

1 **Trees and insectshave microbiomes: consequences for forest health and** 2 **management**

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30**Abstract**

31**Purpose of review**

32Forest research has shown for a long time that microorganisms influence tree-insect
33interactions, but the complexity of microbial communities, as well as the holobiont nature
34of both trees and insect herbivores, have only recently been taken fully into account by
35forest entomologists and ecologists. In this article, we review recent findings on the effects
36of tree-insect-microbiome interactions on the health of tree individuals and discuss
37whether and how knowledge about tree and insect microbiomes could be integrated into
38forest health management strategies. We then examine the effects tree-insect-microbiome
39interactions on forest biodiversity and regeneration, highlighting gaps in our knowledge at
40the ecosystem scale.

41**Recent findings**

42Multiple studies show that herbivore damage in forest ecosystems is clearly influenced by
43tripartite interactions between trees, insects and their microbiomes. Recent research on the
44plant microbiome indicates that microbiomes of planted trees could be managed at several
45stages of production, from seed orchards to mature forests, to improve the resistance of
46forest plantations to insect pests. Therefore, the tree microbiome could potentially be fully
47integrated into forest health management strategies.

48**Summary**

49To achieve this aim, future studies will have to combine, as has long been done in forest
50research, holistic goals with reductionist approaches. Efforts should be made to improve
51our understanding of how microbial fluxes between trees and insects determine the health
52of forest ecosystems, and to decipher the underlying mechanisms, through the development
53of experimental systems in which microbial communities can be manipulated. Knowledge
54about tree-insect-microbiome interactions should then be integrated into spatial models of
55forest dynamics to move from small-scale mechanisms to forest ecosystem-scale
56predictions.

57**Keywords (6):**

58forest tree, insect herbivore, microbial community, ecological interaction, fungal endophyte,
59insect symbiont

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64Introduction

65The disturbances to forest ecosystems caused by insect herbivores are of major ecological
66and economic concern, and are exacerbated by climate change and introductions of exotic
67species [1, 2]. For instance, a mountain pine beetle (*Dendroctonus ponderosae*) outbreak
68resulted in the loss of more than 700 million m³ of timber over 18 million ha of pine forest
69in British Columbia between 1999 and 2011 [3]. Insect herbivores can attack all tree
70organs, including leaves or needles (e.g., the Gypsy moth, *Lymantria dispar*), wood (the
71Asian longhorned beetle, *Anoplophora glabripennis*), seeds (the Western conifer seed bug,
72*Leptoglossus occidentalis*), bark (the pine weevil, *Hylobius abietis*) and roots (common
73cockchafer, *Melolontha melolontha*). The damage they cause is as diverse as the insect
74species themselves, ranging from a decrease in the aesthetic value of trees (e.g., brown
75patches due to the horse chestnut leaf miner *Cameraria orchidella*) to slower tree growth
76(e.g. *L. dispar*), or even tree death (*A. glabripennis*) and impaired forest regeneration (*H.*
77*abietis*). Of course, not all insect herbivores are pests, but even background insect herbivory
78can cause a significant loss of growth in forests [4].

79Like all animals, insect herbivores are holobionts [5]. They have established a wide
80diversity of partnerships with all lineages of the microbial world: bacteria and fungi, but
81also, to a lesser extent, microscopic metazoans, such as nematodes. It has long been
82established that insect-associated microorganisms fulfil several ecological functions in
83forest insects, including chemical communication among conspecific individuals [6], the

84production of essential digestive enzymes [7] or the mediation of interactions with the third
85trophic level [8]. These associations between insects and microorganisms vary in their
86persistence. Some are long-term associations in which the microorganisms are widespread
87in the individual insects within a population, and often shared between parents and
88offspring. These persistent microbial partners, which are often found in specific parts of
89insect bodies, belong to the core microbiota and are considered as symbionts. They may be
90acquired repeatedly from the environment (*e.g.* most gut symbionts) or transmitted
91vertically through the gametes, egg smearing, coprophagy or adult-nymph trophylaxis. By
92contrast, the transient microbiota is assimilated during insect feeding, or is co-opted from
93the plant [9] or the soil [10]. It travels opportunistically with the insect, in its gut or
94mouthparts or on its exoskeleton, and there may be some overlap between its constituents
95and those of the tree microbiota.

96The tree and its microbiota also form a holobiont [5]. Trees have a long history of co-
97evolution with microorganisms, which proved a key asset in the colonisation of land by
98plants [11]. The microorganisms colonising the various organs of trees are highly diverse
99and include bacteria, archaea, fungi, oomycetes and nematodes. These microorganisms are
100acquired horizontally from the surrounding environment (soil, atmosphere) and by vertical
101transmission from the mother tree to its progeny via seeds [12, 13]. The plant microbiota is
102generally defined as the microbial community living on the surface of aboveground tissues
103(the phyllosphere; [14]), belowground tissues (rhizosphere; [15]), seeds (spermosphere;
104[13]), or living within the internal tissues of the plant (endosphere; [16]). The plant
105microbiome is a broader concept. It contains the microbiota (community of living
106microorganisms), the whole spectrum of molecules constitutive of or produced by the

107microorganisms, and the mobile genetic elements (e.g., transposons, viruses) and relic DNA
108embedded in the microbial environment [17]. Some members of the plant microbiota have
109neutral or detrimental effects on their host plant, whereas others are crucial to the plant's
110fitness because their ecological functions extend the ability of the plant to cope with
111environmental stresses, including insect herbivores [18, 19].

112The success of insect herbivores and the damage they cause to trees and forests are
113therefore influenced by a large array of direct and indirect interactions with
114microorganisms from both the insect and tree microbiomes. Multiple studies have shown
115and assessed the influence of microorganisms on tree-insect interactions [reviewed in 20-
11622], but the complexity of microbial communities, as well as the holobiont nature of both
117trees and insect herbivores, have only recently been taken fully into account by forest
118entomologists and ecologists. Here, we present and discuss the consequences of these
119multiple and reciprocal interactions in terms of herbivory. We first review recent findings
120on the microbial groups playing a key role in tree resistance to herbivory and in insect
121feeding behaviour and performance, and highlight the influence on tree health of microbial
122fluxes between the tree and insect holobionts. We then discuss whether and how tree and
123insect microbiomes could be integrated into forest health management strategies. Finally,
124we scale the processes up to forest level and speculate on the consequences of tree-insect-
125microbiome interactions for forest regeneration and biodiversity.

126Part 1 - Tree-insect-microbiome interactions modulate tree health

127The microbiomes of trees and insects form interconnected microbial communities that
128influence the output of tree-herbivore interactions (Fig. 1). Some of the key players in the

129tree microbiota confer resistance to herbivory (section 1.1), whereas the insect microbiome
130enhances the feeding capacities of insects (section 1.2). Finally, direct exchanges of
131microorganisms between insect and tree holobionts (section 1.3) modulate insect
132performance and tree health, defined here as the ability of the individual tree to cope with
133environmental stressors, including insect pests (see also [23] for other definitions of plant
134health).

1351.1. The tree microbiome protects trees against herbivores

136The above- and belowground parts of plants are associated with microorganisms that
137confer resistance to herbivory [21, 24]. Some of these microorganisms act directly on insect
138herbivores, as pathogens or through production of insecticidal toxins. Others act indirectly,
139by influencing plant growth, priming the plant immune system, or inducing resistance in
140plant hosts [24]. Induced systemic resistance involves several phytohormones, including
141jasmonic acid, salicylic acid and ethylene, and can be triggered by both bacteria and fungi
142[24, 25]. Microorganisms also affect the emission of volatile organic compounds from plants
143in response to herbivory (herbivore-induced plant volatiles), to attract predators or
144parasitoids [26, 27].

145Fungal entomopathogens are among the most widely studied protective microorganisms.
146These insect pathogens, which are considered to be natural regulators of insect outbreaks
147in forests, live mostly in the soil [28], but some can also naturally colonise aboveground
148plant organs [29]. For example, fungal entomopathogens have been found as endophytes in
149several tree species, including cocoa (*Theobroma cacao*), ironwood (*Carpinus caroliniana*),
150English oak (*Quercus robur*), European beech (*Fagus sylvatica*), western white pine (*Pinus*

151*monticola*) and Chinese yew (*Taxus chinensis*) [29]. Fungal entomopathogens can be found
152in many phylogenetic groups of fungi [30], but most of those living as plant endophytes
153belong to the order Hypocreales (Ascomycetes) [21, 29], with *Beauveria bassiana* the most
154widely studied species [31]. Hypocreales fungi can infect their insect host through the
155cuticle, causing its death by growing in the internal tissues of the insect and releasing
156toxins; they then thrive by growing on the cadaver before sporulating [28]. The presence of
157fungal entomopathogens in plant tissues generally deters insect herbivores and reduces
158their performance, suggesting that these fungi also have indirect detrimental effects on
159insects mediated by systemic chemical changes in the plant [21].

160In addition to fungal entomopathogens, plant leaves can harbour other fungal endophytes
161that are not insect pathogens, but protect the plant against herbivory. The protective role of
162these fungi, that live within plant tissues at least part of their lifecycle and without causing
163apparent harm or disease to their host [32], has been known for a long time [33]. In the
1641990's, it has been demonstrated for instance that the speckled gall wasp (*Besbicus*
165*mirabilis*) avoids high-endophyte space at the within-leaf scale in Oregon white oak
166(*Quercus garryana*) [34], and that endophytes can indirectly kill these gall-forming insects
167by infecting the gall tissue and cutting off nutrient supply from the leaf to the gall [35]. Such
168protective effect of endophytes against herbivores was however not detected in several
169other biological systems [36-38]. Non-entomopathogenic fungal endophytes can also
170reduce herbivory by producing insecticidal toxins, and/or inducing the production of
171secondary metabolites by plants [21]. These endophytes may also help plants to tolerate
172other stressors and promote growth [39]. Some of these non-entomopathogenic fungal
173endophytes, and the metabolites they produce, are well-described in forest trees [40, 41].

174For instance, the needle endophyte *Phialocephala scopiformis* (Helotiales), isolated from
175white spruce (*Picea glauca*), inhibits the growth of eastern spruce budworm (*Choristoneura*
176*fumiferana*) and several other conifer pests, by producing rugulosin and other toxic
177compounds [41, 42].

178Phyllosphere fungal phytopathogens and bacteria also modulate herbivory levels. A recent
179meta-analysis suggested that foliar infection with fungal pathogens generally reduces
180herbivory, and that negative effects of plant pathogens on herbivore performance tend to be
181stronger for biotrophic than for necrotrophic pathogens [20]. Similarly, phyllosphere
182bacteria can either increase or decrease herbivory levels, by altering plant defence
183pathways and volatile organic compound emissions. For instance, the experimental
184infection of leaves of a wild annual plant with *Pseudomonas* spp. increased herbivory by a
185chewing herbivore, by modifying female oviposition behaviour and larval feeding behaviour
186[43]. Similarly, the inoculation of leaves with *P. syringae* increased herbivory in *Arabidopsis*
187*thaliana* leaves by suppressing the production of reactive oxygen species, a component of
188first-line immunity in plants [44]. Conversely, the inoculation of *A. thaliana* leaves with
189bacteria from the genera *Pseudomonas*, *Xanthomonas* and *Bacillus* increased plant
190performance under herbivory [45]. The inoculation of *Phaseolus vulgaris* leaves with *P.*
191*syringae* was found to alter volatile organic compound emission and repel herbivores [46].
192However, such examples are limited to annual plants. Similar mechanisms are likely to
193operate in trees too, but experimental evidence is still lacking.

194Insect herbivory is also strongly influenced by belowground microorganisms [24, 47].
195Indeed, root mutualists (endophytic fungi, mycorrhizal fungi, rhizobacteria and rhizobia)
196control the performance of aboveground insect herbivores through effects on plant growth

197on the one hand, and plant tolerance and defence on the other [48]. Mycorrhizal fungi and
198plant growth-promoting rhizobacteria can increase growth of plant tissue and/or its
199nutritional value, which benefits insect herbivores. Conversely, they can increase plant
200tolerance to herbivory by facilitating tissue regrowth, and plant resistance to herbivory by
201inducing systemic resistance [47, 49, 50]. Actually, these interactions between belowground
202microorganisms and aboveground insect herbivores are even more complex because
203insects have feedback effects on the colonization of roots by microorganisms. For example,
204early studies in pinyon pine (*Pinus edulis*) revealed that ectomycorrhizal colonization was
205significantly lower in trees susceptible to herbivory by two insect species (*Dioryctria*
206*albovittella* and *Matsucoccus acalyptus*). In addition, the removal of the insects from
207susceptible trees resulted in a rebound of mycorrhizal colonization [51, 52, 53].

208Together, these studies show that tree-associated microorganisms can modulate herbivory
209in forest ecosystems. The underlying mechanisms (e.g., the production of insecticidal
210toxins) have been deciphered for some microbial taxa, but there is a need for more
211experimental approaches. Moreover, future research on microbe-mediated resistance to
212herbivory should be scaled up to community level, by considering all the micro-organisms
213potentially conferring resistance to herbivory, their mutual interactions and their joint
214effects on plant immunity together. This should make it possible to identify the properties
215of microbial communities and microbial networks conferring resistance to herbivory.

2161.2. The insect microbiome contributes to herbivory

217Herbivorous insects face many challenges when it comes to feeding: they have to degrade
218plant tissue, palliate nutrient deficiencies and resist the effects of plant-specialised

219metabolites. This is particularly true for forest insects, which feed on or tunnel through
220woody parts of the plant, as most insects do not synthesise the enzymes required to break
221down lignins or cellulose [54]. The insect microbiome thus plays a key role in the feeding
222process.

223Some microorganisms are essential to herbivores, with which they form obligate
224symbioses. For example, the Asian longhorned beetle (*Anoplophora glabripennis*) has
225evolved a fungal symbiosis in the gut to allow digestion of living woody tissue [55]. Wood
226wasps [56], bark beetles and ambrosia beetles [57, 58] are also dependent on fungi for their
227nutrition. They carry fungi in specific organs on their exoskeleton and inject them into host
228trees. The fungal symbionts enrich the insect diet by providing mycelial material, which
229supplies nitrogen and sterols, and may be the only source of food, in some cases [59]. These
230fungal mutualists are increasingly recognised as playing multiple roles in addition to
231facilitating nutrition. They can degrade plant defence compounds [60], as in the yeasts
232associated with the European spruce bark beetle, *Ips typographus*, which break down the
233stilbene defence compounds of the host tree (*Picea sp.*) [61]. They can also inhibit the
234growth of insect pathogens [62]. In addition to fungal symbioses, which are well-
235represented in forest ecosystems, associations with other microorganisms enable insect
236herbivores to overcome nutritional deficiencies of their food sources. For instance, all
237members of the Hemiptera, which feed exclusively on tree sap (xylem or phloem), are
238dependent on bacteria, generally sheltered in modified insect cells, for the synthesis of
239essential amino acids and vitamins lacking in their diet [63]. These essential nutritional
240partners are probably derived from the plant microbiota and have been co-opted as faithful
241allies by herbivorous insects over the course of evolution. Fungal mutualists probably

242evolved from fungi ingested by insects [64, 65], and phylogenetic reconstructions suggest
243that bacterial symbionts providing nutritional support are derived from phytopathogens
244[66, 67].

245Many insect-associated microorganisms are not obligate long-term symbionts as described
246above, but nevertheless facilitate herbivory by contributing to digestion, participating in
247detoxifying plant allelochemicals, and providing weapons against natural enemies. Multiple
248studies have demonstrated that non-obligate microorganisms present in the insect
249digestive tract (i.e., the gut microbiota) take part in insect digestive functions. For instance,
250experimental cultures demonstrated that fungi and bacteria hosted in the gut of wood
251boring Cerambycidae, Curculionidae and Siricidae bring cellulolytic enzymes to their hosts
252[68, 69]. Likewise, transcriptomic approaches have revealed that midgut microorganisms
253participate in plant tissue degradation and synthesise essential nutrients in Cerambycidae
254[70-72]. Laboratory assays on *Dendroctonus* spp. bark beetles have suggested that gut
255bacteria have nitrogen-fixing and cellulolytic functions [73]. The gut microbiota of the
256emerald ash borer *Agrilus planipennis* is thought to have similar functions [74]. Moreover,
257metagenomic studies have unravelled the detoxifying functions of the gut microbiome of
258several bark beetles of the genus *Dendroctonus* [75, 76]. Combinations of experimental
259manipulation of the gut microbiota and metagenomic approaches have suggested similar
260functions for the gut microbiota in the pine engraver *Ips pini* [77] and the pine weevil
261*Hylobius abietis* [78]. However, the benefits to pine weevil performance were not directly
262linked to the metabolic functions identified [78]. Finally, there is evidence that non-obligate
263microorganisms play a role in defence against natural enemies. For example, in the spruce
264beetle, *Dendroctonus rufipennis*, bacteria present in oral secretions inhibit the growth of

265entomopathogenic fungi [79]. Likewise, fungal symbionts in several siricid woodwasps
266provide protection against nematode parasitism [80]. In the southern pine beetle,
267*Dendroctonus frontalis*, the mutualistic interaction with the fungus *Entomocorticium sp.* is
268maintained by bacteria hosted in the insect mycangia, that produce antifungal molecules
269directed against *Entomocorticium* competitors [81]. However, the insect microbiota can
270also have detrimental side effects. For instance, in the gypsy moth, the action of the
271pathogen *Bacillus thuringiensis* has been shown to be only effective in the presence of a
272specific species of *Enterobacter* in the insect gut [82].

273In all these forest pests, studies have suggested that most gut microorganisms are acquired
274through the opportunistic consumption of plant tissues and are, therefore, probably
275transient and environment-dependent. For instance, the gut microbial communities of
276*Dendroctonus* species and pine weevils have a composition overlapping with that of the host
277tree microbiota, with which they have a number of features in common [83, 84]. Similarly,
278differences in the gut microbiota of larvae fed on different host trees have been found in the
279pine processionary moth *Thaumetopoea pityocampa* [85] and the eastern spruce budworm
280*Choristoneura fumiferana* [86]. In the gypsy moth, both culture-dependent and culture-
281independent methods have shown that the gut bacterial community is influenced by the
282plant species the larvae feed on [87]. Some gut symbionts can however be vertically
283transmitted, as is the case in longhorned beetles where adults smear their eggs with fungal
284symbionts [88].

285In summary, the important contribution of microbial symbionts to the feeding capacities of
286many forest pests is well documented, and evolutionary studies have shown that these
287microbes are probably derived from the plant microbiota. However, we still know little

288about the microorganisms of the transient microbiota of insects, such as gut associates. The
289advent of high-throughput sequencing has led to a large increase in the number of studies
290generating inventories of the diverse microbial taxa associated with insects, but very few
291studies have investigated the stability and transmission of these microbial communities
292over generations and populations, or their role in insect performance and adaptation to
293environmental change.

294**1.3 Insect herbivores alter the tree microbiome and tree health**

295Herbivory is controlled by the tree microbiome, which contains entomopathogenic
296microbes, produces insecticidal toxins, activates tree defences (see section 1.1), and
297contributes to the insect gut microbiome, which enables insects to feed (see section 1.2). In
298this section, we review the evidence for the converse relationship, in which insect herbivory
299alters the tree microbiome, with possible consequences for tree health.

300Herbivory can directly affect the tree microbiome and health through transmission of
301microbial plant pathogens, which may be passive (on the surface of the body or in frass) or
302active (in the mouthparts or ovarial fluids). Several notorious tree pathogens are vectored
303by insects, including fungi [89-90], viruses and bacteria [91-93]. The most emblematic
304example of a fungal disease vectored by insect herbivores is Dutch elm disease, which is
305caused by an ascomycete fungus of the genus *Ophiostoma* (Ophiostomatales). This disease
306caused the massive decline of elm tree populations in Europe, Asia, and North America. The
307spores of the fungus are transported on the body surface of bark beetles and enter the tree
308through the galleries dug by the insect [94]. However, many tree diseases are more complex
309and result from synergistic interactions between several microbial pathogens vectored by

310the insects, the microbial symbionts of the insect and the insect itself [89, 95, 96]. Acute oak
311decline syndrome, which results in necrosis of the inner bark and the larval galleries of the
312bark-boring beetle *Agrilus biguttatus*, involves multiple agents acting sequentially or in
313parallel, with cumulative effects on host tree health [97]. The interaction between *A.*
314*biguttatus* and the microbial component of acute oak decline is not fully understood yet
315[98]. Pine-wilt disease also results from complex interactions, in this case between a
316nematode, its insect vector, the *Monochamus* beetle, and associated bacteria and fungi [99,
317100].

318Herbivory can also alter the tree microbiome, locally or systemically, by influencing the
319chemistry of attacked tissues, and/or the physiology and defence pathways of the whole
320tree. Such changes in the tree microbiome may have consequences for tree health, through
321a mechanism known as microbiome dysbiosis [101, 102]. For instance, Müller *et al.* [103]
322found that leaf consumption by lepidopterous larvae caused local changes in the diversity of
323culturable phyllosphere bacteria, due to increases in the availability of nitrate and ammonia
324in attacked leaves [103, 104]. Several other studies have reported local changes in the tree
325microbiota in the presence of insect endophagous herbivores [105-109]. Massive Scots pine
326defoliation by the nun moth *Lymantria monacha* and the pine lappet *Dendrolimus pini* has
327been shown to be followed by changes in the composition of fungal communities in both the
328phyllosphere and the rhizosphere [110]. Such distant effects of herbivory on the tree
329microbiota are mediated by tree defence pathways. Indeed, herbivores and micro-
330organisms induce and are sensitive to plant defences dependent on the same hormonal
331pathways, so herbivory *per se* can modify the plant microbiome [111, 112], as recently
332demonstrated by the experimental elicitation of anti-herbivore defences [113].

333In summary, insect herbivores can alter the tree microbiome and tree health directly,
334through the transmission and inoculation of microbial plant pathogens, or indirectly, by
335modifying tree chemistry and defences and causing microbiome dysbiosis. Direct effects are
336well documented for forest insect pests, but much less is known about indirect effects.
337Experimental studies are required to decipher the relationships between herbivory,
338microbiome dysbiosis and tree health.

339**Part 2 - Towards the integration of tree-insect-microbiome interactions** 340**into forest pest management**

341In crops, manipulation of the plant microbiome is considered a very promising approach to
342fostering plant protection against abiotic and biotic stressors (including herbivores).
343Indeed, such manipulation is the core idea in the recently developed concept of the
344“phytobiome” [114]. It corresponds to all biotic and abiotic factors acting together to
345determine the health and growth of plants. The phytobiome therefore includes the plant
346microbiome, insect pests and their microbiome, and it should be managed as an integrated
347system [114]. It is generally accepted that plant microbiomes and phytobiomes can be
348manipulated by two approaches — plant breeding and agroecosystem management [115]
349— in addition to the direct inoculation of microbial strains or consortia [116]. Research into
350the management of the phytobiome of planted trees slightly lags behind research into the
351management of the phytobiome of agricultural crop plants, but a few studies have proposed
352tree microbiome management as a potential option for enhancing the health of forest
353plantations [117-119].

354The idea of manipulating the insect microbiome for integrated pest management strategies
355has also recently emerged [120]. Modifications to the insect microbiome might reduce the
356ability of insects to feed on plant tissues and/or improve the ability of parasitoids to control
357insect pests. Symbionts manipulating insect reproduction could also be used to regulate
358pest population dynamics. In human health, the manipulation of endosymbionts has been
359used as a method for controlling the transmission of insect-borne diseases [121, 122].
360Similar manipulations in insect herbivores have been considered as a means of controlling
361insect-vectored plant pathogens but are still rarely applied in crops and orchards (*but see*
362paratransgenic strategies for blocking the transmission of *Xylella fastidiosa* by
363sharpshooters [123]) and have yet to be investigated for use in forest pest management.

364We therefore focus below on the microbiome of planted trees, rather than the microbiome
365of insect pests. We examine how its manipulation could reduce insect pest damage in forest
366plantations (Fig. 2), by drawing parallels with research on the phytobiome of crop plants.

367**2.1. Controlling insect pests with microbial consortia**

368In crops, beneficial microorganisms (including pest antagonists) can be inoculated directly
369onto or into plant organs or the soil, or may be used as a seed coating, for preventive or
370curative treatment [124, 125]. For instance, plant growth-promoting rhizobacteria can be
371used to inoculate the soil or to coat seeds, as a means of increasing plant resistance to
372stresses and fostering plant growth [126, 127]. Current research builds on the development
373of -omic approaches, synthetic communities and microbial network inference to design
374beneficial microbial consortia potentially able to provide broader and more durable plant
375protection than single microbial strains [128, 129]. The introduction of beneficial micro-

376organisms into plant reproductive organs, to promote their maternal transmission, is also a
377promising avenue for research [130].

378Such strategies exist for planted forests, but are rarely used. The biocontrol of insect pests
379through the release of natural enemies is a key component of integrated pest management
380in forestry, and microbial entomopathogens are promising potential biocontrol agents
381[131]. Fibre bands impregnated with fungal entomopathogens fixed around the trunks or
382branches of trees have given satisfactory results for the biological control of several insect
383pests [28]. The toxigenic effect of inoculating white spruce seedlings with the fungal
384endophyte *Phialocephala scopiformis* against spruce budworm *Choristoneura fumiferana*
385persists for 11 years after inoculation [42]. Moreover, several laboratory assays have
386suggested that inoculation of trees with fungal entomopathogens or bacterial endophytes
387may decrease the survival and reproduction rates of major insect pests, including *Ambrosia*
388beetles [132, 133]. Omics and systems biology approaches [128, 134-136] clearly have a
389role to play in the elucidation of complex interactions between trees, insect pests and the
390pathogens they carry, and in the identification of microbial consortia antagonists of insects
391and/or vectored microorganisms. The efficiency of these microbial antagonists should then
392be assessed *in situ* on various tree genotypes, since there may be an interaction between the
393tree genotype and the efficiency of microbial biocontrol agents [137].

3942.2. Breeding trees that support protective microbial communities

395In crops, artificial selection of varieties that associate with a beneficial microbiome is
396considered a promising avenue of research for promoting natural protection against pests
397and pathogens [115, 138-140]. Plant domestication, selection and cultivation, as conducted

398since the advent of agriculture, may have led to the disappearance of the ability of plants to
399associate with a beneficial microbiome [141] and to the disappearance of this beneficial
400microbiome from the environments in which they are currently grown [140, 142]. One
401major challenge is the development of crop breeding strategies taking the plant microbiome
402into account, and the restoration of microbial diversity in agroecosystems through
403inoculations or cultural practices [140, 143, 144].

404To the best of our knowledge, the microbiome has never been considered as a selection
405criterion in tree breeding. This avenue of research should be explored more thoroughly,
406given that several studies have shown that microbiomes of trees are determined, at least
407partly, by genetic factors, for example in olive trees [145], Norway spruce [146] and
408eucalypts [147]. This is however not the case in all tree species [148]. In addition, the
409conditions in which genetic material is produced in seed orchards and tree nurseries could
410help foster the production of trees supporting beneficial microbial populations. The
411maternal environment [118] and early-arriving microbial species [149] can affect the
412assembly trajectory of the tree microbiome, from seeds to adult trees. For instance,
413experiments on *Eucalyptus grandis* showed that the environment of mother trees
414influenced the endophytic fungal communities of their seedlings and their response to pests
415and pathogens [150]. Research on these maternal effects is required for the integration of
416tree microbiomes into tree breeding programs [118]. In particular, it should be recognised
417that the environment in which forestry seed orchards are planted can have an effect on
418seed and seedling microbiomes, and on current and future resistance to biotic and abiotic
419stressors [119]. Several other factors can also influence the seed and seedling microbiomes:
420seed storage conditions [151], the method of plantation establishment (direct seeding vs.

421planting), the type of soil used in tree nurseries, and treatment of the potting mix for
422container stock (with heat, for instance; [152]). It is crucial to take the initial soil
423microbiome into account more effectively, because it can predetermine plant health [153].

424

425**2.3. Fostering microbiome-based resistance to herbivory with silvicultural practices**

426Agroecosystem management practices can be used to favour a beneficial microbiome in the
427crop environment, in both belowground and aboveground compartments. More attention
428has been paid to management of the belowground microbiome [127], because it is more
429diverse than the aboveground microbiome (which contains only a subset of the organisms
430present below ground) [154], and because its relationships with plant health are better
431understood [15]. The soil microbiome can be modified by several different strategies, such
432as inoculating with new microbiomes, adding organic amendments, or growing certain
433plants nearby [24]. The influence of plants on the soil microbiome, and the cascade effect on
434the performance of subsequent plants (including their resistance to herbivory), is known as
435plant-soil feedback, and is the basis of ancient agricultural practices, such as crop rotation,
436intercropping, and the use of cover crops [24]. It is controlled by root exudates, which
437shape the composition of rhizosphere microbial communities, thereby determining the
438growth and defence capabilities of the next generation of plants [155, 156].

439In forests, there is ample evidence to suggest that the composition of the soil microbiome
440depends on tree species and genotype [157-159]. Plant-soil feedback could therefore be
441used to guide the composition of the soil microbiome before establishment of forest
442plantations, to foster tree resistance to multiple stresses and to reduce aboveground

443herbivory [24]. Heterospecific plant-soil feedback, in which another plant species is grown
444in the soil before the crop species, often gives good results [24] and could be exploited
445further. Such management of plant diversity and of the soil microbiome should also affect
446the composition of the aboveground tree microbiome. For instance, tree species richness at
447the forest plot level increased the diversity of leaf epiphytic bacteria [160]. Significant
448effects of tree species richness and silvicultural practices on the composition of foliar fungal
449communities have also been reported in silver birch (*Betula pendula*) [161, 162], but not in
450Norway spruce (*Picea abies*) [163] or Scots pine (*Pinus sylvestris*) [164]. Effects of plant
451diversity on the aboveground microbiome were also found in orchards. For instance, the
452association of banana plants (*Musa* sp.) with Fabaceae trees changed the abundance of
453some phyllosphere bacteria in banana leaves [165]. Management of water and dead wood
454can influence the aboveground microbiome. For instance, in olive tree (*Olea europaea*)
455orchards, phyllosphere bacterial communities have been shown to differ in composition,
456but not in richness and diversity, between 'conventional' and 'sustainable' systems differing
457in terms of the management of soil, water and pruning residues [166, 167]. Similarly,
458agroforestry management practices affect the diversity, composition and function of fungal
459and bacterial endophyte communities in *Theobroma cacao* tree leaves [168]. Oliveira [169]
460also identified a few foliar fungal endophytes differing in abundance between organic and
461conventional cocoa tree plantations. Cropping system (organic vs. conventional) also
462influences the composition of leaf epiphytic bacterial communities in apple tree (*Malus*
463*domestica*) orchards [170].

464Overall, these studies suggest that forest management practices could be used to modulate
465both the belowground and aboveground microbiome in tree plantations, thereby

466modulating the resistance of planted trees to herbivores. Future studies should identify the
467practices favouring beneficial microorganisms for different tree species. Many studies
468(reviewed in detail in [21]) of herbaceous plants have shown that fungal endophytes can
469protect plants against insect herbivores through their entomopathogenic activity [29], and/
470or the production or induction of secondary metabolites [171]. Some of these fungal species
471can also protect trees against pathogens [172]. Forest management should therefore favour
472these protective endophytes naturally.

473In conclusion, microbiome management is a solution increasingly studied and used to
474stimulate growth of crop plants and protect them against pathogens and pests. This
475research is guided by the “phytobiome” concept, which advocates a more holistic view of
476plants and their interactions. The scientific community performing these studies has barely
477considered forest plantations to date. This review shows that the microbiome of planted
478trees could be managed at several stages of production, from seed orchards to mature
479forests (Fig. 2), to improve the resilience of forest plantations to insect pests and other
480biotic and abiotic stresses. More research on managing the microbiome of planted trees is
481needed, particularly for early stages (seeds and seedlings or cuttings), because the
482microbiota acquired during these stages primes the immune system of the tree (see section
4831.1) and controls the subsequent trajectory for microbiota assembly.

484**Part 3 – Scaling up the study of tree-insect microbiomes interactions to** 485**the ecosystem level**

486Interactions between plants, insect herbivores and their microbiomes are often studied
487with a reductionist approach, by considering tripartite interactions between a single plant

488species, a single insect species and a couple of microbial taxa associated with the plant host
489or the insect host (rarely both). There is a lack of community- or ecosystem-scale studies,
490that incorporate multiple plant and herbivore species in interaction, as well as their
491microbiomes and the third trophic level. We speculate that these difficulties in upscaling
492tripartite interactions are partly explained by their spatial and temporal variability [173-
493175]. Below, we review the scant evidence of effects of tree-insect-microbiome interactions
494on three components of forest ecosystem health: the regulation of forest insect
495communities, the regulation of the belowground microbiome and the natural regeneration
496of forests. We are aware that these three topics do not encompass all the biodiversity and
497functioning of forests, but they are the only ones for which we were able to identify active
498research.

499**3.1 Tree and insect microbiomes regulate forest insect communities**

500There is growing evidence to suggest that the microbiome of insect herbivores not only
501affects their feeding behaviour and overall performance (see section 1.2), but can also have
502community-wide effects. There have been no case studies on the cascade effects of the
503insect microbiome on trophic networks in forest ecosystems. However, interesting insights
504can be gained from studies on herbaceous and crop plants. Several studies have shown that
505the microbiome of insect herbivores has a direct influence on the recruitment of its
506parasitoids [8, 176-178], and can also change the way the plant interacts with the natural
507enemies and competitors of the insect herbivore [179]. For instance, an experimental study
508showed that protective symbionts in an aphid species can decrease the density of other
509aphid species competing for the same plant resource and induce the extinction of
510associated parasitoids [180]. Aphid endosymbionts can also attenuate the release of

511herbivore-induced plant volatiles [181]. Moreover, microorganisms and viruses associated
512with insects of the third trophic level also mediate herbivory. For instance, viruses
513associated with parasitoids can affect the molecular dialogue between plants and
514herbivores, and reduce herbivory [182].

515Similarly, the effect of the tree microbiome on insects is not restricted to insect herbivores
516(see section 1.1), but extends to the whole forest insect community. For example, the
517presence of powdery mildew (*Erysiphe alphitoides*) on oak leaves influences the
518composition of insect communities across trophic levels [183]. In Neotropical forests, foliar
519fungal endophytes were shown to increase the top-down control of insect herbivores by
520predatory ants (*Azteca lacrymosa*) [184]. They also modify leaf chemistry and discourage
521leaf-cutting ants (genera *Atta* and *Acromyrmex*). These ants are major defoliator pests in
522tree plantations and ecosystem engineers in natural tropical forests, in which they alter
523forest structure, microclimate and regeneration, thereby affecting the whole trophic web
524[185-187]. The forest insect community is shaped not only by foliar pathogens and
525endophytes, but also by the belowground microbiome. For example, in an evergreen mixed
526broadleaved forest, the belowground microbiome (plant mutualists, pathogens and
527saprotrophs) was shown to modify the composition of the plant community considerably,
528with major effects on the insect community [188].

529Overall, these studies suggest that multipartite interactions, involving macroorganisms,
530microorganisms and viruses, probably play an important role in maintaining forest health
531and biodiversity. In-depth analyses of these interaction networks would undoubtedly
532improve our understanding of the relationships between biodiversity and ecosystem health

533[189], but such analyses remain rare for ecosystems as biodiverse as forests, despite the
534contribution of high-throughput sequencing technologies to ecological network discovery
535[135, 190]. The solution probably lies in the identification of sets of key species and
536deciphering of their functional interactions through application of experimental approaches
537to simplified communities.

538

539**3.2. Above-ground herbivory controls the belowground forest microbiome**

540There is some evidence to suggest that the belowground forest microbiome influences the
541aboveground community of insect herbivores (see section 3.1). Conversely, insect
542herbivores drive the composition of belowground microbial communities, as suggested by a
543recent meta-analysis [191]. Indeed, intensive canopy damage caused by insect outbreaks
544greatly decreases carbon allocation to roots and root exudation, causing shifts in the
545composition of tree root microbial communities. For instance, in subarctic mountain birch
546forests, moth outbreaks have induced a taxonomic and functional shift in mutualistic
547communities, from ectomycorrhizal fungi to arbuscular mycorrhiza-dominated
548communities [192]. A meta-analysis confirmed that herbivory modified belowground
549biogeochemical processes to the detriment of ectomycorrhizal fungi, and showed that
550herbivory effects extended to the entire soil food web [191]. Again, experimental
551approaches are required to improve our understanding of these aboveground-belowground
552relationships and to build a framework capable of predicting the cumulative effects of
553insect outbreaks on forest functioning.

554**3.3 Microbial fluxes control forest regeneration under herbivory pressure**

555 Finally, there is a need to improve our understanding of microbial fluxes, to promote health
556 at the ecosystem scale [193]. In plants, microorganisms pass from one individual to another
557 within a generation, through airborne or insect-vectored transmission (i.e. horizontal
558 transmission), and from one individual to its offspring through seeds (i.e. vertical
559 transmission) [13, 194, 195]. In trees, the horizontal transmission of microorganisms has
560 been studied mostly in the framework of the 'Janzen-Connell hypothesis' [196], according to
561 which, the survival and growth of seedlings is regulated by a density- and distance-
562 dependent mechanism in which microbial pathogens and insect herbivores preferentially
563 kill seedlings at high density near the mother tree. Under this mechanism, the importance of
564 which has been confirmed in both temperate and tropical forests [197, 198], movements of
565 microorganisms and insects act in concert on forest regeneration. Microbial pathogens and
566 insect herbivores are, however, not the only players. The relative importance of their effects
567 on seedling mortality depends on mycorrhizae [199], and may also depend on seed-borne
568 microorganisms. The vertical transmission of the microbiota, which was only recently
569 detected in trees [200-202], may play a role in seedling recruitment under herbivory
570 pressure. The initial, maternally transmitted microbiome may indeed affect the assembly
571 trajectory of the microbiome and its composition at the seedling stage, through priority
572 effects [149]. For instance, studies of crop seeds have demonstrated that vertically
573 transmitted microorganisms foster seedling health [203, 204] and produce volatile organic
574 compounds [205], which are used by both herbivores and their enemies to locate suitable
575 plant hosts (see section 1.1). Future research should improve our understanding of the
576 effects of horizontal and vertical microbial fluxes on seedling recruitment and should

577integrate these fluxes into modelling frameworks, such as forest gap models [206], for the
578scaling up of their effects to the forest ecosystem scale.

579**Conclusion**

580Microbiome acquisition has been a key process in the colonisation of land by plants, and
581some members of the plant microbiota have been co-opted as faithful allies by herbivorous
582insects over the course of evolution. Thus, microorganisms have always been present as a
583third partner in the interactions between plants and insect herbivores, but their diversity
584and the complexity of their interactions with plants and insects have long been
585underestimated by entomologists and ecologists, especially in forest research.

586This review shows that herbivory damage in forest ecosystems is clearly influenced by
587tripartite interactions between trees, insects and their microbiomes. There is ample
588evidence to suggest that the tree microbiome can decrease or increase herbivory in forest
589tree species. Both the aboveground and belowground microbiomes mediate herbivory, by
590direct effects on insects, or indirect effects involving the shaping of tree chemistry and
591defence. The role of the insect microbiome in feeding capacities of many forest pests is also
592well documented.

593As a consequence, the microbiomes of trees and insects should be better integrated into
594forest health management strategies. Based on recent research, only the tree microbiome
595could realistically be managed at the moment. This review suggests that the microbiome of
596planted trees could be managed at several stages of production, from seed orchards to
597mature forests, to improve the resistance of forest plantations to insect pests. Microbiome
598management at early tree stages appears to be the most promising option.

599 Finally, this review shows that the influence of tree and insect microbiomes on processes at
600 the ecosystem scale, such as the regeneration of natural forests, remains poorly understood.
601 Bruggen *et al.* [193] recently expanded the “One Health” concept by proposing that health
602 conditions of all organisms in an ecosystem are interdependent and mediated by microbial
603 fluxes. Forest research should take up this concept to guide forest health monitoring and
604 management strategies. To this end, future research will have to continue combining
605 holistic goals with reductionist approaches. The mechanisms of interactions between trees,
606 insects and their microbiomes should be deciphered by developing experimental systems
607 involving trees, insects and synthetic microbial communities. The stability and transmission
608 of microbiomes across generations and populations should also be investigated by
609 experimental approaches. Knowledge about microbiome interactions and transmission
610 should then be integrated into spatial models of forest dynamics to move from small-scale
611 mechanisms to forest ecosystem-scale predictions.

612 **Figure Captions**

613 **Figure 1:** *Overview of tripartite interactions between trees, herbivores and their own and*
614 *shared microbes.*

615 **Figure 2:** *Overview of strategies that can be used to promote tree and forest resistance to*
616 *biotic and abiotic stresses through manipulation of the tree microbiome.*

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628**Ethics statement**

629Corinne Vacher, Heidy Schimann, Emmanuelle Jouselin and Bastien Castagneyrol declare
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631**Human and animal rights and informed consent**

632This article contains no studies with human or animal subjects performed by any of the
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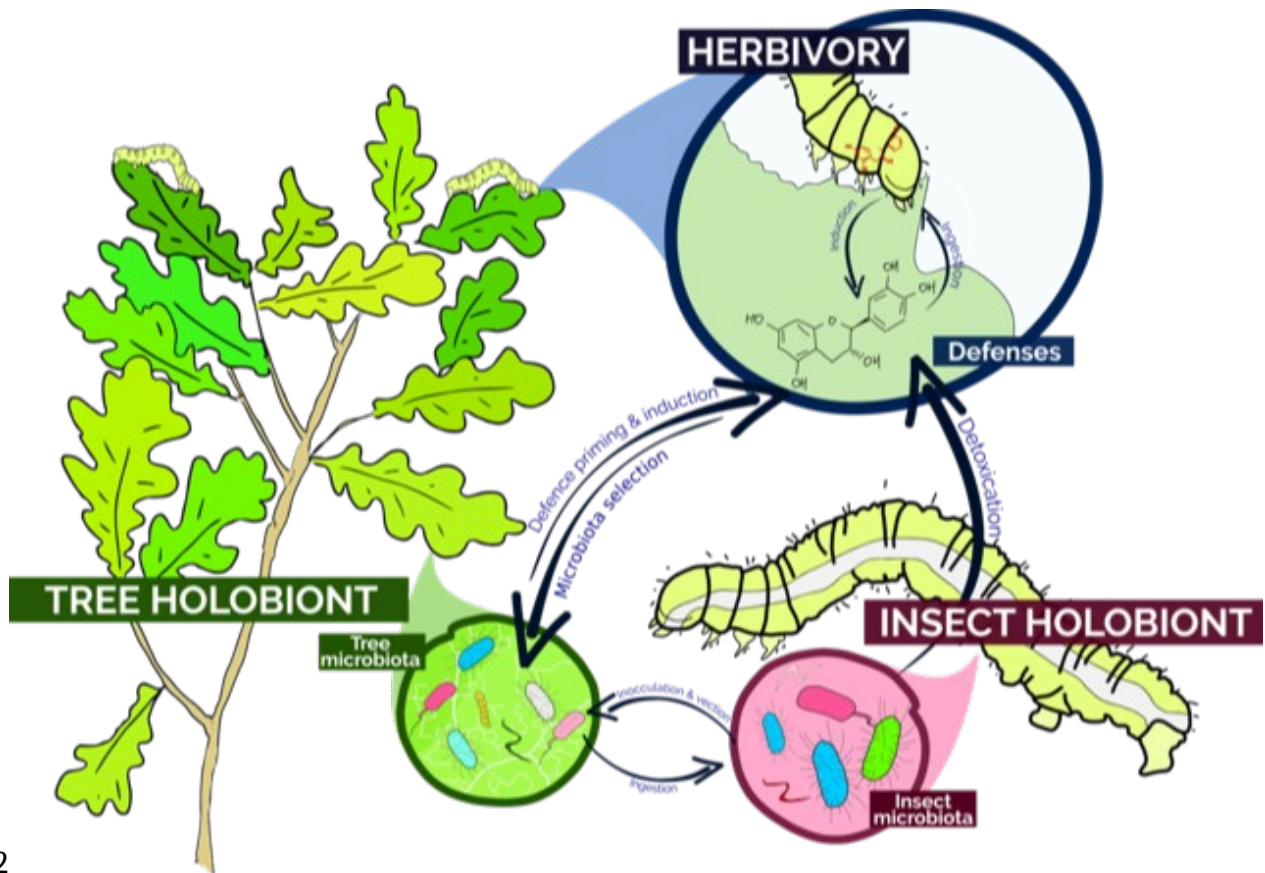
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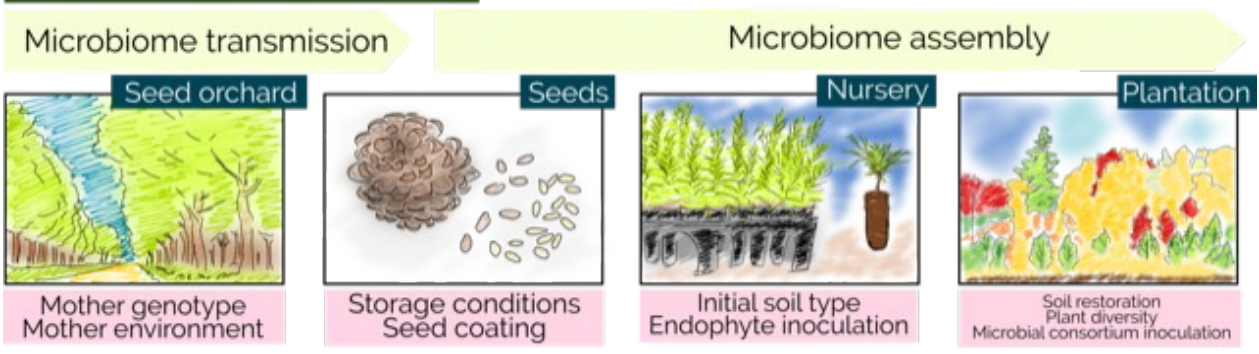
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1192
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1194Figure 1.

Microbiome dynamics



Microbiome management

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1196 Figure 2

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