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## Review Article

# Nesting Associations without Interdependence: A Preliminary Review on Plesiobiosis in Ants

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Plesiobiosis, the most basic form of interspecific associations in ants, denotes occasional or regular nesting of heterospecific colonies of certain species pairs in close proximity to each other without biological interdependence. Plesiobionts differ from each other both in morphology and in behaviour (e.g., in their foraging strategies), and at least one of the plesiobiotic pair is a submissive species. Recent studies on plesiobiosis have revealed that *Formica fusca* and *Lasius flavus* are two of the most frequent plesiobionts. To date, at least 48 different plesiobiotic species pairs have been recorded from various habitat types of the Holarctic region. Two main habitat properties may play a role in the forming of plesiobiosis: the scarcity of suitable nesting sites as a forcing factor and the sufficient amount of food sources available, influencing the abundance of colonies. Thus, high colony density may contribute to the formation of such associations, resulting in (1) frequent nesting in each other's neighbourhood and (2) stronger intraspecific competition, which forces colonies into the vicinity of heterospecific nests. Plesiobiotic associations formed this way may promote persistent coexistence, leading to the formation of other types of interspecific associations (e.g., clepto- or lestobiosis).

## 1. Introduction

Various types of interspecific associations exist among ant species. These can be categorised on the basis of the degree of interactions between heterospecific colonies, ranging from simple cooccurrence with loose interaction to highly specialised social parasitism [1–3]. Following the suggestion by Wasmann [4] and Wheeler [5], Hölldobler and Wilson [6] distinguished two main types of associations between ant colonies, namely, “compound nests” and “mixed nests.” Associations belonging to “mixed nests” mostly result from social parasitism, where one of the species (as a social parasite) depends on its partner, which represents the host. On the other hand, the association types of “compound nests” differ from each other in the degree of interspecific relations ranging from neutral associations through mutualism and commensalism to typical parasitism.

The vast majority of studies on interspecific associations in ants have focused on the forms of typical social parasitism (i.e., temporary parasitism, slavery, and inquilineism) [1, 3, 7–9] or on associations that belong to “compound nests”

representing a higher degree of biological interdependence between heterospecific colonies (i.e., cleptobiosis, lestobiosis, xenobiosis, or parabiosis) ([10–20] etc.). However, few studies have dealt with plesiobiotic associations so far, and most of these reported only observations that might indicate the existence of such associations [5, 21–36].

Although numerous classifications exist for associations related to “compound nests” [2, 4–6, 22, 37], most of them are based on relatively few reports [2]. According to each of the classification systems, plesiobiosis is the most rudimentary form of heterospecific associations. This type of association occurs between species pairs that differ from each other in morphology, in behaviour, and in taxonomy, and it denotes nesting close to each other without biological interdependence. Owing to this close proximity, plesiobiotic partners share not only the nesting shelter, but the same microhabitat, and possibly the foraging area as well.

In this review our aim was to summarise the existing information on plesiobiosis, by listing and discussing (1) the recorded plesiobionts and plesiobiotic partner species and (2) the assumed background factors that may promote

the formation and persistence of plesio-biotic associations. Furthermore, we pose open questions to call attention to the importance of collecting data considering the mentioned ecological approaches.

## 2. General Categorization of Interspecific Associations in Ants

The general classification system of “compound nests” includes five different association types with increasing degree of interactions and biological interdependence between the associated heterospecific colonies. As mentioned above, the most basic form of these associations is plesio-biosis [5, 6, 22]. According to the classical definition, plesio-biotic partner colonies share the same microhabitat without further interactions [1, 5]. In the case of cleptobiosis and lestobiosis, one of the associated colonies gains benefit from being in the vicinity of the other colony. This can be through robbing the stored resources of the other colony, stealing food from returning foragers (cleptobiosis), or preying on the brood of the alien colony (lestobiosis), thereby reducing the costs of searching and handling of food [1, 6, 9, 10]. Parabiosis differs from the other types of “compound nests” since it is a mutualistic relationship between the associated colonies [1, 6]. In these cases, each species gains benefit from its partner (e.g., by protection from enemies or competitors, interspecific trail following, etc.), and these benefits outweigh the costs of the maintenance of the coexistence [11]. Although xenobiosis is considered as a type of “compound nests,” it has more social parasitic features than the previous ones. Xenobiotic species (i.e., “guest ants”) spend their life inside the nest of their host colony stealing food or inducing trophallaxis with host workers [9]; therefore, xenobiosis is a truly parasitic form of interspecific associations [1, 6, 9].

In typical social parasitic associations, individuals of different colonies mix inside the nest, and heterospecific brood is mostly cared for by host workers. These associations imply biological interdependence; that is, the parasite always depends on its host(s) [9]. The queens of temporary social parasitic species use their host colonies during colony foundation, and the mixed colony gradually develops to a pure, monospecific colony of the parasitic species [1]. In this case, the parasitic colony depends on its host only during colony foundation [1, 6, 9, 12]. Unlike temporary social parasitism, slave-maker species depend on their hosts throughout their lives; that is, they are constrained to renew their labour force through robbing brood from host colonies in the course of slave-making raids [1, 6, 9]. The final and most extreme stage of social parasitism is inquilinism. Inquilinous species are the “ultimate social parasites,” as they spend their entire life cycle inside the nest of their host colony. Most of these species lack the worker caste, and their queens invest their energy to produce only reproductive offspring [1, 6, 9].

## 3. Plesio-biotic Association

Regarding the lack of biotic interdependence between the associated colonies [1, 5, 6, 12, 30], plesio-biosis is considered the most rudimentary form of interspecific associations in

ants. This relationship denotes the nesting of mostly two colonies of different species in the direct proximity of each other, which means that the plesio-biotic colonies occupy the same nesting shelter (e.g., in or under logs, stumps, rocks, etc.). On the basis of the currently available data on plesio-biotic associations, this close nesting can occur occasionally or regularly, depending on the species and/or habitat type (as discussed below). Although plesio-biotic nests are adjacent to one another in several cases, they always remain separate as individual units, and the members of heterospecific colonies do not mix [6]. Plesio-bionts are potentially hostile to each other, and if the nest galleries accidentally break in, fighting and brood theft may occur [6, 28, 37]. As a rule, plesio-biotic partner species differ from each other morphologically (e.g., different body size) and/or behaviourally (e.g., different foraging strategies or competitive ability), and they belong to at least different genera [6]. These differences may promote the coexistence of associated colonies according to the “limiting similarity” hypothesis suggested by MacArthur and Levins [38]. Basically, the less similar the species are the more likely they occur together in a plesio-biotic relationship in order to avoid intraspecific competition.

## 4. A Synthesis of the Recorded Cases of Plesio-biosis

**4.1. Plesio-bionts and Plesio-biotic Partners.** In Table 1, we list 49 species that have been observed so far in plesio-biotic associations. 29 of these belong to the subfamily Formicinae, 17 to Myrmicinae, and only 3 to Ponerinae. The four most frequent genera whose members established plesio-biotic relationships were *Formica* (11 species), *Camponotus* (9 species), *Lasius* (8 species), and *Myrmica* (4 species), well representing the general number of genera and species in the Holarctic [6].

Recent studies on plesio-biosis revealed that two species, *Formica fusca* (Linnaeus, 1758) and *Lasius flavus* (Fabricius, 1782), can be considered as two of the most frequent plesio-bionts, on the basis of the total number of their so far known plesio-biotic partner species (Table 1).

Up to the present, at least 48 different plesio-biotic species pairs have been recorded from different habitats of the Holarctic region. Among these, *F. fusca* was involved in 12 cases (25%), *L. flavus* in 8 cases (16.3%), *Monomorium minimum* in 5 cases (10.2%), *M. rubra* and *Myrmecina americana* in 4 cases (8.16%), respectively, and *Pheidole picea* and *Lasius umbratus* in 3 cases (6.12%) each (Table 1). The total number of plesio-biotic associations—where the exact number of the observed cases was given—was 69, from which the two most frequent plesio-bionts participated in 46 associations, *F. fusca* in 28 cases (60.9%) and *L. flavus* in 18 cases (39.1%) (Table 1). *F. fusca* established plesio-biotic associations with species belonging to 6 different genera of two subfamilies (Myrmicinae and Formicinae). Its typical plesio-biotic partners were *Myrmica* spp. (*M. rubra* and *M. ruginodis*), *Tetramorium* spp. (*T. cf. caespitum*), *Leptothorax* spp. (*L. acervorum*), *Lasius* spp. (*L. platythorax*, *L. niger*, and *L. flavus*), and *Camponotus* spp. (*C. vagus* and *C. herculeanus*). Plesio-biotic partners of *L. flavus* belonged to 3 different genera, *Formica* spp. (*F. fusca*, *F. cunicularia*, *F. fuscocinerea*, and *F. aquilonia*),

TABLE 1: Observed cases of plesbiotic associations in ants.

No. of species pairs	Species pairs recorded in plesbiotic associations	Country	Habitats	Location of nests/type of nesting shelter	No. of cases of plesbiotic nests	Source
1	<i>Formica fusca</i> - <i>Myrmica rubra</i>	Finland; UK	Different successional series of rocky habitats; foreshore	In/under moss; under decaying wood; under stone	2; ?	Czechowski 2003, 2004 [32, 34] Morley 1945 [25]
2	<i>Formica fusca</i> , <i>Myrmica ruginodis</i>	Poland	Clearcut of managed forest	In tree stumps	1	Włodarczyk et al. 2009 [36]
3	<i>Formica fusca</i> - <i>Tetramorium caespitium</i>	Poland	Clearcut of managed forest	In tree stumps	3	Włodarczyk et al. 2009 [36]
4	<i>Formica fusca</i> - <i>Leptothorax acervorum</i>	Finland	Different successional series of rocky habitats	Mound of <i>F. lugubris</i>	1	Czechowski 2004 [34]
5	<i>Formica fusca</i> - <i>Lasius flavus</i>	Finland	Different successional series of rocky habitats	Under wood; in rock crevice; under stone	4	Czechowski 2004 [34]
6	<i>Formica fusca</i> - <i>Lasius platythorax</i>	Finland; Poland	Forest on rocks; clearcut of managed forest	In decaying wood; in tree stump	3	Włodarczyk et al. 2009 [36]
7	<i>Formica fusca</i> - <i>Lasius niger</i>	UK	Foreshore	Under stone	?	Morley 1945 [25]
8	<i>Formica fusca</i> - <i>Camponotus herculeanus</i>	Poland	Forest edge	Under wood	1	Czechowski 2005 [35]
9	<i>Formica fusca</i> - <i>Camponotus vagus</i>	Hungary	Pine and poplar forest patches	In/under wood	10	Kanizsai (unpubl.)
10	<i>Formica fusca</i> - <i>Formica lugubris</i>	Finland	Different successional series of rocky habitats	Mound of <i>F. lugubris</i>	1	Czechowski 2004 [34]
11	<i>Formica fusca</i> - <i>Formica aquilonia</i>	Finland	Forest on rocks	Mound of <i>F. lugubris</i>	1	Czechowski and Vepsäläinen 1999 [29]
12	<i>Formica fusca</i> - <i>Formica truncorum</i>	Finland	Different successional series of rocky habitats	In rock crevice	1	Czechowski 2004 [34]
13	<i>Lasius flavus</i> - <i>Formica cunicularia</i>	UK	Foreshore	Under stone	?	Morley 1945 [25]
14	<i>Lasius flavus</i> - <i>Formica aquilonia</i>	Finland	Different successional series of rocky habitats	Mound of <i>F. aquilonia</i>	1	Czechowski 2004 [34]
15	<i>Lasius flavus</i> - <i>Formica fuscocinerea</i>	Poland	Grassy mountain slope	Under stone	1	Czechowski & Czechowska 2000 [30]
16	<i>Lasius flavus</i> - <i>Tetramorium caespitium</i>	Finland	Different successional series of rocky habitats	Under stone	1	Czechowski 2004 [34]
17	<i>Lasius flavus</i> - <i>Myrmica scabrinodis</i>	UK	Foreshore	Under stone	?	Morley 1945 [25]
18	<i>Lasius flavus</i> - <i>Lasius niger</i>	Finland; UK	Rocky outcrop; shore meadow, foreshore	In rock crevice/under stone	12; ?	Czechowski 2004 [34], Morley 1945 [25]
19	<i>Lasius flavus</i> - <i>Lasius platythorax</i>	Finland	Different successional series of rocky habitats	In rock crevice/under stone/overgrown soil	3	Czechowski 2004 [34]
20	<i>Monomorium minimum</i> - <i>Pachycondyla harpax</i>	USA	?	?	?	Wheeler 1901 [5]
21	<i>Monomorium minimum</i> - <i>Pogonomyrmex barbatus</i>	USA	?	?	?	Wheeler 1901 [5]
22	<i>Monomorium minimum</i> - <i>Camponotus festinatus</i>	USA	?	?	?	Wheeler 1901 [5]
23	<i>Monomorium minimum</i> - <i>Camponotus sansabeanus</i>	USA	?	?	?	Wheeler 1901 [5]
24	<i>Monomorium minimum</i> - <i>Formica gnava</i>	USA	?	?	?	Wheeler 1901 [5]

TABLE 1: Continued.

No. of species pairs	Species pairs recorded in plesiobiotic associations	Country	Habitats	Location of nests/type of nesting shelter	No. of cases of plesiobiotic nests	Source
25	<i>Myrmecina americana-Myrmica pinetorum</i>	USA	?	In the sand	1	Wheeler 1905 [21]
26	<i>Myrmecina americana-Pheidole picea</i>	USA	?	?	?	Wheeler 1901 [5]
27	<i>Myrmecina americana-Ponera pennsylvanica</i>	USA	?	?	?	Wheeler 1901 [5]
28	<i>Myrmecina americana-Formica gnava</i>	USA	?	Under stone	1	Wheeler 1901 [5]
29	<i>Myrmica rubra-Lasius niger</i>	Finland	Shore meadow; at road	Under stone; between asphalt edge and grass	2	Czechowski 2004 [34]
30	<i>Myrmica rubra-Lasius platythorax</i>	Finland	Forest	In decaying wood	1	Czechowski 2004 [34]
31	<i>Myrmica rubra-Leptothorax muscorum</i>	Finland	Shore meadow	Under stone	1	Czechowski 2004 [34]
32	<i>Lasius umbratus-Formica sanguinea</i>	Poland	Clearings in a pine forest	In the sandy soil	1	Czechowski & Rotkiewicz 1997 [27]
33	<i>Lasius umbratus-Polyergus rufescens</i>	Poland	Clearings in a pine forest	In the sandy soil	1	Czechowski & Rotkiewicz 1997 [27]
34	<i>Lasius umbratus-Lasius sabularum</i>	Poland	Stand of oak trees	Under stone	1	Borowiec 2011 [40]
35	<i>Pheidole picea-Lasius minutus</i>	USA	Hardwood forest	In a stump	1	Gaige 1914 [23]
36	<i>Pheidole picea-Lasius nearcticus</i>	USA	Hardwood forest	Under rock	1	Gaige 1914 [23]
37	<i>Camponotus fallax-Lasius brunneus</i>	Poland	Urban park	In decaying wood	1	Czechowski 2004 [33]
38	<i>Camponotus herculeanus-Lasius platythorax</i>	Finland	?	In decaying wood	1	Czechowski 2004 [33]
39	<i>Camponotus yogi-Tennothorax andrei</i>	USA	Chaparral	In living stems of <i>Haplopappus pinifolius</i>	1	Creighton & Snelling 1966 [26]
40	<i>Camponotus modoc-Leptothorax calderoni</i>	USA	Pine forest	In log/in stump	?	Wheeler 1917 [24]
41	<i>Camponotus pennsylvanicus-Formica subaenescens</i>	USA	Hardwood forest	Under log	1	Gaige 1914 [23]
42	<i>Camponotus festinatus-Pachycondyla harpax</i>	USA	At road	Under stone	2	Wheeler 1901 [5]
43	<i>Camponotus sansabeanus-Pachycondyla harpax</i>	USA	?	?	?	Wheeler 1901 [5]
44	<i>Camponotus ligniperdus-Aphaenogaster subterranea</i>	Hungary	Pine forest	Under stone	3	Lórinzi (unpubl.)
45	<i>Formica japonica-Tetramorium tsushimae</i>	Japan	Urban area	In the soil	1	Czechowski & Yamauchi 1998 [28]
46	<i>Formica rufa-Leptothorax muscorum</i>	Sweden	?	?	?	Wheeler 1901 [5]
47	<i>Myrmecina graminicola-Ponera coarctata</i>	Hungary	Pine forest	Under stone	2	Lórinzi (unpubl.)
48	<i>Strumigenys pergandei-Formica</i> spp., and so forth	USA	?	In the soil	?	Wheeler 1905 [21]



*Tetramorium* spp. (*T. cf. caespitum*), and interestingly other members of the genus *Lasius* (*L. niger* and *L. platythorax*).

Although plesiobiotic partners usually belong to at least different genera, both *F. fusca* and *L. flavus* occurred in plesiobiosis with species of the same genera. These untypical associations were, however, mostly formed between species of different subgenera with different behavioural features. There was only one exception to this rule in which two species from the subgenus *Chthonolasius*, namely, *Lasius umbratus* and *Lasius sabularum* occurred in each other's close proximity, although the exact nature of this association is unknown [40]. Among the untypical plesiobiotic associations, the ones between *F. fusca* and wood ants (*Formica lugubris*, *F. aquilonia*, and *F. truncorum*) were the most peculiar cases considering the well known temporary social parasitic character of wood ants, whose young queens often use *F. fusca* as host for colony foundation [6]. Nevertheless, in one case *F. fusca* was observed to move into an uninhabited part of the nest mound of a *F. aquilonia* colony, which was possibly queenless, though this *F. fusca* colony still remained there after the reviving of the wood ants [29].

#### 4.2. Background Factors and Driving Forces of Plesiobiosis

**4.2.1. Role of Habitat Type and Food Supply.** Plesiobiotic nests have been recorded from various habitat types, representing different stages of both primary succession and secondary succession. It is important to note, however, that a number of records on plesiobiosis were mere observations without any significant ecological information, for example, on habitat type, nesting site, and/or the number of observed cases of plesiobiotic pairs.

Many of the recorded plesiobiotic species pairs have been described in rocky habitats in Finland. The spectrum of study sites ranged from earlier stages of primary succession, such as open rocky outcrops and shore meadows, to mature pine forests, which represented the last successional stage of rocky habitats. According to this study, most of the plesiobiotic associations involving *Lasius* s. str. were observed in earlier stages of primary succession. This observation confirmed the hypothesis by Czechowski [31], stating that plesiobiosis is especially frequent in habitats lacking suitable nesting sites, and the scarcity of these is one of the main factors promoting the formation of plesiobiotic associations between ant colonies [34].

Another investigation was conducted in a sand dune complex in Finland, where only one plesiobiotic association was observed, which was between *F. fusca* and *M. rubra* [32]. The reason for this may be that each successional stage of the sand dunes represents more homogenous habitats and larger areas optimal for nesting than rocky habitats [32].

Species that prefer to inhabit stumps can be suitable objects for studying the effect of the amount of potential nesting sites on the frequency of plesiobiotic associations. Włodarczyk et al. [36], for instance, studied clearcuts in a managed forest in western Poland, where stumps that were left on clearcuts served as suitable nesting sites for several species. Although clearcuts represented the initial stage of secondary succession, the amount of potential nesting sites

for ants preferring stumps was relatively high, and almost half of the available stumps were occupied by colonies of 9 different ant species [36]. Of the 512 stumps that were checked, five were inhabited by more than one ant species, representing plesiobiotic associations, with *F. fusca* as one of the partners in all cases (*F. fusca*, *Tetramorium caespitum* in three cases; *F. fusca*, *Myrmica ruginodis* in one case and *F. fusca*, *L. platythorax* in one case) [36]. Although clearcuts offered a high number of stumps suitable for nesting, the sparse vegetation cover provided poor trophic conditions for aphid-related ant species compared with forest patches [36], resulting in the presence of fewer species competing for the available nesting sites.

Investigations on plesiobiosis between *F. fusca* and *C. vagus* were conducted in patches of pine and poplar forests in central Hungary (Kanizsai, unpubl.). It was shown that both the density of nests and the number of plesiobiotic associations were influenced by the age of forest patches, and there were more plesiobiotic relationships in older patches than in younger ones. A possible explanation can be that the higher nest density of either species may have facilitated the formation of plesiobiotic associations in older patches.

**4.2.2. Role of Nest Density and Intraspecific Competition.** Two main habitat properties may contribute to the formation of plesiobiotic associations: the scarcity of suitable nesting sites as a forcing factor [34] and the sufficient amount of food sources available, which significantly influence the abundance and reproductivity of ant colonies [41]. When colony density is high, the depletion of food resources by neighbouring colonies may be more intensive, resulting in an increased mortality, especially in the case of incipient colonies [42]. According to former studies ([43] and references therein), the spacing pattern of the nests of *F. fusca* and *L. flavus* (the two most frequent plesiobionts) was, or tended to be regular, when the density of their colonies were high in a suitable habitat. Although competition can produce any type of spacing pattern [44], the regular spatial arrangement of conspecific nests may indicate an intensive intraspecific competition for the same resources [42, 45–49]. Owing to similar food requirements, intraspecific competition supposed to be stronger than interspecific competition [43, 48–50]. The regular dispersion of conspecific nests can reduce the overlapping of foraging areas, thereby minimising intraspecific competition [43, 46, 49]. To effectively utilise foraging areas, it can be advantageous in these cases to maximise the distance between conspecific colonies with similar food requirements and foraging ranges [48]. Thus, it is more favourable for colonies if their nearest neighbours are rather heterospecifics with less overlapping requirements, resulting in a kind of “dear enemy” effect. Therefore, strong intraspecific competition can also contribute to the formation of plesiobiotic associations.

#### 4.2.3. Significance of Differences between Plesiobiotic Partners

**Potential Role of Competition: Position of the Plesiobionts in the Interspecific Competitive Hierarchy.** Recent studies have

revealed that *F. fusca* is one of the most frequent plesio-bionts among the studied ants. Similarly to other common plesio-bionts, *F. fusca* is also a submissive species in the three-level classification of the competitive hierarchy in ants [51, 52]. The submissive behaviour and the opportunistic character of this species can be considered as one of the main features that contribute to its frequent cooccurrence with other species in plesio-biotic associations. Although most of the plesio-biotic partners of *F. fusca* occupied a higher level in the interspecific competition hierarchy, it established plesio-biotic relationships with species that are also submissive (e.g., with *M. rubra*, *L. flavus*, and *Leptothorax acervorum*).

Being also submissive, *Myrmica* spp. are also able to coexist with aggressive ant species. For example, *M. ruginodis* and *M. scabrinodis* were observed to shift their foraging to periods with lower temperature. Accordingly, in areas where territorial competitors were also present, they visited baits at night instead [53].

In the case of the subterranean, cryptic species *L. flavus*, competitive ability may play a less significant role regarding the coexistence with other species. While the two above-mentioned plesio-bionts are surface foragers, that is, they mostly search for food on or above the ground, the colonies of *L. flavus*, however, were found to be associated with various species of root aphids [54]. Thus, for subterranean *Cautolasius* species, the importance of vertical separation in foraging seems more significant than other mechanisms for reducing competition.

Contrary to the afore-mentioned species, several *Camponotus* species are typically regarded as encounter species that is, they defend not only their nests but the discovered resources as well [51, 52]; therefore only submissive species can be expected to be their plesio-biotic partners.

*Conflict Avoidance: Differences in the Foraging Strategy of Plesio-biotic Partners and Resource Partitioning.* As plesio-biotic partner colonies share the same microhabitat [1], they have overlapping foraging area and home ranges owing to the small distances between their associated nests. Accordingly, the probability of an encounter between the members of the two colonies increases as the distance between their nests decreases [55]. Due to the close neighbourhood of the associated colonies, they are expected to interact most intensely with each other. A common outcome of interspecific competition is the minimising of spatial and/or temporal overlapping during foraging, that is, differing from each other in their daily and/or seasonal activity, foraging area, or diet [56–59]. Beside partitioning spatially and/or temporally, different foraging strategies (e.g., individual searching, tandem running and other types of recruitment systems) may also contribute to the coexistence of different species [39, 60, 61]. Although body size can also influence the foraging range, the existence of food recruitment systems makes ants less constrained by their morphology than what can be seen in the case of other animals [60, 62, 63]; thereby, the effects of behavioural features seem more important than those of morphological ones. On the other hand, differences in body size can promote resource partitioning by reducing the overlap in resource use [64]. Although differences in

body size cannot explain food-resource partitioning alone, these can still contribute to the formation of a number of plesio-biotic relationships.

## 5. Conclusions

On the basis of the above considerations, we define plesio-biosis as the occasional or regular nesting of heterospecific colonies of certain species in close proximity to each other without biological interdependence.

Based on the currently available data, members of the subfamily Formicinae establish plesio-biotic relationships the most frequently, and the most common plesio-bionts among them seems to be *F. fusca*. The opportunistic and submissive behaviour of this species makes it a typical plesio-biont, and it is also a frequent host of both temporary social parasites and slave makers [6, 65].

As a rule, plesio-biosis can be formed between ant species that differ from each other in behaviour—primarily in their competitive ability—and in foraging strategies. Other subordinate species with different behaviour or species with higher competitive ability can also be potential partners as plesio-bionts.

Beside the lack of suitable nesting sites, the appropriate amount of available food sources may also play a role in the formation of plesio-biosis, contributing to higher colony densities. The overlap in diet can enhance intraspecific competition, which may force colonies into the vicinity of heterospecific nests. Owing to higher colony density, nesting in each other's close neighbourhood will also occur more frequently. Plesio-biotic associations formed this way may promote a persistent coexistence in cases where the differences are considerable between the partners, which can lead to the formation of other types of interspecific associations with higher levels of biotic interactions.

It is important to note, that the currently available data concerning plesio-biosis are far from being representative. Only a couple of studies have dealt with this topic, and these are restricted to a small number of habitat types of few countries in the northern latitudes. Moreover, most of these studies reported only observations of plesio-biotic cases without additional ecological information, like the regularity of such associations between the species in question. Therefore, to get a more comprehensive picture about plesio-biosis, it would be essential to collect more and detailed data globally.

## 6. Open Questions

Regarding our present knowledge on plesio-biosis in ants, there are still many open questions that need to be answered, which are important for a better understanding of this kind of interspecific relationship.

(1) *Persistence of plesio-biosis.* Plesio-biosis can be formed occasionally between heterospecific colonies, but we still do not know how persistent these associations are. Although ant colonies have typically been treated as spatially fixed entities, inhabiting a given nesting site permanently, it seems that periodic nest relocation is an important aspect of the behaviour of

many ant species [66–68]. It is also uncertain what effects may trigger the disaggregation of plesio-biotic colonies and force the relocation of one of the associated plesio-bionts.

(2) *The role of nesting shelters and “ecosystem engineering.”* It also provides a basis for further investigation, to what extent the type of nesting shelters (e.g., logs, stumps, and rocks) promotes the formation of plesio-biotic associations and how the already established colonies facilitate the settlement of colonies due to their nest constructions. In temperate regions, a large number of species occupy dead logs and stumps or nest in the soil under rocks [6]. Due to their thermal properties, colonies occupying these shelters are allowed to enter to colony growth stage earlier and they are less vulnerable to unsuitable humidity and temperature values. These beneficial conditions can lead to the joint nesting of two or more species in or under the same shelter, especially if the number of suitable nesting sites is low. For example, the nest mounds of wood ants may provide suitable nesting sites for other species owing to their unique microhabitat conditions [69]. This may serve as an explanation for the untypical plesio-biotic associations observed between *F. fusca* and the members of *Formica* s. str., where the former species frequently settles into the uninhabited parts of the nest mounds of wood ants [29]. Similarly, many *Camponotus* species create their nest galleries in trunks and stumps [70–72], which may promote the establishment of colonies of other species in these microhabitats. Owing to this “ecosystem engineering,” plesio-biotic associations may develop from an occasional to a regular relationship even without direct interactions between the associated colonies.

(3) *The “close” proximity of heterospecific colonies.* Former definitions of plesio-biosis emphasise the importance of the close proximity of plesio-biotic colonies, though it is not clear how close this proximity should be or whether these colonies should use the same nesting shelter. In Table 1 we listed only those cases where the plesio-biotic colonies occupied the same nest (i.e., they were under the same stone or in the same log). It is a question, however, whether the frequent neighbouring arrangement of the nests of certain species pairs (when their nests do not necessarily border on one another) can be considered as a plesio-biotic relationship.

(4) *Plesio-biotic associations of arboreal species.* Most of the recorded cases of plesio-biotic associations are between species that inhabit nests located on or under the ground surface. Arboreal species, however, are also known to frequently create their nests in the vicinity of each other on the same tree, as it was, for instance, observed in the case of *Camponotus fallax*, *Lasius brunneus*, and *Temnothorax affinis* [73]. Actually, it was demonstrated that the former two species can occur in a plesio-biotic relationship [33]. It is an interesting question how frequently arboreal species nest in one another’s neighbourhood, and to what extent these cases can be considered as plesio-biosis.

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