found in previous studies, with significantly lower wild bee biomass values close to apiaries as a result of reduced abundances of large (>70 mg fresh body mass) wild bees (Torné-Noguera *et al.*, 2016).

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

| 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 |

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

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

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

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

3.3. *Some perspectives and future directions*

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

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

*How shall we take apiary size into account?* The entire reasoning here is based on an average empiric apiary size of 30.1 ± 21.8 (sd) colonies and lays on the assumption that AIRs are independent from apiary size. In practice, some competition metrics are actually influenced by colony density (Henry et Rodet, 2018), and may therefore respond to both the distance and size of the nearest apiary. AIRs will most probably increase as apiaries will get much larger. This should be explicitly tested with a broader range of realistic professional apiary sizes (e.g. >150 colonies). Conversely, below a threshold that need be determined, small non-professional apiaries may have virtually no influence and could be ignored in the process.

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

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

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

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