Trends in
Parasitology

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Opinion

Darwin's solution: Honeybees survive mite vectors and viruses through natural selection

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Complex host–vector–virus interfaces can impose serious health challenges. Western honeybees have experienced high colony losses globally, mainly driven by the host-shifted, virus-vectoring ectoparasitic mites *Varroa destructor* and *Tropilaelaps mercedesae*. Host populations can survive mite infestations through natural selection, offering a long-term strategy for colony health. However, host–vector–virus coevolution requires local adaptations of this triad, which is poorly understood. We propose harnessing natural selection through a global approach focused on standardized monitoring of colony survival, mite infestation levels, and control of reproductives. Studying native and adapted mite hosts, host shifts, and comparing susceptible to surviving hosts will enhance understanding of this host–vector–virus system. This strategy promotes colony health in both managed and wild host populations and provides insights into other host–vector–virus interfaces.

Highlights

High losses of western honeybee colonies occur in many regions globally and are mainly driven by virus-vectoring ectoparasitic mites (*Varroa destructor* and *Tropilaelaps mercedesae*).

Due to the variable host–vector–virus interactions, conventional breeding is unlikely to provide a solution.

Even though hosts can survive through natural selection, this has not been sufficiently considered.

We propose harnessing natural selection through a concerted global approach, using colony survival and mite infestation numbers as selection criteria.

A better understanding of this host–vector–virus system, through studying native mite hosts, host shifts, and comparing susceptible hosts with surviving novel hosts, will provide general lessons.

Taking advantage of naturally selected mite-resistant populations will enable the production of more western honeybees that survive without treatments.

Honey bee host–parasitic mite vector–virus interface underlies colony losses

Although the number of managed western honeybee (*Apis mellifera*) colonies has increased globally [1], beekeepers continue to struggle with unsustainably high colony losses [2,3], particularly throughout the Northern Hemisphere. Together with well-documented declines in wild insects [4], this raises concerns for pollination services essential for biodiversity and food security.

There is clear evidence that ectoparasitic mites, most notably *Varroa destructor* [5], act as potent virus vectors [6] and underlie these global losses [2,7]; for example, in 2024 and 2025, colony losses in the United States were unusually high (>50%), due primarily to acaricide-resistant mites [3]. Mites continue to evolve resistance [8]; thus, strategies based on chemical mite treatments are not sustainable. As obligate ectoparasites (Table 1), these mites are also adapting to their hosts [8]. This sets up a complex **triad** (see Glossary) of host–vector–virus interactions, because mites both parasitize bees and transmit viruses, forming the central link in a three-way host–vector–virus system that remains poorly understood. Genomic work shows that the mites have shifted hosts multiple times, each time changing the selection scenarios on all triad members [15,20]. However, our understanding of pathogen evolution to support honeybee health is still limited (Box 1). Interestingly, some populations of hosts, their mites, and some virus strains have coevolved an equilibrium through **natural selection**, where infestations do

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not lead to colony death [35]. Understanding this triad is therefore critical for a holistic control strategy.

Although four *Varroa* species are recognized [5], only *V. destructor* has spread worldwide (Table 1). Roughly 80–100 years ago, *V. destructor* independently and repeatedly shifted hosts between eastern (*Apis cerana*) and western (*A. mellifera*) honeybees, spreading globally on the novel host [20]. About 20 years ago, *Varroa jacobsoni* also shifted hosts but so far remains restricted to Oceania [15].

V. destructor feeds on both honeybee adults and brood and reproduces on pupae within brood cells [7]. Because males are produced parthenogenetically and sib mating is common, even one mite can establish a full colony infestation [7,36]. Transmission to other colonies occurs through hitching rides on food-stealing workers (robbing) and orientation errors of both drones (male sexuals) and workers (drifting) [7]. Another mite genus, *Tropilaelaps* spp., shifted hosts from giant honeybees to *A. mellifera* (Table 1) and has a similar life cycle to *Varroa* spp., but with a higher dependency on host brood [37]. Currently, *Tropilaelaps mercedesae* is expanding its range [38,39], presenting a growing threat. Furthermore, global warming, which allows honeybees to increase their brood-rearing period, will promote both brood parasites [40]. Although mites directly compromise hosts [7,41], most damage results from these mites vectoring a range of viruses [6,7,18]. These mite-vectored virus loads correlate with *A. mellifera* colony mortality [6,42].

Dynamic triad interactions of host–vector–virus system drive context-dependent outcomes

The severity of mite impacts varies widely across and within regions, reflecting local host–vector–virus coadaptations and the impacts of climate, environment, and beekeeping management. This evolution occurs in real time [43] resulting in a spatiotemporal mosaic of hosts, vectors, and viruses (Box 2). Indeed, most honeybee viruses, including deformed wing virus, are RNA viruses that evolve as populations of variable ‘quasispecies’ through a combination of highly error-prone replication/recombination and rapid selection [7,48]. Parasitic mites exert strong selective pressure on transmitted viruses [7,49] and impact nontransmitted ones (‘mite-hitchhikers’) [34]. Moreover, there is flexibility in both host and parasite traits [7,50–55]. Finally, external factors such as mite management (e.g., acaricide use) [7,29] and the availability of resources to the hosts (i.e., pollen, honey, and propolis) further influence these dynamics, generating endless interactive combinations and locally variable mechanisms of host survival. Therefore, a single *A. mellifera* population that survives mites without intervention globally is impossible. Indeed, while some of the numerous breeding programs for **resistance** to *V. destructor* have locally succeeded, none has produced a resistant bee for universal use [51,56]. Nevertheless, local mite-resistant *A. mellifera* host populations have evolved numerous times through natural selection [35,57,58]. Thus, the most promising avenue is to take advantage of natural adaptation locally in each region.

Natural selection

Resistance against *V. destructor* has evolved in African and Africanized *A. mellifera* populations repeatedly through natural selection across Africa, Latin America, and the Caribbean [35]. More localized, often smaller surviving populations have also been reported among European and European-derived honeybees [35,57,58]. Some beekeepers across Europe and North America have managed their colonies without mite control for many years [35], but the majority still rely on widespread acaricide use, which prevents host–vector–virus coevolution [59]. This creates a fundamental challenge: how to balance immediate colony protection to ensure survival with the need to maintain sufficient selection pressure for long-term resilience. Addressing this dilemma

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requires a more deliberate integration of evolutionary principles into honeybee management and breeding.

The way forward: Harnessing natural selection for resilient colonies

Here, we outline a long-term strategy that integrates evolutionary principles [59,60], comparative research across host–vector–virus systems, and practical management to accelerate the development of resilient honeybee populations capable of surviving mite infestations with minimal intervention (Figure 1).

Research priorities: Addressing fundamental knowledge gaps

A successful strategy must embrace the full complexity of the host–vector–virus system and move beyond single-trait explanations. We suggest addressing five fundamental research gaps:

1. Investigate mite evolution (Box 1).
2. Develop a deeper understanding of the spatiotemporal variation in this host–vector–virus system (Box 2).
3. Investigate the native hosts of *Varroa* spp. and *Tropilaelaps* spp. (Box 3).
4. Conduct comparative research between susceptible and resistant host populations.
5. Invest in large-scale studies with thousands of host colonies and global reach.

Additional complexity of the system is due to the high polyandry of host queens, which typically mate with more than 10 males [67], the colonies inherent buffering capacity [68], and the impact

Table 1. Honeybee, *Apis* spp., hosts and ectoparasitic mites, *Tropilaelaps* spp. and *Varroa* spp., with virus vector capacity

	Host species	Parasite species							
		Tropilaelaps clareae	*Tropilaelaps koenigerum*	*Tropilaelaps mercedesae*	*Tropilaelaps thaii*	*Varroa destructor*	*Varroa jacobsoni*	*Varroa rindereri*	*Varroa underwoodi*
Dwarf honeybees	*Apis andreniformis*								
	Apis florea	? [9]							
Giant honeybees	*Apis breviligula*	X [10], O							
	Apis dorsata	X [10], O	X [10], O	X [10], O				? [11]	
	Apis laboriosa		? [12]	? [12]	X [10], O				
Cavity nesting honeybees	*Apis cerana*	? [13]		X [10] (very rare)		X [14], O	X [14], O		X [14], O
	Apis koschevnikovi							X [14], O	
	Apis mellifera	X [10]		X [10]		X [14]	X [15]		? [16]
	Apis nigrocincta						X [16]		? [16]
	Apis nuluensis						? [17]		? [16]
Vector of honeybee viruses		–	–	V [18]	–	V [6,7]	V?	–	V [19]

It is apparent that there are major gaps in our knowledge of this one host genus and two parasitic mite genera systems. Especially the original hosts and the virus vector capacity deserve more attention. Also, it would be worthwhile investigating why *Varroa* have not expanded into open nesting species. Empty cell: no evidence of parasitism reported to date; O: original host species; V: mite is vector of honeybee viruses; V?: virus presence reported, but most likely belong to *V. destructor*; X: infestation confirmed, with mite reproduction; –: lack of data; ?: infestation not finally confirmed, successful reproduction missing.

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Box 1. Understanding pathogen evolution to support honeybee health

Understanding how viruses and their mite vectors adapt to new hosts, and how this shapes virulence, is key to reducing their long-term impact. Three research avenues remain undeveloped yet hold major promise for improving honeybee health: (1) retracing and tracking host shifts among *Apis* species, (2) characterizing phenotypic plasticity of hosts and parasites, and (3) assessing **local adaptations** across mites, bees, and viruses. Recent accessibility to high-quality mite genomes [21,22], genomics-derived tools [23–25], and standardized rearing protocols [14,26,27] provide new insights into the invasive success of parasitic mites.

Under what conditions and how do mites shift hosts?

Host shifts in *Varroa* and *Tropilaelaps* provide parallel systems to understand how parasitic mites shift hosts, establish themselves, and evolve under different ecological and management pressures. Genomics highlight that the global invasion of *V. destructor* did not originate from only two lineages (K1 and J1). Instead, multiple independent host shifts have now been detected across *V. destructor* and *V. jacobsoni* [7,20], sometimes involving large founding populations [20]. Low gene flow from *A. cerana*'s mites may have facilitated rapid adaptation to *A. mellifera* [20]. Yet, major questions remain: why does the more virulent K1 displace J1 lineages [28] and why has only a small subset of the mite diversity present on *A. cerana* successfully established on *A. mellifera* [7]? This suggests potentially intriguing limits in the unsuccessful mite lineages compared with those that successfully made the host jump. Still, the frequency, drivers, and constraints of host-shift events currently remain unresolved.

The missing genotype–phenotype link

Despite genomic divergence across mite populations, except for acaricide resistance [29] and mite oogenesis [30], most variants remain unlinked to functional traits. Comparative studies identify which mite lineages can reproduce on different hosts [31], but not the underlying mechanisms. Multiomics approaches now make it feasible to link genomic variation with reproduction, feeding, orientation, and vectoring capacity. However, progress depends on standardized phenotypic assays, which have long been restricted by the mites' obligate parasitic lifestyle and limited advances in artificial rearing [26,32].

Assessing local adaptation in the host–vector–virus system

Independent evolution of acaricide resistance [29], rapid divergence of mite and virus populations [20,33,34], and regional differences in the outcome of infestation [3,7] demonstrate that no universal scenario for host–vector–virus interactions exists. Colony damage depends on local host–vector–virus variants and management. Region-specific genomic and phenotypic assessments are essential to identify local adaptations and develop context-specific mitigation strategies. Therefore, coordinated global comparisons are overdue for sustainable honeybee health.

of resource variance (pollen, nectar, and propolis) that strongly influences colony dynamics and resilience [69]. More comparative research is needed between surviving and nonsurviving populations from this host–vector–virus perspective, drawing on both large-scale populations of

Box 2. The spatiotemporal mosaic of hosts, vectors, and viruses

The evolutionary trajectory of any species is affected by its interactions with the local environment [44]. This will inevitably result in local adaptations, creating a landscape of different interspecific relationships [44]. Variation between spatially distinct host populations is therefore expected at both small and large temporal scales [45]. Describing and understanding this spatial–temporal variation is key to understanding host–parasite relationships and how to favor such sustainable situations through beekeeping practices. So far, most studies conducted on naturally surviving *A. mellifera* colonies in the northern hemisphere have been conducted on one or only a few populations, typically at a few and distant time points. Research, therefore, currently lacks comparative studies that illustrate the variation in coevolutionary interactions across space and time and thus represents a snapshot of the strategies employed by hosts and parasites at a specific place and time. This, therefore, fails to describe the changing dynamics of this triad system. In the context of globalization and climatic change, the increasing movement of bees and parasites may disrupt host–vector–virus coevolution. Conversely, movements may also spread beneficial alleles, depending on the local context (see Scenario 2). Understanding when migration facilitates or constrains local adaptation is therefore critical, particularly during the early stages of host population recovery or resistance evolution. Addressing this question requires studies that explicitly track changes in population dynamics across space and time. These studies should follow the coevolutionary interaction across multiple generations, for example, by measuring mean values of adaptation at a series of time points during the experiment at biologically relevant intervals [46] or by employing repeated comparisons of the evolved players against nonevolved references, that is, time-shift experiments [47]. Leveraging global collaborative scientific networks (e.g., COLOSS), future research should examine spatially distinct populations simultaneously and over time. Coordinated, standardized sampling across regions and time points will quantify variability in coevolutionary outcomes and clarify how local adaptation shapes this and other host–vector–virus systems.

Glossary

Black box selection: in this method of selection, we do not know the mechanisms underlying the adaptations; hence, it is a black box into which we do not peer. Instead, we are selecting based on the 'visible' phenotypic outcome; in this case, low mite infestation levels and colony survival.

Drones: the male haplotype sexuals in a honeybee colony, which are raised from unfertilized eggs and thus inherit chromosomes only from their mother.

Integrated pest management: an ecologically based, multidisciplinary strategy that combines biological, cultural, physical, and chemical control methods to manage pests in the most effective, economically viable, and environmentally sustainable way.

Local adaptation: the process by which honeybee populations evolve genetic, behavioral, or metabolic traits that enhance their survival and performance in response to the specific environmental conditions of their local habitat.

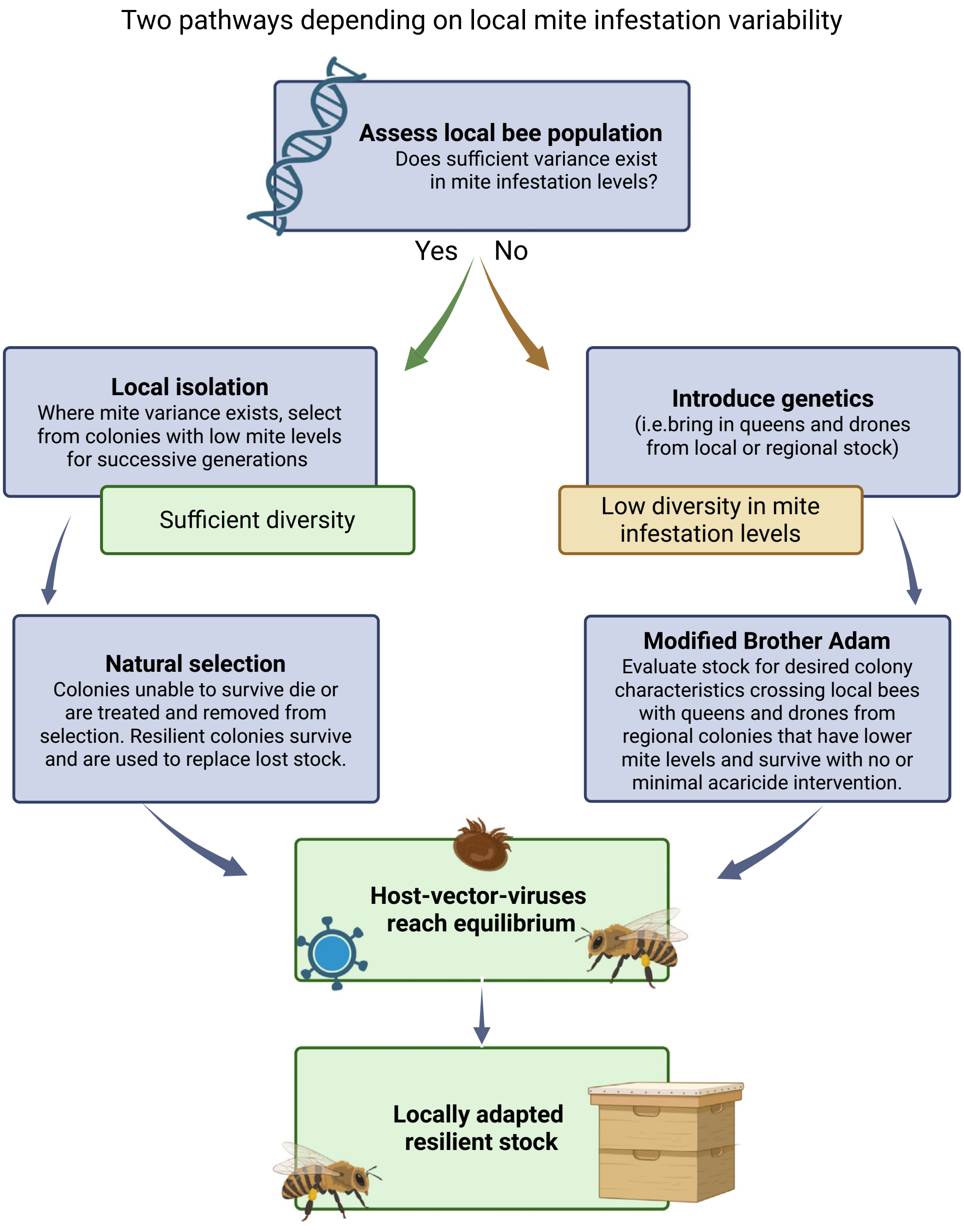
Mite monitoring: the systematic process of regularly assessing and quantifying the population levels of mites (such as *V. destructor* in beekeeping or spider mites in agriculture) within a specific environment.

Natural selection: the process by which honeybee populations develop resistance to mites through the survival and reproduction of individuals with traits that enhance survival against parasitic mite burdens. Over time, these adaptive traits become more common in the population, improving the colonies' ability to cope with the parasitic threat.

Resistance: we define resistance as the ability of honeybee colonies to minimize the growth of mite populations and survive mite infestations without acaricide treatments. Colonies that have resistance traits will, therefore, have lower mite levels compared to nonresistant colonies. This is in contrast to tolerant colonies that survive despite high mite infestations, though they often do not thrive. We do not advocate for tolerance, as these colonies can harbor high Varroa and viral loads, which can be shared with other bee populations through plant or bee interactions.

Triad: here we refer to the complex interactions and evolutionary dynamics of the host–vector–virus systems that are established when *V. destructor* or

T. mercedesae parasitize honeybees and vector a suite of viruses.



Trends in Parasitology

Figure 1. Two pathways to enhance natural selection. On the left side, the population has variance in mite infestation levels across colonies, suggesting a sufficient basis for selection and can enter directly into Darwinian black box 2.0 selection (see Box 4), where colonies are only permitted to produce drones and queens when *V. destructor* infestations are low, while colonies with high infestation levels are requeened and drone production is limited. Thus, the colonies reach an equilibrium between the host–vector–viruses, though the mechanisms remain unknown. On the right-hand side, we have populations that do not have enough variance in mite infestations, and thus, importations from diverse populations are required. Local or regional queens and drones from surviving populations are integrated into existing populations, which are backcrossed and/or hybridized to select for natural resistance. Then, a similar selection program can be continued as on the left-hand side.

naturally adapted hosts [35] and smaller 'islands' of resistance [58,59]. These populations should not be treated as discrete categories but as points along a continuum of adaptation. Comparing their shared and divergent traits will reveal whether some mechanisms are essential for resistance

Box 3. The need to study the natural hosts

Studying the natural hosts of parasites that have shifted to *A. mellifera* is crucial to better understand how these host–parasite systems have reached long-term coevolutionary equilibria, in contrast to the collapse-prone parasitism seen on the novel host. In their natural hosts, the parasite populations are regulated by host individual and colony-level traits (Figure I). In *A. cerana*, reproduction of *Varroa* mites is halted by the mite's inability to reproduce in worker brood [63], most likely due to a combination of factors, such as altruistic suicide of the host brood [64], hygienic behavior by the attending nurse bees, and missing signals from the brood that trigger reproduction. When *V. destructor* mites from *A. mellifera* colonies are inserted into *A. cerana* worker brood cells, the larvae and pupae die, thereby arresting parasite reproduction. Thus, *V. destructor* reproduction in *A. cerana* is limited to seasonally available drone brood, and when multiple foundress mites invade a single cell, the drones often fail to emerge, trapping the mites in the cell. Efficient allogrooming by *A. cerana* workers also reduces mite survival, but see a recent review [65].

In giant honeybees, several colony-level traits halt parasite growth. Seasonal migratory behavior produces brood breaks [66], which stop mite reproduction. When parasite populations increase dramatically, *A. dorsata* abscond, leaving all brood parasites and brood diseases behind on the abandoned comb. *A. dorsata* are excellent groomers, and thus, *Tropilaelaps* spp. will often attach to adult bees near the wing buds, where they are more difficult for the bees to reach but are also more susceptible to falling off. Unlike *V. destructor*, which shows a clear preference for drone brood, *Tropilaelaps* spp. parasitize worker and drone brood in similar proportions. Understanding these natural host–vector systems can reveal important mechanisms that could be utilized in breeding schemes or management (see the main text).

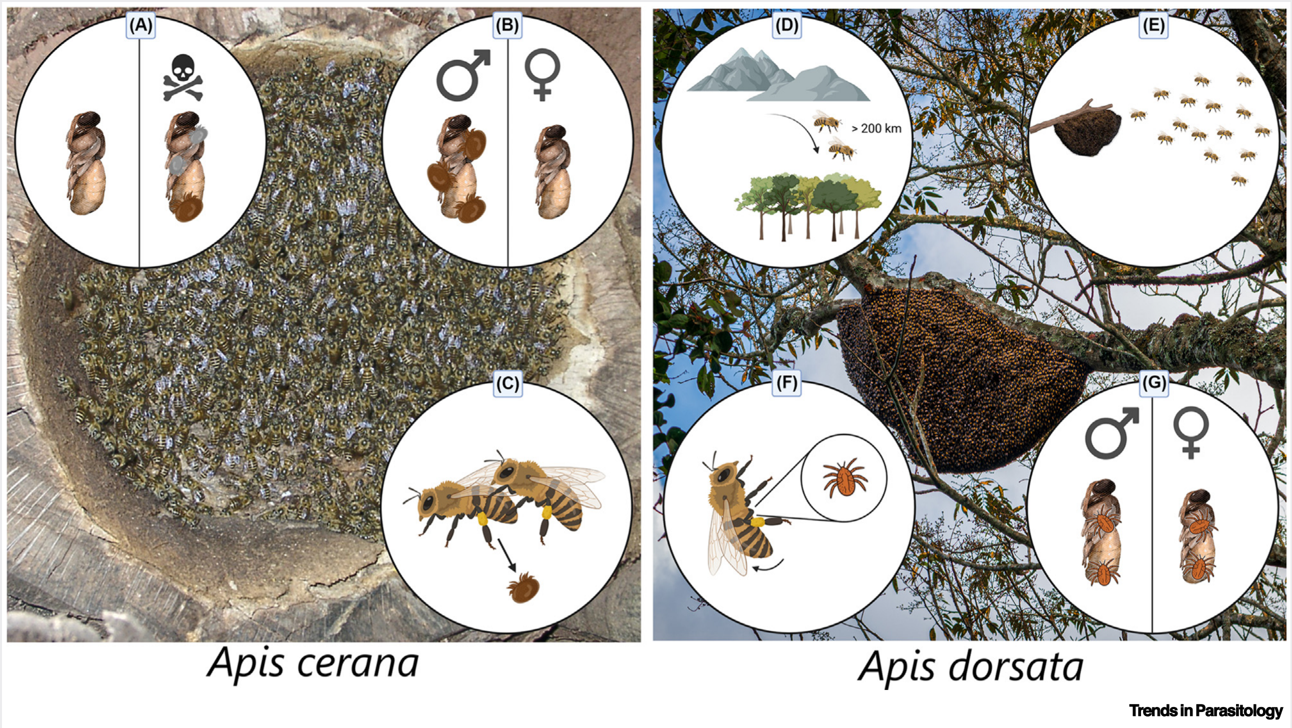


Figure I. Native host adaptations. The eastern honeybee, *A. cerana* (left), is the original host of *V. destructor* and has evolved several strategies to minimize growth of this parasite, including nonreproduction in worker brood and (A) social apoptosis, forcing *V. destructor* to reproduce in (B) seasonally available drone brood. The bees also engage in successful (C) allogrooming. The giant honeybee, *A. dorsata* (right) engages in (D) seasonal migrations and when parasite populations rise dramatically, they will (E) abscond. These bees are excellent self-groomers (F). Both (G) worker and drone brood are equally attractive to *Tropilaelaps* spp., a strong contrast to *Varroa* spp.

and others are more context-dependent. Current studies typically involve a restricted number of colonies, which limits our understanding of the diversity within these host–vector–virus systems. Addressing these challenges requires coordinated, global efforts that generate comparable datasets involving thousands of colonies to establish a robust baseline of host–parasite dynamics. Such collaborative projects would permit simultaneous **mite monitoring** and experiments across space and time using standard protocols (COLOSS *BEEBOOK*[i]) to disentangle the complexity of these host–vector–virus systems. Such a holistic, broad approach would help us to better understand the prevalence of mechanisms (i.e., rare vs. common vs. universal) and their relative importance for local colony survival via a host–vector–virus triad coevolutionary equilibrium.

The importance of studying the natural hosts

Studying the natural hosts of *Varroa* spp. and *Tropilaelaps* spp. is crucial because these associations represent long-term coevolutionary equilibria, rather than the collapse-prone parasitization seen when they shifted to the naïve host *A. mellifera* (Box 3). Unfortunately, detailed studies on the natural hosts remain sparse; for example, the spatial–temporal variation (Box 2) within these natural host–parasite systems is poorly understood. This hampers the development of evolution-informed management that anticipates mite adaptations rather than reacting after colony-level damage occurs. Filling this gap by characterizing parasite life history, host resistance traits, and host–vector–virus interactions in natural host systems would provide critical insights for sustainable control and improve risk assessment for future host shifts.

Where have mites shifted hosts, and where has the natural adaptation of the honeybee succeeded in achieving triad equilibrium?

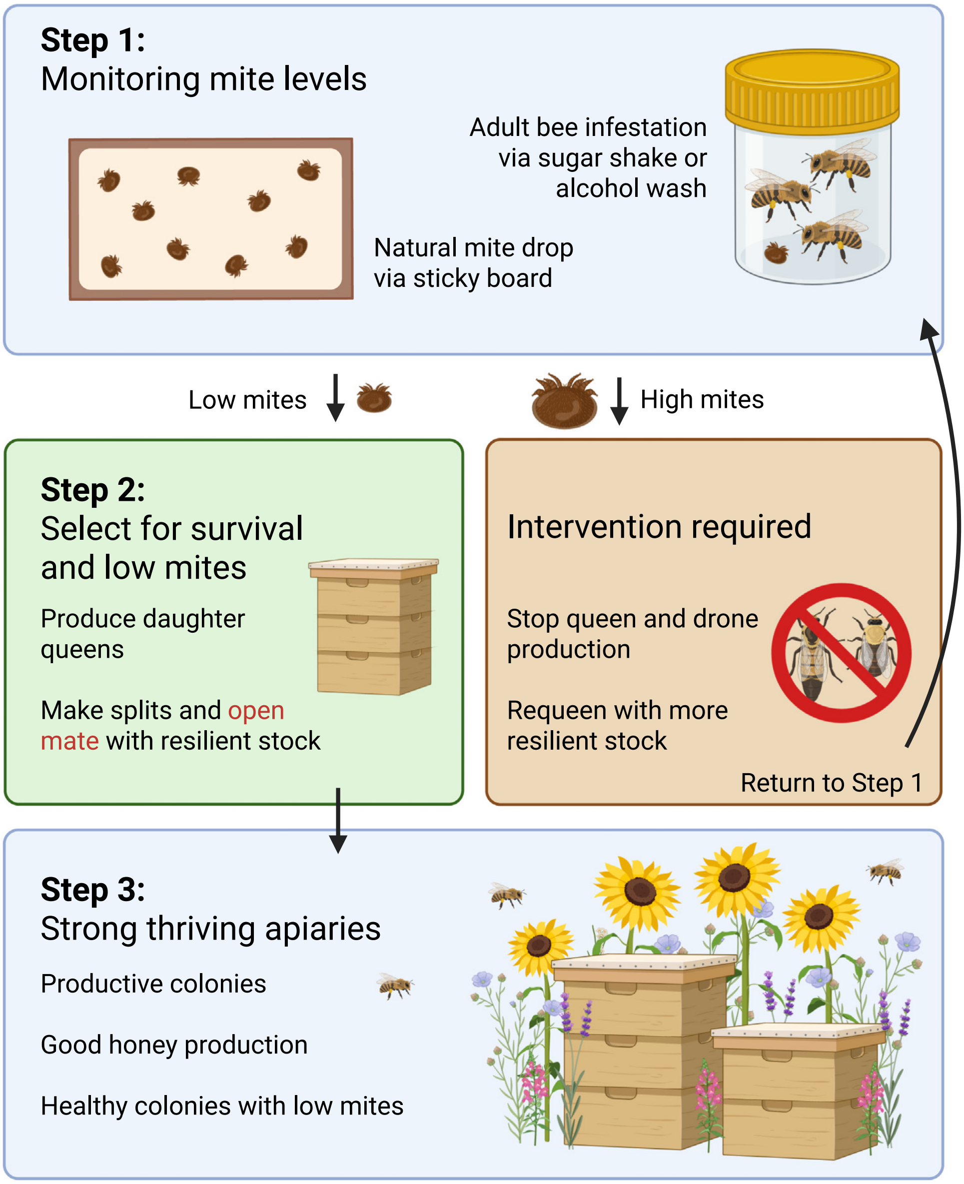
In Asia, beekeepers often keep western and eastern honeybee colonies in the same apiaries [70], thereby promoting interspecific parasite transmission. Sometimes these new hosts evolve successful adaptations or possess pre-adaptations that minimize mite population growth. Interestingly, it appears as though *T. mercedesae* can only rarely reproduce in the brood of the novel host *A. cerana* [12]. It is unknown whether the same mechanisms are responsible for suppressing parasite reproduction from *Varroa* spp. and *Tropilaelaps* spp.

Comparisons both within and across multiple natural and new honeybee hosts, mite species, and populations will enable a better mechanistic understanding of host–vector–virus coevolution and successful host shifts, as well as promote field action (see Scenario 2).

Selection pathways for adaptations to mites

Scenario 1: Darwinian black box selection 2.0. In several regions, managed populations have evolved resistance through a process that can be described as '**black box selection**' [71], where colonies are not treated against mites and thus only those capable of surviving contribute to the next generation [35,42]. However, in many regions, not treating colonies would lead to massive losses. Thus, we suggest using integrated treatments to minimize colony losses during the process, excluding susceptible colonies from reproducing (Figure 2). The critical first step is, therefore, to determine whether the local population has significant variation in mite infestation levels as a basis for selection (Figure 1). This can be achieved by monitoring mite infestation levels across large numbers of colonies over the beekeeping season. If some colonies repeatedly display lower mite infestations in comparison to others, there is probably a genetic basis for selection available. However, if infestation levels show no variance, a modified approach may be required (see Scenario 2).

Selection should be applied at the colony level, focusing on survival and low mite populations. Considering the endless variation over space and time, this appears to be the way forward rather than targeting individual traits. The practical endpoint of such selection is simple: colonies that survive under any given beekeeping management regime with no or minimal acaricides and lower parasite levels become the genetic basis for future colonies. Daughter queens from these colonies can then be used to replace queens in colonies with higher infestation levels, thereby increasing the frequency of resistance traits within the population. In addition, mating guidance is required [72]; for example, stimulating drone production in colonies with lower mite populations (e.g., via the introduction of drone brood comb) will help disseminate adaptations through open mating in surrounding populations. Furthermore, colonies with high mite infestations should be treated to minimize their impact on surrounding colonies and prevent them from producing reproductives, for example, by removing drone comb and queen cells. Such interventions turn 'mite



Trends in Parasitology

Figure 2. The road to success. Beekeepers monitor mite levels and colony survival. They should produce splits, nucleus colonies, and daughter queens from the colonies with low mite levels. Any colonies with high mite levels should be requeened with more resilient stock at the earliest opportunity and prevented from producing reproductives (queens and drones). They should also be treated to minimize mite pressure on other colonies and to keep the colonies alive. Once requeened with more resilient stock, they should re-enter Step 1, monitoring mite levels. By continuously breeding from the colonies with the lowest mite numbers, beekeepers can wean themselves off the chemical treadmill and eventually reach a healthy, sustainable apiary that no longer needs mite treatments.

bombs' into eunuchs, hindering highly infested colonies from spreading their genes [73]. This approach has already been successfully used [74] and by treating susceptible colonies, it minimizes unnecessary colony losses, ensuring food security and livelihoods can be maintained while still promoting the spread of resilience.

Scenario 2: Brother Adam 2.0, transfer of resistance from one apiary to enhance resistance in another. Natural selection can only succeed if the underlying genetic variation for resistance already exists within the population (Figure 1). The key to success is, therefore, sufficient variation in mite infestation across colonies. If mite infestations are high but with too little variance to enable selection, resistance traits need to be introduced from nearby local populations that have lower mite populations. Such an approach would combine natural selection with controlled integration of genes from surviving local bee populations with low mite infestation levels and low colony mortality. The key difference from the original approach of Brother Adam [61] is that only local or regional source populations are used. This would enable us to integrate missing components into susceptible honeybee populations from nearby resilient ones without interrupting local adaptations. However, an enhanced mechanistic understanding of host resilience will be required (see 'Addressing fundamental knowledge gaps' section). For this strategy to gain acceptance among beekeepers, it must integrate selection for desirable apicultural traits such as productivity, gentleness, and manageable swarming behavior. Such selection for resilience and colony productivity proved successful in Norway [57].

Implementation in beekeeping: Integrated pest management—An interim solution

Large colony losses destroy beekeeping operations, threaten livelihoods, and imperil food production through lost pollination services. We thus need an interim solution that allows colonies to continue to survive while coevolving with mites and the viruses they transmit. This will require training beekeepers to implement selection according to scenarios 1 or 2 outlined earlier (Box 4). Management solutions must include regular mite monitoring to make appropriate intervention decisions. Effective management strategies use **integrated pest management** to treat only when specific thresholds have been exceeded, rotate chemicals to slow the evolution of miticide resistance [29], and employ more biotechnical methods. Large-scale beekeepers who monitor mites in only a subset of colonies may conduct selection only in that subset and should minimize the production of reproductives (drones and queens) from their unmonitored colonies. To protect their colonies, beekeepers must monitor the efficacy of treatments.

A shift in colony management away from traditional acaricide treatment needs to respect beekeepers by understanding their needs, current practices, and beliefs. This includes

Box 4. Darwinian beekeeping

Darwinian beekeeping is an evolutionary approach to apiculture that promotes honeybee colony health by fostering natural selection [59,61,62]. This approach goes far beyond using colony survival and low mite levels as selection criteria to enhance resilience to mite infestations. It requires understanding which methods of beekeeping are likely to interfere with natural selection, thereby limiting local adaptations [59]. By minimizing or adapting human intervention, beekeepers allow environmental pressures, including parasites and climate change, to shape colony reproduction and survival. Core practices include the use of local stock, allowing for natural queen and drone rearing in colonies, open mating, and providing adequate housing and food after honey harvest [59,62]. Darwinian beekeeping shifts the focus of apiculture from maximizing short-term productivity to ensuring long-term sustainability and ecological balance. By aligning beekeeping practices with evolutionary principles, it offers a promising strategy to mitigate widespread honeybee colony losses, ultimately supporting the development of self-sustaining honeybee populations. It is obvious that large-scale commercial beekeeping operations cannot adopt all aspects of Darwinian beekeeping but could at least focus on those that can be integrated (e.g., natural queen rearing and open mating). Furthermore, using principles of natural selection will not solve all the problems currently impacting apiculture, as the current methods of keeping bees also create new problems, especially by importing and exporting bees to distant locations, which disrupts local adaptations. Therefore, despite intense breeding over centuries, natural selection appears to be much more relevant for the health of managed *A. mellifera* colonies than previously thought [59], because it enables colonies to better cope with whatever challenges may arise in the future, for example, climate change or novel invasive species. It therefore appears that sustainable solutions for the apicultural sector can only be achieved by taking advantage of natural selection and not by attempting to limit it. Darwinian beekeeping appears to be an important strategy for promoting colony health and well-being beyond the suggested scenarios for surviving mite infestations.

supporting strategies that permit economic security, offering a variety of clear guidelines suited to the different types [75] and acknowledging that change requires time to break old habits. The needs of commercial beekeepers, whose livelihood depends on their managed livestock, differ greatly from those of hobby beekeepers. They need management strategies that are practical, cost-efficient, and effective, as the cost of treatment and labor, along with impacts on colony survival, are the driving factors influencing their management decisions. They may be more interested in purchasing verified resilient stock than selecting such stock within their own operations.

Despite their very different outlooks and needs, honeybees from hobbyists and commercial operators have the potential to interact when kept within the flight radius of each other, exchanging pathogens and parasites during encounters, as well as interbreeding due to mating flights. To integrate these human and biological factors into current and future mite control strategies, trusted and open knowledge transfer between researchers and beekeepers is needed, guided and facilitated by extension, advisory services, and social science experts who understand how farming behaviors can be changed [76]. Initial success among small-scale beekeepers could drive adoption by larger operations.

Concluding remarks

In many regions of the world where *A. mellifera* beekeeping management is limited, natural selection has produced locally stable host–vector–virus systems. However, in many managed systems, these equilibria have not yet been achieved, in part due to the complex and often conflicting influences of the environment and commercial beekeeping. In this context, integrating natural selection into beekeeping and breeding represents a necessary and sustainable path toward long-term resilience and prepares us for new threats, for example, *Tropilaelaps* spp.

To date, breeding efforts that emphasize single traits or specific colony-level responses to these mites have yielded important insights but have not translated into widespread colony survival. Such selection is often cost-intensive to conduct, and simpler solutions are needed. Evidence from naturally varroa-surviving populations across diverse regions indicates that resistance can arise through multiple, distinct pathways. This pluralism highlights a critical need for a concerted effort to understand the mechanisms underlying resistance (see Outstanding questions), including how hosts, mite vectors, and viruses interact across environments. It appears, therefore, overdue to help beekeepers—for example, to ease mite diagnostics for commercial beekeepers using automated and affordable systems. Furthermore, it is high time to conduct global joint monitoring and experiments with standardized research methods (*BEEBOOK*[i]) and, ideally, tens of thousands of colonies to better understand this complex host–vector–virus interface. Such mechanistic knowledge is critical for predicting the stability of resistance, integrating survivor traits into susceptible apiaries, and preparing managed pollinators for future and yet unknown challenges.

Effective selection does not require full knowledge of the underlying mechanisms. Thus, we advocate for a complementary Darwinian ‘black box’ approach that prioritizes colony-level phenotypes: colony survival coupled with low mite populations, regardless of the underpinnings. This selection framework leverages naturally occurring variation in mite infestation as a robust and practical basis for selection, while remaining agnostic to the specific traits involved. If variability is locally insufficient, the introduction of regional stock from colonies with low mite levels should occur to speed up selection for regionally adapted stock. We caution against the long-distance import–export of ‘resistant’ bees, as this will disrupt local adaptations in the interacting host–

Outstanding questions

What are the fundamental mechanisms of host switches by parasites, and why do some switches seem to be impossible?

What are the fundamental mechanisms driving the host–vector–virus, beekeeper, and environment interface?

What is the prevalence of underlying mechanisms (i.e., rare vs. common vs. universal) and their relative importance for local colony survival?

How do vectoring mites alter virus virulence, load, and transmission within and between colonies?

Why are *Varroa destructor*-resistant eastern honeybees (*Apis cerana*) also resistant to *Tropilaelaps* spp., although they are not the native host for this parasite?

Are there colony productivity trade-offs when colonies are resistant to mites?

Can we model the potential of saturating an area with reproductives to select for resistance?

vector–virus triad. The export of 'resistant' bees to exotic places should be avoided, as such imports can bring unexpected consequences for bee health.

This Darwinian beekeeping and breeding strategy, which emphasizes the importance of natural selection for colony reproduction and survival, puts beekeepers and their needs front and center (e.g., maintenance of desirable colony traits), providing a feasible pathway to reduce reliance on chemical treatments while limiting unsustainable colony losses (Box 4). The key is to prevent colonies with high mite infestations from contributing to the next generation via queens and drones. Although implementation in open mating systems presents challenges, aligning breeding practices with selection pressures at the colony level offers a realistic and scalable route toward sustainable management. In general, it appears overdue to harness the intuitive knowledge of beekeepers by integrating their in-depth experience into our understanding of colony health. Therefore, we call for more collaborative future interactions between beekeepers and bee scientists globally [e.g., via the largest global beekeeping organizations (Apimondia[ii]) and bee research organizations (COLOSS[iii])]. Harnessing both mechanistic understanding and the power of natural selection will safeguard managed and nonmanaged honeybee colonies against future challenges beyond the present mite challenges. Ultimately, coordinated efforts to disentangle the fundamental interactions within the host–vector–virus system, combined with natural selection, will open exciting new avenues for research in parasitology.

Author contributions

All authors contributed to writing and editing the manuscript.

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Declaration of interests

The authors declare no competing interests.

Resources

[i] https://coloss.org/activities/beebook/

[ii] https://apimondia.org/

[iii] https://coloss.org/

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