Wild Bees in Switzerland: Biology, Significance, Threats and Conservation

Abstract

Wild bees form a group of exceptional diversity, with 632 species recorded in Switzerland, of which 575 are considered currently present (Praz et al., 2023). Unlike the honey bee (Apis mellifera), the vast majority of these species are solitary, with an annual cycle, and depend for their reproduction on a precise combination of floral resources and specific nesting microhabitats — soil substrates, cavities, stems or woody structures — that are often spatially separated. Approximately 37% of species nesting in Central Europe are oligolectic, specialised on a narrow pollen spectrum, a constraint resting on behavioural, morphological and physiological mechanisms. This specialisation is directly associated with extinction risk: oligolectic species appear significantly more often on the Red List than generalists. Functionally, wild bees contribute to the pollination of wild and cultivated plants in a manner complementary to the honey bee, which they cannot replace; their diversity increases the inter-annual stability of pollination services. The Swiss Red List (Müller & Praz, 2024) indicates that 45.4% of evaluated species are threatened and that 59 are considered extinct on national territory. The main causes of decline are the loss and fragmentation of semi-natural habitats, the reduction of relevant floral resources, the disappearance of nesting substrates and, in certain contexts with high hive densities, exploitative competition with the honey bee. The conservation of wild bees requires a landscape approach integrating botanical diversity, structural heterogeneity of habitats and spatial proximity between resources, and cannot be reduced to promoting

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1. Introduction: Why Wild Bees Matter

In public debate, the word "bee" still very often refers to the honey bee. This focus is understandable, since Apis mellifera is visible, associated with beekeeping, honey and crop pollination. It nonetheless masks a much broader biological reality. Worldwide, bees form a highly diverse group, with approximately 20,000 described species and recent estimates suggesting that the actual richness may be even higher. Within this context, Switzerland harbours a remarkable diversity for a country of this size, with 632 recorded species, of which 575 are considered currently present (Rasmussen et al., 2020; Dorey et al., 2026; Praz et al., 2023).

This diversity is frequently underestimated, largely because many wild bees are inconspicuous, solitary, seasonal and sometimes highly localised. They do not live in permanent, easily visible colonies and do not produce honey for human use. Yet their unobtrusiveness says nothing about their ecological importance. International syntheses show that animal pollinators are involved in the reproduction of a very large proportion of flowering plants, and that bees constitute one of the most important groups within this ensemble (Klein et al., 2007; Ollerton et al., 2011; Potts et al., 2010).

One of the main reasons to pay attention to wild bees lies in their role in pollination. They contribute both to the maintenance of the spontaneous flora and to the pollination of certain crops. This dual function must nonetheless be stated carefully. The work of Garibaldi et al. (2013) showed that wild pollinators increase fruit set independently of honey bee abundance, indicating that their contribution is not simply redundant. Their relative importance, however, varies with crop type, landscape, agricultural practices and local conditions. It would therefore be excessive to pit wild bees against the honey bee in general terms.

The importance of wild bees also lies in their functional diversity. Species differ in body size, flight period, foraging behaviour, tolerance to weather conditions and degree of floral specialisation. Some are active very early in spring, others later in the season; some exploit complex flowers efficiently or forage under conditions where the honey bee is less active. This diversity reinforces the complementarity of pollinating communities and contributes to the stability of the pollination service over time (Garibaldi et al., 2013; Rogers et al., 2014; Senapathi et al., 2021).

In the Swiss context, this question is of particular importance. Recent work shows that Switzerland harbours an exceptionally rich bee fauna, with especially pronounced diversity hotspots in the dry inner-Alpine valleys, notably in Valais and Graubünden (Praz et al., 2023). This richness places a particular responsibility on the country with regard to knowledge, conservation and management. This responsibility is all the more significant given that the conservation status of the group is concerning. The new Swiss Red List indicates that 279 of the 615 evaluated species, i.e. 45.4%, appear on the Red List, and that 59 species are considered extinct in Switzerland (Müller & Praz, 2024). Even if historical comparisons must remain cautious because of changes in knowledge and taxonomy, this result clearly signals a high vulnerability of the group.

It is finally important to distinguish clearly between wild bees and the honey bee. The dynamics of the two groups are neither identical nor necessarily correlated. An increase in the number of hives does not automatically imply an improvement in the situation of wild bees, just as the presence of honey bees does not guarantee the persistence of the most demanding species. This distinction is essential to avoid confusion both in public debate and in management measures.

In sum, wild bees are important because they participate in ecosystem functioning, contribute to the pollination of many wild and cultivated plants, enrich the functional diversity of pollinating communities and constitute a sensitive indicator of the ecological quality of landscapes. In Switzerland, this group is characterised both by high richness and marked vulnerability. This dual reality justifies treating it as a front-rank scientific, ecological and management issue.

2. What Are Wild Bees?

In this article, the expression "wild bees" is used in its common practical sense in Switzerland and more broadly in Central Europe: it denotes all bees other than the honey bee managed by beekeeping, and therefore includes bumblebees. This way of naming the group is useful for biology, ecology and conservation, but does not correspond to a formal taxonomic rank. It is a functional and descriptive category, not a natural boundary within the classification of bees. This is an important point, because part of the confusion arises precisely from the fact that the opposition between "wild bees" and "honey bee" is often understood, incorrectly, as if it had strict systematic value. In reality, Apis mellifera is indeed a bee like all others, but occupies, in the human and beekeeping context, a particular status that justifies separate treatment in an article devoted to wild bees.

From a biological standpoint, bees belong to the group Anthophila within the Apoidea. Recent phylogenetic and evolutionary work strongly supports the idea that bees are descended from ancestors related to predatory apoidan wasps, and that one of the major innovations in their evolutionary history was the shift to larval nutrition based on pollen rather than animal prey. Pollinivory, in the sense of using pollen to nourish offspring, thus constitutes a central and defining trait of bees. It is this point, more than any unique external appearance, that allows us to understand what unites the group as a whole.

The pedagogical formula that bees are "vegetarian wasps" can help situate this evolutionary transition, but remains simplistic. It is useful for conveying that there is an ancient kinship between bees and certain wasps, and a major shift in the diet used for larval rearing. However, it should not cause us to forget that bees today form a very ancient, very diverse group deeply specialised in exploiting floral resources. The difference from many aculeate wasps therefore lies not simply in a change of diet, but in an entire ecological, behavioural and morphological reorganisation linked to the collection, transport and use of pollen.

This floral orientation is expressed in several shared characteristics. In many species, pollen is transported using specialised structures located on the hind legs or on the ventral surface of the abdomen. These transport devices are not all identical, but they illustrate the same biological logic: bees do not merely visit flowers to feed, they actively collect and transport pollen for reproduction. This is why the truly defining criterion is not the occasional pollen consumption by the adult, but its deliberate transfer to the nest for larval nutrition. This point also helps better distinguish bees from other flower-visiting insects that visit flowers without organising comparable larval provisions.

However, one should not imagine that there is a single "typical bee" of which all others are merely secondary variants. Bees form a highly heterogeneous ensemble in terms of size, morphology, hairiness, behavior, floral regime and social organisation. Some species are tiny and pass almost unnoticed; others are much larger and immediately visible. Some live alone, others show more or less elaborate forms of cooperation, and some lineages, such as bumblebees or bees of the genus Apis, attain high levels of sociality. The diversity of bees therefore concerns not only species number, but also the variety of ecological and evolutionary solutions they represent.

Within the specific framework of wild bees as understood here, most species are solitary. This means that a mated female builds her own nest, collects her own provisions, lays her own eggs and does not benefit from the assistance of workers in rearing the brood. Bumblebees constitute an important intermediate case for understanding the group: they are eusocial, but their colonies are annual, which clearly distinguishes them from the honey bee, whose colonies are perennial and can persist over several years. This distinction is essential, because it already shows that the honey bee cannot serve as a general model for describing "bees" as a whole. Even within a group commonly called "wild bees", lifestyles remain highly diverse.

The honey bee, Apis mellifera, therefore appears as a special case in several respects. It is strongly eusocial, forms perennial colonies, stores substantial food reserves and is subject to continuous human management. In contrast, most wild bees have neither comparable permanent colonies, nor honey reserves in the beekeeping sense, nor densities determined by human husbandry. It is precisely for this reason that confusion between the honey bee and wild bees is so problematic: it readily leads to projecting onto the whole group a lifestyle that in reality concerns only a small proportion of bees. Understanding this discrepancy is a prerequisite for correctly interpreting the biology, diversity and conservation of wild bees.

Finally, it should be emphasised that the term "wild bees" also has a practical utility for conservation. It allows very diverse taxa to be grouped in a single perspective, sharing several important characteristics from a management standpoint: absence of beekeeping management, strong dependence on specific habitats and microhabitats, often annual cycles and marked sensitivity to the fine ecological quality of landscapes. This utility does not erase the conventional character of the category, but it explains why it remains widely used in Central European literature and in Swiss synthesis works. The correct formulation is therefore to say that wild bees form a biologically coherent category for ecology and conservation, without making them an autonomous taxonomic entity separated from the honey bee by an absolute natural boundary.

3. Diversity of Wild Bees

The diversity of wild bees constitutes one of the indispensable starting points for any serious examination of their ecology and conservation. It cannot be summed up in the general notion that there are "many species". It refers to a taxonomic, morphological, behavioural, phenological and biogeographic diversity of such scope that no simple generalisation can suffice to capture the group. This diversity is scientifically important for at least two reasons. On the one hand, it explains why wild bees fulfil varied and often complementary ecological functions. On the other hand, it shows why responses to landscape change, agricultural practices, urbanisation or conservation measures differ strongly from one species to another (Michener, 2007; Westrich, 2019).

Worldwide, bees form a group of approximately 20,000 described species, and some estimates suggest the actual number could be higher if one takes into account taxa still poorly known in certain world regions (Michener, 2007). At the European level, the figure of approximately 2,000 species is generally cited in recent synthesis works (Nieto et al., 2014). Within this context, Switzerland stands out for its remarkable richness. The most recent annotated checklist records 632 bee species in the country, including the honey bee Apis mellifera and the exotic species Megachile sculpturalis, and considers 575 species as currently present in Switzerland (Praz et al., 2023). This richness is particularly high when related to the country's area. It justifies Switzerland being considered an important zone for the study and conservation of bees at the Central European scale.

These figures must nonetheless be handled with precision. On the one hand, numbers vary depending on whether one is speaking of all historically recorded bees, species currently present, only wild bees in the practical sense excluding the honey bee, or taxa retained after certain taxonomic revisions. On the other hand, the national checklist is not a fixed object once and for all. It depends on the state of knowledge, examination of old collections, field rediscoveries, taxonomic progress and the detection of newly established species. The best way to approach this subject is therefore to present the numbers not as absolute and timeless truths, but as the documented state of knowledge based on available reference works, particularly those of Praz et al. (2023) and the national Red List (Müller & Praz, 2024).

Swiss diversity concerns not only the total species count. It is also expressed in the taxonomic composition of the group. The bees recorded in Switzerland are distributed across six families: Melittidae, Andrenidae, Halictidae, Colletidae, Megachilidae and Apidae (Amiet et al., 1996–2010; Praz et al., 2023). This distribution is not anecdotal. It reflects different evolutionary histories, morphologies, nesting strategies and flower relationships. Andrenidae and Halictidae include many ground-nesting species, often inconspicuous and difficult to identify. Megachilidae include several well-known genera, such as Osmia, Megachile or Chelostoma, many of which use cavities or particular building materials. Apidae, for their part, include not only bumblebees, but also various genera that differ greatly from an ecological standpoint. In other words, speaking of wild bees in the singular often amounts to concealing a deep diversity of biological lineages.

To this taxonomic diversity is added a spectacular morphological diversity. In Switzerland as elsewhere in Central Europe, wild bees range from very small species of a few millimetres to large bumblebees or much more conspicuous carpenter bees. Colours vary from matt black to bluish or greenish metallic shades; hairiness can be dense or almost absent; pollen collection structures differ greatly between groups; body shapes, antenna proportions and integument characters vary in ways that are often subtle but taxonomically important (Michener, 2007; Westrich, 2019). This diversity is not merely aesthetic or descriptive. It corresponds to very different ecological adaptations: flower size exploited, flight distance, nesting type, activity period, thermoregulatory capacity or trophic specialisation.

From a biogeographic perspective, Switzerland offers a particularly interesting situation. Its richness in bees is not explained solely by an intensive inventory effort, even though this plays a major role. It also stems from the juxtaposition, over a relatively limited territory, of strong altitudinal gradients, contrasting climatic situations and several biogeographic influences. Regions with more Mediterranean influence, dry inner valleys, alpine zones, alluvial habitats, intensively exploited lowland sectors and cooler forested massifs do not offer the same possibilities to all species. This territorial heterogeneity favours the coexistence of very different assemblages and contributes to the overall national richness (Praz et al., 2023).

The dry inner-Alpine valleys play a particular role here. Recent work shows that they constitute major diversity hotspots for bees in Switzerland, notably in Valais and in parts of Graubünden (Praz et al., 2023). This finding is important for several reasons. First, it underlines the exceptional interest of inner-Alpine xeric habitats for conservation. Second, it shows that species richness is not uniformly distributed across the territory. Finally, it invites us to avoid any overly homogeneous representation of the country. Switzerland is not a uniform ecological block; certain regions concentrate a particularly high diversity and faunistic singularity, with rare, thermophilic or steppe-affinity species that do not find favourable conditions everywhere.

Local examples from Valais illustrate this situation well. Studies conducted at Erschmatt have shown exceptionally high species richness levels over small areas, reaching values among the highest documented in Central Europe (Oertli et al., 2005). These results should not be mechanically extrapolated to the whole canton or the whole of Switzerland, but they show concretely how much certain structured, dry, warm and heterogeneous landscapes can concentrate a remarkable diversity.

A methodological point often underestimated also deserves emphasis: the actual diversity of wild bees is more difficult to observe and document than that of other more visible groups. Many species can only be identified under a microscope, sometimes from very fine characters, and some series of closely related species remain challenging even for experienced specialists (Amiet et al., 1996–2010; Westrich, 2019). This has several consequences. First, inventory data depend strongly on available taxonomic expertise. Second, citizen science programmes can cover only a limited fraction of total diversity, especially for readily recognisable species. Third, knowledge remains more complete for certain groups or regions than for others. One must therefore be careful not to confuse actually absent diversity with inadequately detected diversity.

This identification difficulty explains in part why Switzerland has a particularly valuable documentation thanks to the long-term work of specialists coordinated by the competent national institutions. The Fauna Helvetica volumes devoted to bees, as well as the databases linked to the Swiss Centre for Faunal Cartography and info fauna, constitute an exceptional knowledge infrastructure for a country of this size

(Amiet et al., 1996–2010; Praz et al., 2023). This investment in taxonomic knowledge is not an academic luxury. It directly conditions the possibility of detecting distributional changes, monitoring rare species, evaluating conservation status and defining conservation priorities.

Finally, it should be recalled that the diversity of bees cannot be reduced to species richness. Two sites may harbour a comparable number of species while differing greatly in their composition and conservation value. A site dominated by common, generalist and widely distributed species does not have the same ecological significance as a site harbouring several rare, specialised or narrowly distributed species. This distinction is central to avoiding a purely quantitative reading of diversity. In conservation, the quality of a community also depends on its originality, its functional composition and the presence of species with high heritage value or high ecological sensitivity (Müller & Praz, 2024).

4. Lifestyles and Life Cycles

Wild bees do not all follow the same lifestyle, and this is precisely one of the reasons why the well-known model of the honey bee should not be projected onto the entire group. In the public mind, the word "bee" spontaneously evokes a large perennial colony, a marked division of labour, a long-lived queen, numerous workers and honey reserves. Yet this scheme describes only one particular case: that of Apis mellifera. Among wild bees of Central Europe, and therefore in Switzerland, the vast majority of species are solitary. This means that a mated female builds her own nest, collects her own provisions, lays her own eggs and does not benefit from workers for brood rearing. This biological reality is fundamental, as it conditions both the rhythm of the annual cycle, the vulnerability of species and their relationship to the landscape (Michener, 2007; Westrich, 2019).

In solitary species, the general biological sequence is relatively simple in principle, even if it varies in detail between taxa. After emergence, adults mate. Males often die after a relatively brief flight period, while females enter an active reproductive phase during which they search for a nesting site, prepare a first cell, provision it with pollen and nectar, lay an egg, close the cell and then build another. Larval development then proceeds inside the nest, hidden from observation, until pupation and then overwintering in a form that depends on the species. The key point is therefore: in most wild bees, the visible adult phase on flowers is short, while the bulk of the life cycle takes place in the nest, often over many months (Michener, 2007; Westrich, 2019).

Under the temperate conditions of Switzerland, the annual cycle is the general rule. Many species are univoltine, meaning they produce only one generation per year. Adults emerge in spring or summer depending on the species, mate, females establish their nest, provision cells and then die before the emergence of their offspring. The latter spend most of the year in the nest, as larvae, prepupae, pupae or sometimes as newly formed adults ready to emerge, until the following season. The synthesis in the background document rightly emphasises this point: the typical cycle of Swiss wild bees is a simple annual cycle, strongly synchronised with the flowering season and with the availability of resources needed for reproduction. Work on the phenology of wild bees outside the tropics points in the same direction, recalling that an annual cycle with obligate diapause constitutes the most common biological framework in temperate zones (Bartomeus et al., 2011).

It is important, however, not to elevate this typical cycle to a universal law. Several exceptions exist. Some species may exhibit a prolonged diapause, so that not all individuals from the same cohort emerge in the same year. Others may show partial or occasional bivoltinism under favourable climatic conditions, particularly in warmer regions or during exceptionally mild autumns. This remains an active area of research, and caution in phrasing is warranted: one can mention the existence of cases of partial bivoltinism without generalising them to the whole Swiss fauna or claiming they represent a durably advantageous strategy for populations. The same caution applies to the effects of climate change on phenological plasticity: they are plausible and already observable in some datasets, but their demographic implications remain highly species- and context-dependent (Bartomeus et al., 2011).

The seasonality of wild bees is indeed very marked. Each species has a flight period characteristic of it, often relatively brief, sometimes only a few weeks. This activity window generally corresponds to the availability of the floral resources used by the species, especially when it is specialised on a restricted plant group. Phenology is therefore an integral part of the ecological identity of wild bees. It does not merely describe "when the species is seen", but also when it reproduces, forages, mates and invests in its offspring. Recent literature shows that this phenology varies with local climate, altitude, aspect and landscape characteristics, which explains why the same species can appear at quite different dates in different Swiss regions or in different years. Caution is therefore necessary when attempting to provide a general calendar of "wild bees": one must reason by species, or at minimum by ecologically comparable groups.

Reproduction itself presents several remarkable features. As in Hymenoptera generally, sex determination follows a haplodiploid system: females come from fertilised eggs, males from unfertilised ones. The female therefore has, to some degree, control over the sex of her offspring at the time of oviposition. This particularity illuminates several aspects of the reproductive cycle, notably the organisation of cells in the nest and the fact that males frequently emerge before females. Protandry, i.e. the earlier emergence of males, is well documented in many solitary bees and is interpreted as a strategy increasing mating opportunities at the time females appear (Heimpel & de Boer, 2008; Westrich, 2019). The literature establishes this point solidly, and also shows that males often have a shorter flight duration than females.

This difference between males and females concerns not only emergence, but also the ecological function of the adults. Males do not build nests and do not collect pollen for the brood. Their activity is mainly oriented towards finding mates and personal nutrition. Females, by contrast, bear the entire reproductive investment. This asymmetry has several implications. First, females often have a longer active lifespan because they must build and provision several cells. Second, they are far more directly dependent on the simultaneous availability of flowers and nesting sites. Third, the reproductive success of the population rests largely on their ability to convert a relatively brief adult life phase into viable offspring. This point is essential for understanding why localised disturbances — floral drought, destruction of a nesting site, increased foraging distances — can have disproportionate effects on the reproduction of solitary species.

Larval nutrition constitutes another fundamental feature of the life cycle. In wild bees, larvae are fed through a provision deposited in each cell before oviposition. This provision consists mainly of pollen and nectar, sometimes floral oils in a few specialised groups, but is not distributed progressively as in the honey bee colony. The dominant model in solitary species is therefore that of comprehensive prior provisioning: the female prepares all the resources needed for larval development, lays an egg, then closes the cell. This means that each cell represents a closed reproductive unit, whose success depends on the quality and quantity of the collected provisions as well as on the microclimatic and sanitary conditions of the nest. The principle of "one cell – one egg – one provision" constitutes one of the fundamental features of the wild bee life cycle.

Overwintering is also highly variable among species. In the most common typical cycle of temperate zones, individuals overwinter in the nest as immatures or as newly formed but still inactive adults, protected in their cell until emergence the following season. Not all species overwinter at the same stage: some overwinter as larvae or prepupae, others as adults, and the modalities of diapause vary between groups. This diversity has important consequences for climatic vulnerability. Depending on the overwintering stage, species respond differently to mild winters, late frosts or shifts in spring flowering.

Even among species sharing an annual cycle, adult lifespans remain modest. In many solitary bees, males live for a few days to a few weeks, and females for only a few weeks or slightly longer, depending on species and conditions. This apparent brevity of adult life should not be interpreted as an inherent weakness; it is part of a biological strategy highly concentrated on a brief seasonal window. However, it does make species sensitive to any disturbance that further shortens the effective reproduction period. An unfavourable climatic episode or a gap in floral supply during this window can suffice to substantially reduce the number of cells produced by a female.

Bumblebees constitute an important case, as they show that social forms exist within wild bees without reproducing the honey bee model. In bumblebees, only a young mated queen overwinters. In spring, she establishes a colony alone, rears the first workers, and these then take on part of the foraging and brood care work. The colony then disappears at the end of the season, and only the new mated queens survive until the following cycle. This social model is therefore annual, not perennial like that of Apis mellifera. An important comparison with the honey bee follows: even when a wild bee is eusocial, its cycle can remain very different from the classic beekeeping model (Plowright & Laverty, 1984; Westrich, 2019).

Some Halictidae, particularly in the genera Lasioglossum and Halictus, show simpler forms of sociality, sometimes described as primitive or facultative. These cases are biologically interesting because they show that the boundary between solitary and social life is not always absolutely clear-cut. There is a gradient of sociality in bees, and the evolution of these lifestyles has been the subject of much work. For the purposes of this article, the essential point is not to enter into phylogenetic detail, but to make the reader understand that "wild bees" do not form a uniform block from a social standpoint. Most are solitary, some are social, certain ones may even vary depending on context, and therefore none can be described using a single organisational scheme. On this point, the synthesis rightly recommends maintaining careful phrasing and presenting bumblebees and certain Halictidae as important exceptions within a predominantly solitary group.

A particularly instructive example is Osmia spinulosa, which the structure correctly uses as an illustrative thread. This Central European species has a well-documented annual cycle. Females nest in empty snail shells, build and provision their cells during a relatively brief flight period on a yearly scale, and the offspring spend most of the remainder of the cycle in the nest. Available data indicate a flight period that can reach approximately ten to eleven weeks at most, with males whose activity duration is shorter than that of females. Particularly interesting is the finding that females can regularly inspect their nests even several weeks after closing them. This example very well illustrates the general logic of solitary bees: a visible, concentrated and active adult phase, followed by a long development hidden within the nest (Müller, 1994, 2018).

This example also helps to understand why it is methodologically important to reason in full cycles and not only in "flight periods". If one only observes adults present on flowers, one perceives only a small part of the species' biology. Yet reproductive success also depends on the location of nests, the quality of provisions, winter survival rate, diapause stage and the protection of cells against pathogens, parasitoids and climatic hazards. This is why the following chapters on nesting, flower relationships and habitat requirements should not be understood as themes separate from the life cycle, but as the ecological dimensions that condition its course.

The climate question finally deserves mention, but without overinterpretation. Work on phenological shifts shows that bees and plants are already responding to warming, with observable date advances in several datasets (Bartomeus et al., 2011). However, for most Swiss species, long time series remain limited; the effects of climate change on wild bee cycles and distribution must therefore still be stated cautiously, particularly in the Alpine context. The most rigorous formulation is therefore to say that wild bee phenology is potentially sensitive to climate change, but that the magnitude, direction and consequences of these changes remain very species- and ecological-context-dependent.

In summary, wild bees are characterised by great diversity of lifestyles, but a general biological framework emerges clearly for the species of temperate Switzerland: predominantly solitary species, annual cycle as the general rule, brief adult phase, reproductive investment concentrated in females, prior cell provisioning, overwintering in the nest and phenology tightly linked to floral resources. The exceptions — annually social bumblebees, some Halictidae with more flexible sociality, cases of prolonged diapause or more complex voltinism — do not contradict this framework; they rather show its limits and richness. This reading is important for the entire article, as it reminds us that wild bees can only be understood by articulating biological cycle, floral resources, nesting site and landscape temporality.

5. Nesting Modes and Nesting Ecology

In wild bees, nesting is not a secondary aspect of biology, but one of the cores of their reproductive ecology. The success of a local population certainly depends on the presence of floral resources, but equally on the ability of females to find a suitable nesting substrate, prepare it, protect it and assemble there the materials necessary for cell construction. In this regard, the nest should not be understood as a mere shelter. It represents the complete infrastructure of reproduction: oviposition site, larval development site, often overwintering site, and the space where much of the offspring's survival is at stake. This centrality of the nest explains why wild bees respond so strongly to the fine structure of habitats, well beyond the mere availability of flowers (Müller & Praz, 2024; Westrich, 2019; Zurbuchen & Müller, 2012).

The convergent literature on Central Europe indicates that a large majority of wild bees nest in the ground. Depending on the datasets and geographic perimeter considered, ground-nesting species generally represent approximately two-thirds to three-quarters of the fauna, while the remainder is distributed among species nesting in pre-existing cavities, in stems, in dead wood, in particular substrates or following other specialised strategies (Antoine & Forrest, 2021; Westrich, 2019). Caution is nonetheless warranted with exact percentages for Switzerland, since fine national quantifications remain less abundant than the syntheses available for Central Europe. The robust conclusion is therefore not that there would be a single unvarying proportion, but that ground nesting is very strongly dominant in wild bees, with major consequences for their vulnerability to soil sealing, tillage, systematic greening or the disappearance of pioneer surfaces.

Ground-nesting species excavate their own nest in the soil, often in the form of a main tunnel from which lateral or terminal cells branch off. This general scheme nonetheless encompasses a strong diversity of solutions. Some species establish isolated nests, while others form dense, sometimes spectacular aggregations when local conditions are favourable. These aggregations do not generally imply sociality comparable to that of bumblebees or the honey bee; they primarily reflect a concentration of independent females on a particularly well-suited substrate. This distinction is important, because the "colonies" of ground-nesters observed on a bank or sparse meadow are in reality often spatial groupings of solitary individuals attracted by the same physical soil properties (Westrich, 2019; Antoine & Forrest, 2021).

The nesting preferences of ground-nesting species are much finer than is often supposed. Synthesis reviews show that texture, particle size, compaction, moisture, soil temperature, slope, aspect and degree of vegetation cover strongly influence the choice of nesting site (Antoine & Forrest, 2021). Some species prefer sandy or loamy soils easy to excavate; others readily use more compact soils, clay banks, sparsely vegetated tracks or gravelly zones. This heterogeneity prevents speaking of "the ideal soil" in the singular. What matters is rather the coexistence, at the landscape scale, of a diversity of microconditions likely to suit different guilds.

Among the most robust findings in recent literature is the importance of bare or sparsely vegetated soil for many ground-nesting bees. Gardein et al. (2022), on calcareous grasslands in Germany, showed that ground-nesting bees strongly preferred bare soil areas and that nest density there increased very substantially compared to vegetated control surfaces. This type of result is particularly useful because it provides an experimental argument where many studies remain correlational. It would nonetheless be excessive to deduce that any bare soil is favourable to all species. The presence of open soil is an important factor, but its value depends on context, substrate type, surface stability, thermal exposure and proximity to the resources used by reproductive females (Antoine & Forrest, 2021; Gardein et al., 2022).

It should also be emphasised that ground nesting does not necessarily require spectacular or rare habitats in a landscape sense. Many species use very ordinary but now rare structures in intensively managed landscapes: exposed banks, sparsely vegetated path edges, areas of compacted but unsealed soil, pioneer brownfields, gravel pit margins, small eroded surfaces, well-drained slopes or patches of bare soil in dry grasslands. This point is central to understanding nesting ecology: the quality of a landscape for bees often depends on barely visible microstructures, easily eliminated by management aimed at uniformity or the "tidiness" of surfaces.

Alongside ground-nesting species, a second major ensemble consists of species using pre-existing cavities. These cavities can be galleries of wood-boring insects in dead wood, hollow stems, pith-filled stems, cracks in stone, holes in old walls or other interstices already available in the habitat. Here again, simplifications must be avoided. The literature shows that so-called cavity-nesting species do not settle for "any hole"; they select diameters, depths, orientations and microclimates compatible with their size, nesting behaviour and building materials (Beyer et al., 2023; Westrich, 2019). The cavity is therefore not just a container, but a complete microhabitat whose quality directly influences larval development.

Cavity-nesting species reveal the ecological importance of dead wood, standing stems and certain old landscape structures. In strongly simplified landscapes, the disappearance of old hedgerows, rich ecotones, bramble thickets, dry stems and dead woody elements mechanically reduces nesting possibilities for this group. However, it should be kept in mind that cavity-nesters remain a minority relative to ground-nesters across wild bees as a whole. This precision is important to avoid a frequent error in popular writing: public attention easily focuses on cavity-nesting bees because they are most directly concerned by insect hotels, while the majority of species depend primarily on suitable soil substrates (Antoine & Forrest, 2021; Westrich, 2019).

Some species show even more striking specialisations. Osmia bees nesting in snail shells constitute one of the best-known examples in Central Europe. In these cases, the shell is not merely passively occupied; it is integrated into a genuine reproductive architecture, with sealing, cell partitioning and sometimes camouflage of the nest (Müller, 2018). These cases are ecologically important because they show how far nesting site specialisation can go. They also remind us that a microstructure very ordinary at the landscape scale can be of major importance for certain species.

Beyond site choice, the internal construction of the nest constitutes an essential dimension of nesting ecology. Cells are not simply arranged in a bare tunnel or cavity. They are separated, lined and sealed using materials whose choice varies greatly between species. Some use earth or mud; others cut leaf or petal fragments, collect resin, plant hairs, sand, mineral debris or composite materials. In Megachilidae, for example, the use of leaves, petals, plant hairs or resin for cell lining is particularly well known and constitutes a classical feature of their biology (Michener, 2007; Westrich, 2019). This architectural dimension has direct ecological implications: for a site to be genuinely favourable for reproduction, it must not only offer a nesting location but also allow access to appropriate building materials in the vicinity of the nest.

The spatial proximity between the nest and floral resources also plays a role in nesting ecology. The point is not to turn this chapter into one about flowers, but to indicate that the nesting site is never chosen independently of the cost of foraging trips. In solitary bees, increasing the distance between nest and floral resources greatly increases energy costs and reduces offspring production, as Zurbuchen et al. (2010) showed experimentally. It is therefore plausible, and supported by several studies, that the quality of a nesting site depends also on its relative position in the landscape. A physically adequate substrate that is too far from the necessary resources may be less attractive than a slightly suboptimal substrate that is better connected. This interaction between nesting and resource proximity constitutes a robust point in the literature, even if detailed data remain limited for many Swiss species.

The microclimatic conditions of the nest are another important dimension. Temperature, humidity, sun exposure, protection from runoff and mechanical substrate stability influence the survival of eggs, larvae and pupae. For ground-nesting species, a well-exposed slope can offer a warmer and drier microclimate favourable to development. For cavity-nesters, the orientation of the entrance, tunnel depth and support material modify internal conditions. These parameters are not always documented in equal detail across groups, but the literature converges on the idea that the nest constitutes a very sensitive microenvironment, not a neutral cavity (Antoine & Forrest, 2021; Westrich, 2019).

It is also necessary to integrate the pressure of natural enemies into this nesting ecology. Wild bee nests can be parasitised by mites, fungi, flies, beetles, parasitoid Hymenoptera and, above all, kleptoparasitic bees. The latter do not build nests or provision cells; they exploit the nests of host species in which they lay or introduce their own offspring. Their presence is therefore intimately linked to that of their hosts and to the permanence of nesting sites. Sheffield et al. (2013) have proposed considering kleptoparasitic bees as interesting indicator taxa for assessing the quality and completeness of bee communities. In the logic of this chapter, their interest is twofold: they show on the one hand that nesting ecology includes complex biotic interactions, and on the other hand they remind us that a landscape favourable to a given bee may also be favourable to a whole suite of ecologically associated species.

Alongside kleptoparasitism, there is also true social parasitism in certain bees. This is notably the case for certain so-called "cuckoo bumblebees", whose females enter the nest of another species, take control of it and have their offspring reared by the host workers. This lifestyle differs from kleptoparasitism in the strict sense, but it also shows that the nesting ecology of wild bees includes several forms of parasitic dependence on the nests of others (Plowright & Laverty, 1984; Westrich, 2019).

An important methodological point deserves emphasis. The literature on wild bee nesting remains still unevenly developed across groups and regions. Antoine and Forrest (2021) emphasise that, despite the abundance of naturalistic descriptions, few experimental studies rigorously isolate the precise factors determining the choice or success of a nesting site. In Switzerland, data remain fragmentary and comparative quantifications of nesting site availability by landscape type are still few. Appropriate caution is therefore needed in overly sharp causal formulations. One can state that the lack of nesting substrates constitutes a plausible and often important factor in declines, but it is more difficult to quantify its exact share relative to floral scarcity, especially across guilds and landscape contexts.

6. Bee–Flower Relationships and Trophic Specialisation

The relationships between wild bees and flowers cannot be reduced to a general visitation of flowering vegetation. They constitute one of the cores of bee biology, because flowers provide both the energy needed by adults and the resources essential for offspring development. This dual function immediately imposes a central distinction. Nectar serves mainly as an energy food for adults, while pollen plays a decisive role in larval nutrition. In bees, the most important ecological question is therefore not only which flowers are visited, but above all which flowers provide the pollen actually collected for the brood. It is on this basis that the literature defines the trophic specialisation of bees, far more than on the simple observation of adult nectar-collecting visits (Rasmussen et al., 2020; Müller & Praz, 2024).

This distinction is essential, because a bee may appear relatively generalist when one observes its floral visits in the field, while remaining biologically specialised for the pollen destined for larvae. Adults can drink nectar from a broader range of flowers than that used for making up the nest's pollen provisions. In other words, the apparent breadth of the floral spectrum observed at the level of individual adults does not automatically reflect the actual breadth of the trophic regime relevant to reproduction. The synthesis by Rasmussen et al. (2020) emphasises precisely this point: bee specialisation must be conceived at the intersection of behaviour, morphology, pollen transport and actual resource use for larval development, and not as a superficial floral preference (Rasmussen et al., 2020).

A further distinction must be made between trophic specialisation and the floral constancy observed during foraging. Many bees, including some non-strictly-specialised species, tend to visit relatively homogeneous flower types during the same foraging trip. This floral constancy behaviour often improves foraging efficiency, reduces learning costs and, from the plants' standpoint, favours more targeted pollen transfer between compatible flowers. Grüter and Ratnieks (2011) nonetheless recall that this constancy must not be confused with strict long-term specialisation: a bee can be faithful to a floral type during a given trip without being closely dependent on that plant type throughout its whole biology (Grüter & Ratnieks, 2011).

In the literature on wild bees, specialisation is often described using a gradient from polylecty to oligolecty. Polylectic species collect pollen from several, sometimes numerous, plant families. Oligolectic species, by contrast, restrict themselves to a much narrower set of host plants, defined by different authors at the level of a genus, tribe or family. This is not a perfectly binary opposition. Some species occupy intermediate positions, and the exact boundaries between categories depend partly on the taxonomic resolution adopted and the quality of available data. Despite this grey zone, the distinction remains useful, because it reflects very different ecologies and very contrasting degrees of dependence on the floristic composition of habitats (Rasmussen et al., 2020).

In the Swiss context, the Red List provides particularly illuminating results on this subject. It first recalls that, unlike other pollinator groups, bees visit flowers not only to meet their own energy and protein needs, but also to feed their larvae. It then shows that the degree of floral specialisation is known for 449 non-parasitic evaluated species, of which 149, or 33.2%, are oligolectic. Most strikingly, the proportion of Red List species is markedly higher among oligolectic species than among polylectic ones: 56.5% versus 37.5%. The same source further specifies that oligolectic species linked to Brassicaceae, Carduoideae and Dipsacoideae are among the most strongly threatened. These data are important because they show that floral specialisation is not a marginal or anecdotal trait, but a factor closely associated with extinction risk in the current Swiss fauna (Müller & Praz, 2024).

The experimental work of Praz et al. (2008) provides a major result here. By rearing larvae of several specialist species on non-host pollens, the authors showed that these bees could not develop correctly on these alternative resources. The strongest finding of this study is that certain pollens apparently available in the environment are not biologically interchangeable for specialists. This non-interchangeability suggests the existence of important physiological constraints, possibly linked to pollen chemistry, its digestibility or the ability of larvae to assimilate certain nutrients and tolerate certain secondary compounds. In other words, in some specialist bees, specialisation is not only a behavioural choice; it is also a functional constraint of development (Praz et al., 2008).

The results of Sedivy et al. (2011) further reinforce this reading. By comparing two closely related species of the genus Osmia, both described as very generalist, the authors showed that they differed markedly in their ability to complete their development on the same pollen diets. This result is particularly instructive, as it shows that even polylecty does not mean unlimited plasticity. Closely related species using a broad range of plants may nonetheless show marked physiological differences in their ability to exploit certain resources. The practical consequence is equally significant: in managed landscapes, one cannot assume that a general increase in floral supply will automatically compensate for the disappearance of the plants most important for larval development (Sedivy et al., 2011).

Floral specialisation also rests on fine sensory and cognitive mechanisms. In Chelostoma rapunculi, a specialist on bellflowers, Milet-Pinheiro et al. (2013) showed that particular volatile compounds, notably rare spiroacetals in floral signals, play a central role in host plant recognition. The results indicate that females use precise chemical cues to locate appropriate flowers. The interest of this study extends beyond the particular case of Chelostoma. It shows that specialisation is not only a matter of larval physiology; it also involves specialised detection and orientation systems in the adult. Bee–flower relationships thus appear as multi-level relationships, combining perception, learning, foraging behaviour and developmental constraints (Milet-Pinheiro et al., 2013).

At the ecological level, this specialisation has several major consequences. First, the quality of a habitat for wild bees depends on its fine botanical composition, not merely on the total number of visible flowers. Second, there is a phenological dimension: host plants must not only be present, but flowering sufficiently abundantly during the flight period of reproductive females. Third, there is a spatial dimension: floral resources must be accessible within a distance compatible with the location of nests. These three dimensions — composition, temporality, accessibility — explain why specialist species are particularly sensitive to landscape simplification and habitat fragmentation (Müller & Praz, 2024; Rasmussen et al., 2020).

The most robust conclusion for the current Swiss context is therefore: bee–flower relationships are at the heart of wild bee ecology, not only because flowers provide food and energy, but because a significant proportion of the fauna depends on relatively close trophic relationships with certain plant groups. This dependence is strongly linked to extinction risk at the national scale, as the Red List shows. Any reflection on their conservation must therefore go beyond the simple idea of "adding flowers" and concern itself with the precise botanical structure of habitats, the host plants actually used and their maintenance in time and space (Müller & Praz, 2024; Praz et al., 2008; Rasmussen et al., 2020; Sedivy et al., 2011).

7. The Importance of Wild Bees as Pollinators

The importance of wild bees as pollinators can only be correctly understood by avoiding two common simplifications. The first would consist of reducing pollination to the honey bee alone, as if all pollen transfers useful for plant reproduction or agricultural production could be attributed to Apis mellifera. The second would, conversely, consist of presenting wild bees as systematically more important than the honey bee in all contexts. The state of knowledge is more nuanced. What it allows to be affirmed with the greatest solidity is that wild bees play a major functional role, both in the reproduction of many wild plants and in the pollination of various crops, and that this role is neither uniformly substitutable nor reducible to the mere abundance of one managed species (Garibaldi et al., 2013; Drossart & Gérard, 2020; Sutter et al., 2017).

One of the most robust findings at the international level comes from Garibaldi et al. (2013), who showed across 41 crop systems worldwide that wild pollinators increase fruit set independently of honey bee abundance. This result is particularly important, because it shows not only that wild bees participate in pollination; it indicates that their contribution does not disappear when honey bees are present. In other words, there is a specific effect of wild pollinators. The most solid interpretation is therefore not that wild bees "replace" the honey bee, but that they add complementary functions to it that increase total pollination (Garibaldi et al., 2013).

This complementarity is largely explained by the diversity of biological traits in wild bees. Some species are active earlier in the year, others later. Some forage at lower temperatures or under less favourable weather conditions than the honey bee. Some exploit complex, deep or less accessible flowers more effectively. Others show foraging behaviours or body sizes that modify the way pollen is collected, transported and deposited on the fertile organs of flowers. Wild bees prove particularly useful in demanding crops or under marginal climatic conditions, precisely because their morphology and behaviour differ from those of the honey bee.

One of the major findings of recent literature is precisely that pollinator diversity matters in itself. Rogers et al. (2014) showed in a perennial crop that bee species richness improved both productivity and its stability. Senapathi et al. (2021) concluded at the global scale that wild insect diversity increases the inter-annual stability of crop pollinator communities. These results do not mean that each species contributes in equal proportions, nor that all rare species have equivalent functional weight in all systems. They show, however, that a more diverse assemblage tends to make the pollination service more robust in the face of weather fluctuations, resource variations or inter-annual abundance changes. This robustness constitutes a central point for both agriculture and landscape ecology.

In the Swiss context, the most solid data show that entomophilous pollination has real economic importance. Sutter et al. (2017) estimate that insect-dependent crops represent approximately 5% of Swiss agricultural land and that the direct economic value of insect pollination lies between 205 and 479 million Swiss francs per year. This estimate must be interpreted carefully, as it rests on categories of crop dependency and not on a direct measurement, crop by crop, of the exact share of wild bees. In Switzerland, quantitative studies rigorously comparing the respective contributions of wild bees and the honey bee to specific crops remain few. Nevertheless, these works are sufficient to show that wild pollinators represent not merely a theoretical or heritage issue; they also concern concrete agronomic functions.

On the question of compensation by the honey bee, reviews and syntheses converge rather towards a cautious answer: compensation is at best partial and strongly dependent on crop type, landscape and ecological conditions (Garibaldi et al., 2013; Drossart & Gérard, 2020). This conclusion is important not only for agriculture but also for conservation. It means that multiplying hives does not in itself constitute a strategy equivalent to conserving wild communities.

Ultimately, the importance of wild bees as pollinators can be summarised in four points. First, they contribute substantially to the pollination of many wild and cultivated plants. Second, their contribution is largely complementary to that of the honey bee, not merely redundant. Third, certain species or guilds can be particularly effective in certain crop systems or under certain climatic conditions. Fourth, wild bee diversity increases the stability and robustness of the pollination service. This is why the conservation of wild bees falls not only within a biodiversity heritage objective, but also within the maintenance of an essential ecological function of landscapes.

8. Threats to Wild Bees

The conservation status of wild bees in Switzerland requires treating the question of threats precisely, but also methodically. It is not sufficient to enumerate a series of possible pressures; one must distinguish, as far as possible, what corresponds to a documented decline, what corresponds to well-supported factors, and what remains more difficult to rank due to the often correlational nature of the data.

The first, most solid finding is the scale of the problem itself. The most recent Swiss Red List evaluates 615 species and concludes that 279 of them, or 45.4%, appear on the Red List; of these, 59 species are considered extinct in Switzerland (Müller & Praz, 2024). This result is particularly striking at two levels. On the one hand, it confirms that bees are among the insect groups most severely affected by biodiversity threats. On the other hand, it shows that the phenomenon concerns not only a diffuse decline in abundance, but also the effective national disappearance of a significant number of species. An essential methodological clarification must however be added immediately: the new Red List does not permit a simple and direct comparison with that of 1994, due to differences in method, taxonomic progress, the very substantial increase in available data and changes in evaluation criteria. It would therefore be unwise to assert, on this basis alone, that the situation has linearly deteriorated, improved or stabilised between the two assessments. What can be said with confidence is that the current situation remains concerning and that a very large proportion of the indigenous fauna is threatened (Müller & Praz, 2024).

This diagnosis does not mean that all species are equally exposed. One of the most important findings of the Swiss Red List is precisely to show that certain categories of species are overrepresented among threatened taxa. Oligolectic species — those specialised on a narrow pollen spectrum — appear markedly more threatened than polylectic ones. Similarly, ground-nesting species appear more frequently on the Red List than those nesting above ground. Finally, species flying late in the season, as well as those associated with narrower ecological niches, appear particularly vulnerable. These results are consistent with those of Hofmann et al. (2019), who show at the Central European scale that a narrow habitat niche and late-summer emergence strongly increase extinction vulnerability. This convergence between Swiss data and macroecological analyses is important, as it suggests that threats do not strike randomly: they affect more severely the species most dependent on specific resources, fine habitat structures or more critical seasonal windows.

Habitat loss and degradation constitute, in this picture, the best-supported factor. Major syntheses on pollinators identify, in a recurring fashion, land use change, habitat fragmentation, reduction of semi-natural habitats and landscape homogenisation as major drivers of wild bee decline (Potts et al., 2010; Goulson et al., 2015). In the Swiss context, this reading is strongly confirmed by the Red List. It underlines that wild bees have high habitat requirements, often depend on the juxtaposition of several distinct resources in the landscape, and that the most diverse species persist mainly in habitats that have today become rare or fragmented, such as dry grasslands and pastures, certain alluvial habitats, pioneer brownfields, gravel pits or strongly structured extensive mosaics (Müller & Praz, 2024).

In agricultural landscapes, this habitat transformation often takes the form of progressive intensification. Plot enlargement, disappearance of hedgerows, fallow land, lean meadows, extensive strips, structured ecotones and pioneer surfaces lead to a landscape simplification that directly affects wild bees. The most generalised species can sometimes partially persist in such contexts, but more specialised species or those with small foraging ranges quickly become disadvantaged.

The loss of floral resources constitutes a specific component of this habitat degradation. It should not be understood only as a decrease in the total number of visible flowers, but as a simplification of botanical composition and a reduction of temporal continuity of flowering. For wild bees, especially when they are specialised, the question is not only whether flowers exist, but whether the relevant host plants are present, at the right time, in sufficient quantity, and within a radius compatible with foraging trips from the nest. The Swiss Red List establishes a strong link between floral specialisation and extinction risk, showing clearly that the loss of specific pollen resources plays a major role in the decline of many species (Müller & Praz, 2024).

The loss of nesting structures constitutes the other essential facet of this same dynamic. Many wild bees nest in the ground, others depend on cavities in dead wood, stems, mineral fissures or very fine microstructures. In intensively managed landscapes, systematic greening, bank levelling, disappearance of bare soils, scarcity of dead wood, removal of dry stems or standardised renovation of old walls and structures directly reduce the number of available reproduction sites. This point is important, because it explains why simply increasing floral supply is not always sufficient to support populations. A species may find food resources locally without being able to reproduce if nesting sites or necessary building materials are lacking.

Urbanisation constitutes another major factor, but its effects deserve to be stated with nuance. Syntheses on urban bees show that increasing impermeabilisation and standardisation of urban spaces are generally accompanied by a decrease in species richness, particularly for specialised species or those dependent on certain soil types and structures (Buchholz & Egerer, 2020). However, it would be incorrect to conclude that cities are uniformly unfavourable to all wild bees. Certain large cities can locally harbour rich communities, notably in diversified gardens, urban brownfields, railway banks, old walls or sparsely managed mosaics.

Pesticides represent another pressure often invoked in wild bee decline. Major reviews on pollinators clearly identify pesticides among the important risk factors, alongside habitat loss, climate change and pathogens (Potts et al., 2010; Goulson et al., 2015). In the Swiss context, the effects of pesticides on wild bee communities remain still poorly directly documented, and their interactions with other threats are rarely studied in an integrated manner. The most rigorous conclusion is therefore that pesticides constitute a credible and well-supported threat at the general level, but that their exact relative weight in Switzerland, compared to habitat loss or fragmentation, remains more difficult to quantify.

Climate change should also be integrated into this analysis, but without overinterpretation. Global reviews now consider it an important factor in modifying pollinator communities (Potts et al., 2010; Goulson et al., 2015). For Central European wild bees, several mechanisms are plausible: shifts in flight periods, modification of synchronisation with flowering, increased summer droughts, shifts in distribution ranges and differential effects depending on species traits. It is more accurate to speak of an increasing and differentiated pressure rather than a uniform effect on all Swiss wild bees.

The most defensible conclusion for this chapter is therefore the following. Threats to wild bees in Switzerland are mainly linked to human landscape transformations: agricultural intensification, loss and fragmentation of semi-natural habitats, simplification of the landscape mosaic, reduction of floral resources and nesting sites, urbanisation, pesticide exposure and, increasingly, climatic effects. These threats do not act in isolation and do not affect all species in the same way. Specialised species, summer species, species linked to precise microhabitats and ground-nesting species appear particularly vulnerable. Scientifically, it would be excessive to designate a single factor as the main culprit in all contexts. However, it is strongly supported that habitat loss and the structural impoverishment of landscapes constitute the common foundation on which other pressures are grafted, whose relative importance varies by habitat, species and regional context.

9. Habitat Requirements: What Wild Bees Need

In the study of wild bees, the term "habitat" cannot be understood in the vague sense of a more or less natural or more or less flower-rich habitat. For bees, a functional habitat is a system of combined resources. It must offer, within an ecologically coherent space, flowers suited to the needs of adults and larvae, nesting sites compatible with the reproductive strategies of present species, nest-building materials when necessary, and a landscape configuration allowing these different resources to be connected without excessive movement costs. Wild bees do not depend on a single favourable element, but on a set of minimum and optimal conditions combining floral resources, nesting possibilities and landscape structure.

This precision is important because it helps avoid a frequent misunderstanding. A habitat may appear favourable at first glance because it shows abundant flowering at a given moment, while remaining mediocre for many wild bees if nesting sites are lacking, if crucial plants are absent at other times of the season, or if resources are too far apart. Conversely, a floristically unspectacular site may have great value for certain species if it combines, over short distances, an adequate nesting substrate, a few determining host plants and a favourable microclimate. This is why habitat quality for wild bees must always be thought of functionally and not merely visually.

Spatial proximity between resources is not a secondary detail of the habitat, but a central ecological condition. In many wild bees, efficient foraging trips occur over a scale of a few hundred metres rather than kilometres, such that an apparently flower-rich landscape can remain poorly functional if these resources are too far from nesting sites. The experimental work of Zurbuchen et al. (2010) shows that increasing the distance between nest and floral resources clearly reduces reproductive performance: in Hoplitis adunca, an increase of 150 m led to a decrease of approximately 23% in the number of provisioned cells, and in Chelostoma rapunculi, an increase of 500 m led to a decrease of approximately 46%. These results should not be transformed into a universal threshold valid for all species, as flight distances depend strongly on body size, behaviour and landscape context. They nonetheless robustly show that a favourable habitat depends not only on the presence of resources, but also on their effective proximity in space (Zurbuchen et al., 2010; Zurbuchen & Müller, 2012).

The first requirement is a diversified and temporally continuous floral supply. It is not sufficient for a landscape to produce abundant flowering over a brief spring or summer period. Swiss wild bees have very different flight periods, and their needs change depending on whether they are early, summer, generalist or specialist species. A high-quality habitat must therefore offer a succession of floral resources from early spring to the end of summer, with a sufficiently varied botanical composition to meet different trophic spectra.

The second fundamental requirement is the availability of appropriate nesting sites. A large proportion of wild bees nest in the ground, which implies the presence of permeable surfaces, suitable substrates, sometimes bare or sparsely vegetated soil, banks, well-exposed slopes or pioneer areas. Other species depend on pre-existing cavities in dead wood, hollow stems, pith stems, old walls, mineral interstices or comparable structures.

Spatial proximity between resources constitutes a third central requirement. Wild bees do not exploit the landscape as an abstract space; they must physically connect their nest to the floral resources necessary for adult nutrition and brood provisioning. Foraging distances are related to body size, flight behaviour, landscape type and local resource abundance (Greenleaf et al., 2007). Experimental work has shown that increasing the distance between nest and floral resources reduces offspring production in solitary bees (Zurbuchen et al., 2010). This spatial constraint leads to a key idea: a high-quality habitat for wild bees is often a networked habitat. What matters is not only the isolated presence of favourable resources, but their articulation within a sufficiently dense network to allow bees to complete their life cycle.

Hedgerows, ecotones and transitional zones play a particularly important role in this logic. They often offer, over short distances, a rare combination of flowers, woody structures, stems, warmer zones and vegetation breaks favourable to nesting. Pfiffner et al. (2018) show that high-quality habitats on organic farms complement one another and that linear landscape elements contribute to this complementarity.

Extensive meadows and dry grasslands appear in many studies as particularly favourable habitats. They often combine floral richness, varied soil structures, microtopographic heterogeneity and favourable thermal conditions. However, one must avoid making them magical habitats valid for all species. The complementarity of habitats counts more than any single habitat type.

Wildflower strips and other biodiversity promotion measures deserve discussion here, as they are often presented as a simple response to wild bee needs. Available results show that they can indeed increase wild bee abundance and sometimes diversity, especially when they increase floral supply in simplified agricultural landscapes (Albrecht et al., 2021; Hellwig et al., 2022). Their effectiveness is however neither uniform nor necessarily durable if these strips are not maintained or renewed appropriately.

In summary, what wild bees need can be formulated synthetically, but not simplistically. They need diversified floral resources spread over time; nesting sites adapted to their respective strategies; building materials when their biology requires them; microclimatic conditions compatible with their activity and the development of their offspring; and a landscape structure that keeps these resources sufficiently close together. The more specialised a species is, the more these requirements tend to be strict. The more homogeneous, intensive or fragmented a landscape is, the more difficult it becomes to combine all these conditions. This is why the notion of habitat, applied to wild bees, always refers to a functional mosaic of resources and not a mere botanical backdrop.

10. The Honey Bee as a Special Topic: Utility, Limits, Competition

The honey bee, Apis mellifera, occupies a singular place in an article devoted to wild bees. It is at once an important pollinator for certain agricultural productions, the central species of beekeeping, and an organism managed by humans at densities that do not necessarily correspond to the spontaneous ecological capacity of habitats. For this reason, it can be treated neither as a simple equivalent of wild bees, nor as a uniform problem whose effects would be identical everywhere. A rigorous approach requires distinguishing several levels of analysis: the agronomic utility of the honey bee, the overlap of resources with wild bees, the possible existence of effective competition, measured effects — or lack thereof — on wild bee reproduction and fitness, as well as the distinct question of pathogen transmission.

On the functional level, the utility of the honey bee for agriculture is hardly in doubt. In Switzerland, Agroscope work estimates the direct economic value of insect pollination at between 205 and 479 million Swiss francs per year, and entomophilous crops represent approximately 5% of agricultural land and 14% of cultivated land. It would therefore be wrong to treat the honey bee as an ecologically negligible or purely problematic organism. Beekeeping also has its own economic value, linked to honey and other product production, as well as a social and cultural importance beyond ecology alone (Sutter et al., 2017).

The results of Garibaldi et al. (2013) show, across more than 40 crop systems, that wild insects increase fruit set independently of honey bee abundance, and that wild insect visits improve fruit set more strongly, on average, than an equivalent increase in honey bee visits. The most solid conclusion is therefore not that the honey bee is useless, but that it acts mainly as a complement, not as a complete substitute for wild pollinators (Garibaldi et al., 2013).

The first delicate question is that of floral resource overlap. It is well established that the honey bee is a very generalist species capable of exploiting a broad floral spectrum, and that it can reach very high local densities due to managed hives. This simple finding is sufficient to make a significant overlap with many wild bees plausible. But here two things must be clearly distinguished: resource overlap and effective competition. The former is widely documented; the latter cannot be automatically deduced from the former. As the systematic review of Mallinger et al. (2017) recalls, many studies show a shared use of the same flowers, but far fewer then demonstrate a direct negative effect on wild bee abundance, diversity or fitness (Mallinger et al., 2017).

The review of Mallinger et al. (2017) is particularly useful because it synthesises precisely this heterogeneity. For studies on competition, 53% report negative effects on wild bees, 28% observe no net effect and 19% find mixed results. This balance rules out two excessive conclusions: on the one hand, the idea that honey bees always and everywhere harm wild bees; on the other, the idea that no concerning effects would exist. The literature does not deliver a uniform verdict, but clearly shows that negative effects are possible, sometimes marked, and strongly depend on ecological context, hive density, floral availability, landscape and the taxa considered.

The most recent results confirm this need to reason by context. The study of Pasquali et al. (2025), conducted on the protected island of Giannutri, is methodologically remarkable because it combines experimental manipulation, measurement of floral resources and monitoring of wild bee responses. The authors show that daily temporary exclusion of honey bees increases nectar and pollen availability, modifies wild bee foraging behaviour and occurs in a context of strong decline of certain large wild bees over several years. This study therefore provides a strong empirical argument in favour of possible exploitative competition at high density, at least in a protected island system with limited resources. But it is precisely because the demonstration is strong that one must be rigorous about its scope: it shows what can happen in a particular context, not what necessarily occurs in all habitats where hives are present (Pasquali et al., 2025).

Conversely, Swiss urban studies invite a more nuanced reading. The City4Bees report, commissioned for the FOEN based on the case of Zurich, shows on the one hand that honey bee densities have strongly increased in cities and that every urban green space now lies within the action radius of an apiary. On the other hand, the results indicate that wild bee species richness is mainly linked to local resource availability and that direct competition with honey bees does not appear to be the main factor explaining the composition of the urban community studied. The central scientific message is therefore contextual: in cities, the effects of honey bees depend strongly on resource richness and the quality of the urban fabric (Casanelles Abella et al., 2023).

Pathogen transmission constitutes another dimension, distinct from food competition. Fürst et al. (2014) showed that the prevalence of deformed wing virus and Nosema ceranae was linked between honey bees and bumblebees, and that DWV strains were shared, making spillover very plausible for at least some infectious agents. The review of Mallinger et al. (2017) concludes that 70% of studies examining pathogen transmission report potentially negative effects of managed bees on wild bees. However, methodological strictness must be maintained: the detection of a shared pathogen, or even the probable existence of transmission, does not automatically demonstrate a major impact on the dynamics of all wild populations (Fürst et al., 2014; Mallinger et al., 2017).

The most scientifically defensible conclusion is therefore: the honey bee is both useful and limited. It provides agricultural services and supports beekeeping, but it does not replace the functional diversity of wild bees. The overlap of floral resources with the latter is well established, but does not in itself constitute proof of demographically significant competition. Negative effects exist in certain contexts, especially when hive density is high and resources limited; other contexts show relatively peaceful coexistence, or even the absence of detectable effects on certain reproduction indicators. Pathogen transmission represents a plausible and documented risk, but still unevenly quantified in its population-level consequences. Any simplistic formulation of the type "the honey bee harms wild bees" or, conversely, "the honey bee helps wild bees", must be avoided. The most rigorous analytical framework remains that of case-by-case evaluation, depending on landscape, hive density, floral availability, site status and the wild groups concerned (Garibaldi et al., 2013; Mallinger et al., 2017; Casanelles-Abella et al., 2023; Pasquali et al., 2025).

11. What Can Be Done? Action Principles for Promoting Wild Bees

Available knowledge suggests that no single measure is capable, on its own, of lastingly promoting all wild bees. Observed responses depend on the species concerned, the quality of the surrounding landscape and the resources already present. It is nonetheless possible to derive some relatively robust action principles, provided they are formulated with caution and adapted to local contexts (Westrich, 2019; Zurbuchen & Müller, 2012; Antoine & Forrest, 2021).

Think about habitat functionally

A first principle is to think about habitat functionally rather than simply visually. For wild bees, a favourable habitat is not defined only by the presence of flowers, but by the combination of floral resources, nesting sites and a spatial organisation allowing these resources to be connected within distances compatible with species biology. A richly flowering surface can therefore remain of low value if it is remote from nesting substrates or provides resources only over a brief period (Zurbuchen et al., 2010; Zurbuchen & Müller, 2012; Maurer et al., 2022).

Ensure a diversified and continuous floral supply

A second principle concerns the floral supply. In many contexts, it appears favourable to increase floristic diversity and ensure a continuity of flowering throughout the activity season. This orientation must not, however, be reduced to the simplistic idea that "more flowers" would suffice. The botanical composition of the habitat remains decisive, particularly for specialist species, which sometimes depend on a limited number of host plants. When local knowledge permits, it is therefore preferable to reason not only in terms of flower quantity, but also in the ecological quality of the resources offered (Rasmussen et al., 2020; Ganser et al., 2021; Tonietto et al., 2018).

Preserve genuine nesting resources

A third principle, often less visible, concerns nesting resources. A large proportion of wild bees nest in the ground, while others use pre-existing cavities, hollow stems, dead wood or mineral structures. In practice, this argues for maintaining or restoring open or sparsely vegetated soils, well-exposed banks, structured ecotones, dry stems and woody elements, rather than placing excessive confidence in artificial devices alone. Insect hotels can have complementary value for certain cavity species and for awareness-raising, but they replace neither the diversity of natural substrates nor the needs of the many ground-nesting species (Antoine & Forrest, 2021; Gardein et al., 2022; Westrich, 2019; MacIvor & Packer, 2015).

Manage habitats in an extensive and differentiated way

A fourth principle concerns habitat management. Available results suggest that overly intensive management tends to impoverish floral resources and microhabitats, while complete abandonment can lead, depending on the context, to progressive habitat closure unfavourable to many species. The most coherent approaches therefore appear to be forms of extensive and differentiated management: staggered interventions over time, maintenance of refuge zones, limitation of homogenising practices and conservation of a certain structural heterogeneity (Pfiffner et al., 2018; Kratschmer et al., 2019; Albrecht & Ganser, 2023).

Reason at the landscape scale

A fifth principle is to think about measures at the landscape scale. In agricultural landscapes, positive effects seem most plausible when extensive meadows, wildflower strips, hedgerows, ecotones, fallow land and other semi-natural elements complement rather than being planted in isolation. In the dry inner-Alpine valleys, notably in Valais and parts of Graubünden, priority should first be placed on conserving habitats already recognised as particularly rich, rather than on generic measures detached from local ecological realities (Maurer et al., 2022; Pfiffner et al., 2018; Praz et al., 2023).

Accompany measures with monitoring

Finally, these orientations should, as far as possible, be accompanied by some form of monitoring. In many cases, available studies measure primarily local variations in abundance or species richness over the short term, without always allowing conclusions about lasting improvement of populations. Even simple monitoring, repeated over time and combined with observations on vegetation and habitat structure, can help distinguish genuinely useful measures from those producing only an apparent or transient effect (Klaus et al., 2024; Marshall et al., 2024).

Adopt an overall logic rather than a single recipe

In sum, what the current state of knowledge allows to be asserted with the most confidence is not that a universal recipe exists, but that effective conservation of wild bees rests on the complementarity between floral resources, nesting sites, spatial habitat organisation, adapted management and long-term evaluation. This overall logic, more than any isolated measure, appears today the most defensible for the Swiss context (Zurbuchen & Müller, 2012; Westrich, 2019; Praz et al., 2023).

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