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A comparative study of the fauna associated with nest mounds of native and introduced populations of the red wood ant *Formica paralugubris*

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Highlights

- Comparison of nest fauna associated with native and introduced populations of *Formica paralugubris*
- Differences in community compositions among sites, nest fauna more similar than soil fauna
- Higher oribatid mite diversity in nests than soils, unlike springtails
- Several oribatid species associated with nest habitats, whereas only a few springtails
- Weak evidence of multiple relocations of mesofauna species during transplants

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Abstract

In the second half of the twentieth century, many red wood ant populations were transferred from the Alps to the Apennines as biological control agents. Since the introduction involved the relocation of entire nest mounds, it is presumable that the associated fauna was also relocated. While the introduction of these ants has raised several concerns about their ecological impact, there has been no attempt to investigate the introduction of other nest-associated species. In this study, we collected samples of soil and nest material from three populations of the red wood ant *Formica paralugubris*, one Alpine native and two imported into the Apennines. We aimed to confirm that nest mounds are hotspots for soil fauna, detect the occurrence of new myrmecophilous species, and compare the nest-associated fauna among sites, to test the hypothesis of mass species relocation. We focused our analyses mainly on two taxa, springtails and oribatid mites, two highly representative groups of the mesofauna inhabiting nest mounds. The results showed higher richness and diversity in nests than soil for oribatids but not for springtails. We found 17 myrmecophilous oribatid species, but only two springtail species. Finally, native and imported sites shared only a few oribatid and springtail species, suggesting that massive relocation did not occur with nest transplants or it was likely limited. Additionally, we found some species never before collected in Italy.

Keywords: red wood ants, myrmecophily, soil fauna, *Formica paralugubris*, oribatid mites, springtails, new species

1. Introduction

Red wood ants (RWA) are typical in Central and Northern Europe, where seven species of *Formica* s.s. or the *F. rufa* group are known [1]. In contrast to other ants, these species are mostly associated with coniferous trees and require cold climates [2]. In the southern portion of their distribution area, their presence is limited to higher altitudes [3,4,5,6]. In Italy, the species of *Formica s.s.* are widespread along the Alpine chain, and only the more thermophilic *Formica pratensis* Retzius, 1783 naturally occurs at more southern locations in the Apennine mountains [7], although its exact distribution is still unknown. In the mid-twentieth century, nests of several alpine RWA species, such as *F. paralugubris* Seifert, 1996, *F. polyctena* Förster, 1850, and *F. aquilonia* Yarrow, 1955, were repeatedly introduced to the Apennines as biocontrol agents for forest insect pests, and in some cases, viable populations established and started to spread [8,9,10]. Their impact on the arthropod fauna inhabiting the newly occupied area has been demonstrated [9]. All RWA species are known to profoundly affect local communities, from plants to vertebrates, due to their predatory ability, dominant status, and capacity to modify the physical properties of the habitats they colonize [1,11,12,13]. The large aboveground nest mound is one distinguishing characteristic of these ants. They are formed to maintain stable humidity and temperature in the nest chambers, and often contrast with harsh external conditions [14,15,16]. For example, in *F. polyctena* mounds, the difference between the nest and air temperature during the winter can exceed 20 °C [17]. In cold habitats, this microclimatic stability may turn the RWA mounds into “warm islands”, which can be attractive for a wide array of organisms [18,19]. More in general, that ant nests can provide shelter, food and favorable physical conditions for many litter animals has been established for several ant species [e.g. 20,21,22,23,24].

The invertebrate fauna hosted in RWA nest mounds, assessed in multiple studies, includes a broad range of taxa: isopods, spiders, mites, nematodes, springtails and a long list of insects, from flies to several beetle species [25,26,27,28]. More than 120 obligate myrmecophilous species have been found in RWA nest mounds, as well as several other species that occasionally inhabit nests because of their combined and often favorable moisture, pH and temperature conditions [19]. Myrmecophily can be defined as the partial or complete dependence on ant colonies by non-ant species [29]. This relationship can be based upon parasitic, commensal or even mutualistic interactions [30,31]. Thus far, more than ten thousand myrmecophilous arthropods are known, and they have evolved numerous strategies to inhabit or have access to ant nests [32,33,34], such as chemical camouflage, morphological mimicry and pheromonal attractors [35,36,37].

In this study, we analyze the invertebrate fauna hosted in the nest mounds of *F. paralugubris*, a highly polydomous and polygynous RWA species [38]. Since this species was one of the most often introduced into the Italian peninsula [10], we focus our study on the comparison of the nest myrmecophiles from native and introduced populations. Ant translocation involved the movement of entire nest mounds [8], and this likely translocated all the associated fauna as well. The main aims of this study are: i) to confirm that nest mounds can be attractive for the soil fauna, both in the native and imported populations, by comparing assemblages inhabiting nest mounds and soil; ii) to identify potentially myrmecophilous species not previously described in the literature; iii) to compare soil and nest fauna across sites and evaluate if this difference supports the hypothesis of species relocation. We focused on springtails (Hexapoda, Collembola) and oribatid mites (Acari, Oribatida), which were used in previous studies as common representative taxa of the mesofauna inhabiting RWA nest mounds [39,40,41,42]. Among microarthropods, springtails and oribatid mites constitute two of the most species-rich taxa of the soil ecosystem [43]. Although quite distant phylogenetically, the two groups share several ecological and behavioral features because of their adaptation to similar ecological niches. Both groups feed on litter and soil micro-organisms and graze on fungi, and thereby affect the dispersion of saprophytic and mycorrhizal species and control fungal populations [44,45,46,47]. Their community structure is modulated by several natural factors, including plant diversity, litter quality and meta-population dynamics. However, these two key groups are also sensitive to anthropogenic factors such as land use, soil tillage, environmental pollution, physical disturbance and fire [48,49,50,51].

2. Materials and Methods

2.1 Study area and sampling design

The sampling was carried out between June and August 2017. Samples of nest material and soil were collected from three sites, one in the Alps in the Giovetto di Paline Nature Reserve (abbreviated as GP, 45° 57’57’’N, 10° 7’48’’E), and two in the Apennines, in the Abetone forest (abbreviated as AB, 44° 08’50’’N, 10° 40’24” E) and the Campigna Biogenetic Nature Reserve (abbreviated as CA, within the Foreste Casentinesi, Monte Falterona e Campigna National Park, 43° 52’00’’N, 11° 44’14’’E) (Fig. 1). The Alpine site, GP, is the site of origin, where nests later imported to both Apennine sites were collected [52]. Nests used for sampling in the Campigna Biogenetic Nature Reserve were imported in 1958 [9, 52], whereas the exact year of transplants is not available for the Abetone forest. However, the period was probably similar (Groppali, personal communication). The habitats of the three sites are similar, a mixed forest composed of a dominant conifer species and beech (*Fagus sylvatica* L. 1753). The dominant species in the Alpine site is the red fir (*Picea abies* (L.) H. Karst, 1881), while in the Apennine sites, it is the white fir (*Abies alba* Mill, 1759). The geographic position of all ant nests—including sampled nests—was recorded in five hectares per site by a GPS locator (Garmin eTrex® 10, accuracy ~ 3 m), and the density per hectare was evaluated.

Five nests of *F. paralugubris* of similar size (height range, 1.3–1.5 m; diameter at the base of the mound, 2.3–2.6 m) were chosen in each area. Nests were spaced at least 15 meters apart to ensure independent sampling of the nest fauna. Moreover, we preliminarily checked for the presence of ant trails connecting the selected nests. From each mound, we collected three 1-dm^3 samples of nest material (total number of samples = 45, 15 per site) and two 1-dm^3 samples of soil three meters from each nest (as control) utilizing a soil corer (15 cm diameter) to a depth of 50 cm. Nest material was collected at 40 cm depth from the surface of the mound. Each sample was separately stored in a plastic bag. All samples were transferred to the laboratory within 6 hours from the time of collection. The material was gently stirred and homogenized in a plastic basin and then placed into a Berlese funnel. Samples were left in the funnels for 5 days, following Parisi et al. [53]. The specimens collected were examined using a stereomicroscope. Oribatids and springtails were identified to the species level, while most of the other organisms were identified to a higher taxonomic level. All samples were stored in pure ethanol for further analysis.

2.2 Statistical analyses

Species diversity at the three sites was estimated following Chao et al. [54], using as input the abundance data for oribatids and presence/absence for springtails. The use of presence/absence for springtails is motivated by the strongly aggregated distribution of several species of this taxon [55,56], which may hamper diversity estimates [54]. The method for evaluating diversity is based on the estimation of Hill numbers, qD, and yields estimates of total (rarefied and extrapolated) species richness ($q = 0$), and the exponential values of the Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$) indices. The 95% confidence intervals were obtained from bootstrapping, based on 4999 replications of the reference sample set. Finally, differences in observed species density among sites (defined as the number of species captured in each sample) were assessed using mixed-effect modelling with Poisson error distribution, including the nest as a random variable [57]. A Tukey post-hoc test was then performed to assess the differences in pairs.

Association of a species with either nests (i.e., myrmecophily) or soil was evaluated by analyzing the probability of occurrence in the respective material. Generalized Linear Mixed Models (GLMM) were used for this analysis, with the type of habitat (nest or soil) as the main factor. For springtails, we used binomial distribution (presence/absence data) in the model, whereas for oribatids, given the high difference in abundance between samples, we log-transformed data and used a Gaussian distribution. For springtails, we analyzed only species that occurred in at least three samples in each site in which they were present. For oribatids, following Elo et al. [42], we tested only species that occurred in at least three samples and with at least ten individuals per site. Sites in which the species did not occur were omitted from the analysis.

Compositional differences among sites were investigated using multivariate techniques. Rare species (those with less than three observations) and empty samples with no specimens were omitted from the following analyses [58]. The multivariate distances among samples were computed with the Bray-Curtis dissimilarity index after log transformation of the data, and the resulting distance matrix was analyzed by non-metric multidimensional scaling (nMDS) according to Clarke and Warwick [58]. Species composition differences were tested with a permutation-based non-parametric multivariate analysis of variance (PERMANOVA), using the factor “site” (fixed) and “nest” (random, nested) to account for non-independence of observations. β-diversity was computed following Anderson et al. [59], and permuting model residuals were compared to generate a permutation distribution of F under the null hypothesis of no difference in dispersion between groups. All analyses were conducted using the R software package (ver.3.6) using the libraries “vegan”, “iNEXT” and “ecodist”.

3. Results

The estimate of nest density was similar among sites (AB ~ 13 nests/ha, CA ~ 12 nests/ha, GP ~ 12 nests/ha). We collected a total of 32 springtail species (11 in GP, 21 in CA and 16 in AB) belonging to 21 genera, 122 oribatids (49 in GP, 39 in CA and 51 in AB) belonging to 62 genera, 53 morphospecies of other arthropods, 2 morphospecies of Annelida (Haplotaxida) belonging to the Enchytraeidae and Lumbricidae families, and one nematode morphospecies. Of the 53 morphospecies of arthropods, 39 were insects, subdivided into Coleoptera (23), Diptera (6), Hemiptera (4), Lepidoptera (2), Hymenoptera (2), and one each of Thysanoptera and Psocoptera.

Other arthropods included four Diplopoda, three Chilopoda, three Arachnida, one Protura, one Diplura and one Symphila. A detailed list of the morphospecies collected (Collembola and Oribatida excluded) and their abundance at each site and type of habitat (nest or soil) is reported in Supplementary material S1.

Except for springtails and oribatids, the most represented group was that of beetles. Overall, most coleopteran morphospecies were found in nests (20 out of 23, 17 of them exclusively in nests), whereas only seven out of 23 morphospecies were collected in soil samples (three of them exclusively in soil). Among Coleoptera, Staphylinidae was the most represented taxon, with ten total morphospecies collected. Diptera (6 morphospecies) were collected only in the soil samples. All three spider morphospecies collected were associated with nests only. None of the other groups with more than one morphospecies was exclusive for either of the two types of samples.

We found three oribatid species new to Italy: *Damaeus selgae* Pérez-Íñigo, 1966 and *Scheloribates tuberculatus* Pérez-Íñigo jr., Herrero and Pérez-Íñigo, 1987 only known from Spain [60], and *Dissorhina ornata peloponnesiaca* Mahunka, 1974, recorded in Spain [61], Greece [62] and recently, Poland [63]. Moreover, the myrmecophilous beetle *Monotoma conicicollis* Chevrolat, 1837 (Monotomidae), previously recorded only in the Alps, was recently recorded for the first time in the Apennines [64]. Several species of insects, previously known only in the Alps, have often been overlooked, and their populations only recently recorded in the northern Apennines and surrounding areas [65,66].

In total, we found 19 species that preferred ant nests (2 springtails and 17 oribatids), whereas seven species preferred soil (2 springtails and 5 oribatids) (Table 1). Pooling all sites, no difference in the number of springtail species in soil and nests was found (Fisher exact test $p = 0.805$), whereas oribatid species richness was significantly higher in nests than soil (Fisher exact test $p = 0.022$). The number of species shared between soil and nests differed among sites for springtails (Fisher exact test $p = 0.022$, Figure 2), but not for oribatids (Fisher exact test $p = 0.310$). The number of species shared among sites is summarized in Table 2. There was no difference between the proportion of shared species both in soils and in nests with respect to the total number of species in that habitat (Mantel-Haenszel chi-square test with continuity correction: $\chi^2 = 2.1$, $p = 0.147$).

Focusing on nest samples, CA generally had slightly higher springtail species richness and diversity than either AB or GP, although the confidence intervals of the three sites overlapped widely (Figure 3). Species density did not differ among sites for springtails (Type III Wald test: $\chi^2 = 1.727$, df = 2, $p = 0.422$). For oribatids, CA had lower α-diversity than AB and GP, while species density was significantly lower than at AB and GP ($\chi^2 = 18.943$, df = 2, $p < 0.001$; multiple comparisons: CA vs AB: z = -3.572, $p < 0.001$; CA vs GP: z = -4.078, $p < 0.001$; AB vs GP: z = -0.525, $p = 0.859$).

The nMDS ordination plot for springtails (Figure 4a, stress = 0.06) showed a separation among groups, whereas nest samples were partially separated by site. The PERMANOVA (Table 3) revealed a significant effect of the factor site, but also significant variability among replicate nests within each site. A clearer picture emerged from the nMDS ordination plot of oribatids (Fig. 4b, stress = 0.17). In this case, the three sites clearly had different soil assemblages, but the two introduction sites AB and CA were closer to each other (i.e., more similar) than to GP. The data points of the former two were located on opposite sides of the plot of the latter one. Nest assemblages were also fairly distinct by site but were more similar than soil samples. All soil samples were located in the central part of the plot, in close connection to each other. Notably, while the soil samples from the Apennine sites were clearly separated by those from the Alps, the nest samples were more similar. Even in this case, PERMANOVA revealed significant differences in nest assemblages among sites, both also significant within-site variability (Table 3). Finally, no significant difference in β-diversity among sites was found for either springtails ($p = 0.054$) or oribatids ($p = 0.431$).

4. Discussion

4.1 Richness and diversity of soil and nest fauna

The predictions that higher species richness would be found in nest mounds of *F. paralugubris* than in the surrounding soil was confirmed for oribatids, but not for springtails. As for this latter group, the presence of red wood ants is known not to be a determining factor affecting their occurrence (see Lenoir et al. [40] for a study with *F. polyctena*). However, little is known about the difference in richness and diversity between ant nests and the surrounding soil. Conversely, for oribatids, our finding is consistent with Laakso and Setälä [18], who found higher mite richness in nests of *F. aquilonia* than in the nearby soil.

Our results contrast with those of Elo et al. [42], who found different species but comparable species richness in the nest mounds of *F. polyctena* and the surrounding soil. As no other replicate studies on the same ant species are available, it is not possible to know if these differences represent specific features of the three species assessed, or, instead, they are driven by local environmental determinants, as suggested by Elo et al. [42]. These authors hypothesized that this incongruence could be due to differences in the quality of the leaf litter, which is assumed to be poorer in coniferous stands than in broadleaf forests. This relative lack of litter might compel mites to aggregate within nest mounds more strongly in the former than in the latter. A second suggested factor could be nest density: the higher density may drive species to be more distributed and less concentrated among ant nests. In our study, the hypothesis regarding leaf litter quality might be supported, because all three sites were dominated by coniferous trees (*Abies alba* and *Picea abies*), as in Laakso and Setälä [18], although a denser understory is present in the Alpine site. Nest density may have an effect as well, but we do not have any reference to verify whether the density in our sites is relatively high or low, and therefore how it might influence the aggregative behavior of nest symbionts. However, density was very similar among sites; hence this factor should similarly influence all three populations.

4.2 Myrmecophilous or soil-preferring species

Springtails and oribatid mites showed different degrees of potential myrmecophily. Only two springtail species, *Cyphoderus albinus* Nicolet, 1842 and *Lepidocyrtus cyaneus* Tullberg, 1871 selectively chose ant nests, and both are known myrmecophilous inhabitants of RWA nest mounds [19,26], and other ant species (e.g., *C. albinus* in *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, 1990 nests [67]). In contrast, two species, *Folsomia penicula* Bagnall, 1939 and *Pseudosinella apuanica* Dallai, 1970, both known to occur in Italy [68], preferred soil habitats, even though in both cases, the preference was not absolute, as they also occurred in some ant nest samples, though to a lesser extent.

Conversely, a higher number of oribatid species (17 out of 122) were found to be potentially myrmecophilous. Four of these, *Carabodes labyrinthicus* Michael, 1879, *Carabodes ornatus* Storkán, 1925, *Liacarus coracinus* Koch, 1841, and *Pergalumna nervosa* Berlese 1914, have previously been described as preferring the nest habitat [42]. Most of the species collected are quite common, such as the ones belonging to the *Carabodes* genus, which can be found both in European and American forests, mainly in tree bark where lichens, mosses, and fungi are present [69,70]. Since all these latter organisms (or parts of them) can be found within nest mounds, either alive or as nesting material [71,72], it is possible that nest habitat is suitable for some *Carabodes* species. Two *Pergalumna* species were recognized as potentially myrmecophilous, *P. nevosa* and *P. altera*. Both species have previously been collected in central Italy [73,74]. The species within this genus are known predators of nematodes [75,76], which, in turn, may find the particular nest conditions favorable for proliferation [77]. Unfortunately, the Berlese funnel is not an accurate tool for detecting nematodes, so we cannot provide reliable information on nematode communities.

Regarding the linkage between *Phauloppia lucorum* Koch 1841 and ant nests, usually, most species of the *Phauloppia* genus are known to inhabit and feed on lichens [78,79,80]. Thunes et al. [81] found that the occurrence of the RWA *F. aquilonia* negatively impacted the lichen community, probably because of the chemical changes in the environment or by the direct collection of thallus fragments, which can be found within RWA nest mounds [72]. However, to our knowledge, it is hitherto unclear whether those lichen fragments came from active harvesting by ants or merely from the collection of detached lichen fragments. In any case, *P. lucorum* may feed on the lichens transported by ants into the nests, making the nest mound a suitable habitat for this species as well.

Only a few species, such as two *Oppiella* species and *Minunthozetes pseudofusiger* Schweizer, 1922 showed a preference for soils. For the latter, the preference for soil instead of other habitats, such as grass, roots or litter, is known [82], although studies on their avoidance of ant nests are not available. The generalist and eurytopic *Oppiella* species are known to occur in harsh habitats, such as newly burned soils [83], suggesting that in this context, they prefer to occupy habitats with more extreme temperatures and moisture conditions [84].

4.3 Comparison of assemblages among sites and species relocation hypothesis

We detected differences in species richness and diversity across sites only for oribatids but not for springtails. Lower oribatid diversity was found at Campigna, whereas the native site of Giovetto di Paline and Abetone were very similar. This result is quite surprising, because the two imported populations, Campigna and Abetone, are geographically close and very similar in their general features (fir-dominated forests, altitude and climate). The Alpine site, although similar in dominant tree composition, shows denser understory (F. Frizzi, personal observation), which may potentially affect both springtails and mite diversity [85,86]. However, many factors may influence diversity, such as altitude, climate conditions, and geographic location [2]. Moreover, metapopulation rules apply to the nest mound fauna of RWA populations, and inter-nest distances may affect diversity [87]. Although the mean nest density was similar among sites, the distances between sampled nests with neighboring ones were not measured in a precise manner, and a different exchange of mesofauna between nests among sites cannot be ruled out. Thus, the reasons behind this apparent incongruence are not yet determined and could be a subject for future studies.

According to the multivariate analysis, the three sites had different springtail and oribatid assemblages, both for soil and nest communities. No springtail species and only three oribatid species were shared among the three soil sites. The difference in the soil assemblages probably reflects the geographic distance, which is shorter between the two imported populations than between native and imported sites. On the other hand, notably, the oribatid fauna was more similar among nests than among soils, irrespective of the site, which may suggest a wider geographic diffusion of some nest-preferring species than of the soil fauna. Indeed, the proportion of shared species was nearly twice among nest than soil samples (12 out of 102 in nests, 3 out of 54 in the soil). To our knowledge, this is a novel finding and a targeted genetic analysis of these taxa in soils and nest mounds could shed light on the effective dispersion history of the species [88,89].

Nonetheless, the number of species sampled in nests and shared among sites (2 springtails and 12 oribatids) was rather low compared to the total number of species collected in all nest samples (22 springtails and 102 oribatids). This result may suggest that the number of species transferred from the Alps and established in the Apennines was not high or that some of the species already occurred in central Italy. For example, the two springtail species, *C. albinus* and *L. cyaneus*, are known myrmecophilous species in many parts of Europe [26,67]. Hence it is likely that they spontaneously occur at all sites independent of introductions. Thus, possible relocation with nest material can be hypothesized only for a few species. For example, we collected a few specimens of the oribatid mite *Jugatala angulata* Koch, 1839 in the nests of all three sites, even though this species has never been recorded in Italy except for the Alps [90,91]. Similarly, *Cymbaeremaeus cymba* Nicolet, 1855 was found only in nest samples in both introduction sites, although this species has already been recorded in the Italian peninsula, but only in northern and southern sites and not in the central regions [73]. For the other nest-preferring species, it is challenging to hypothesize a relocation process, because some of them were also recorded in soil samples (*Adoristes ovatus* Koch, 1839, *C. labyrinthicus*, *Hermannia gibba* Koch, 1839, *Scheloribates pallidulus* Koch, 1841). It cannot be excluded that individuals of some species—not strictly dependent on ants to survive—shifted toward inhabiting the soil.

5. Conclusions

In conclusion, this is the first study to include an introduced population in a comparative analysis of the nest-associate fauna in red wood ants. We confirmed that RWA nests are hotspots for arthropod biodiversity, particularly for oribatid mites. We found several potentially myrmecophilous species that preferred the nest habitat instead of soil, though the symbiotic relationships with ants should be further investigated to verify myrmecophily. We used for the first time a comparative approach in the analysis of the nest fauna, assessing the differences between a native Alpine population and two introduced Apennine populations of the RWA *F. paralugubris*. Although we might expect some clear traces of a large species relocation given the massive transport of nest material during introductions, we found only a few species that potentially could have been transferred, suggesting that it probably did not occur. More comparative studies are recommended, e.g. on RWA imported populations, since the fate of most of them—and the fauna inhabiting their nests—are hitherto almost wholly unknown.

Fig. 1. Map of the three sampling sites. In light grey is the alpine site of the original population, and in dark grey, the two Apennine sites of the two introduced populations.

Fig. 2. Cumulative number of species observed at the three study sites for a) springtails and b) oribatids. Black bars = nests, white bars = soil, grey bars = species shared between soils and nests. Sites: AB = Abetone (Apennines), CA = Campigna (Apennines), GP = Giovetto di Paline (Alps).

Fig. 3. Species diversity in the three sites (red = Abetone, Apennines; blue = Campigna, Apennines; green = Giovetto di Paline, Alps). Sample-based plots with 95% confidence intervals for species richness (q=0), Shannon (q=1), and Simpson (q=2) diversity indexes. Continuous lines = observed values; dashed lines = extrapolated values.

Fig. 4. nMDS ordination plots for a) springtail and b) oribatid datasets. Colors indicate the sites (red = Abetone, Apennines; blue = Campigna, Apennines; green = Giovetto di Paline, Alps), symbols indicate sample types (triangles = samples from nests; circles = samples from soils).

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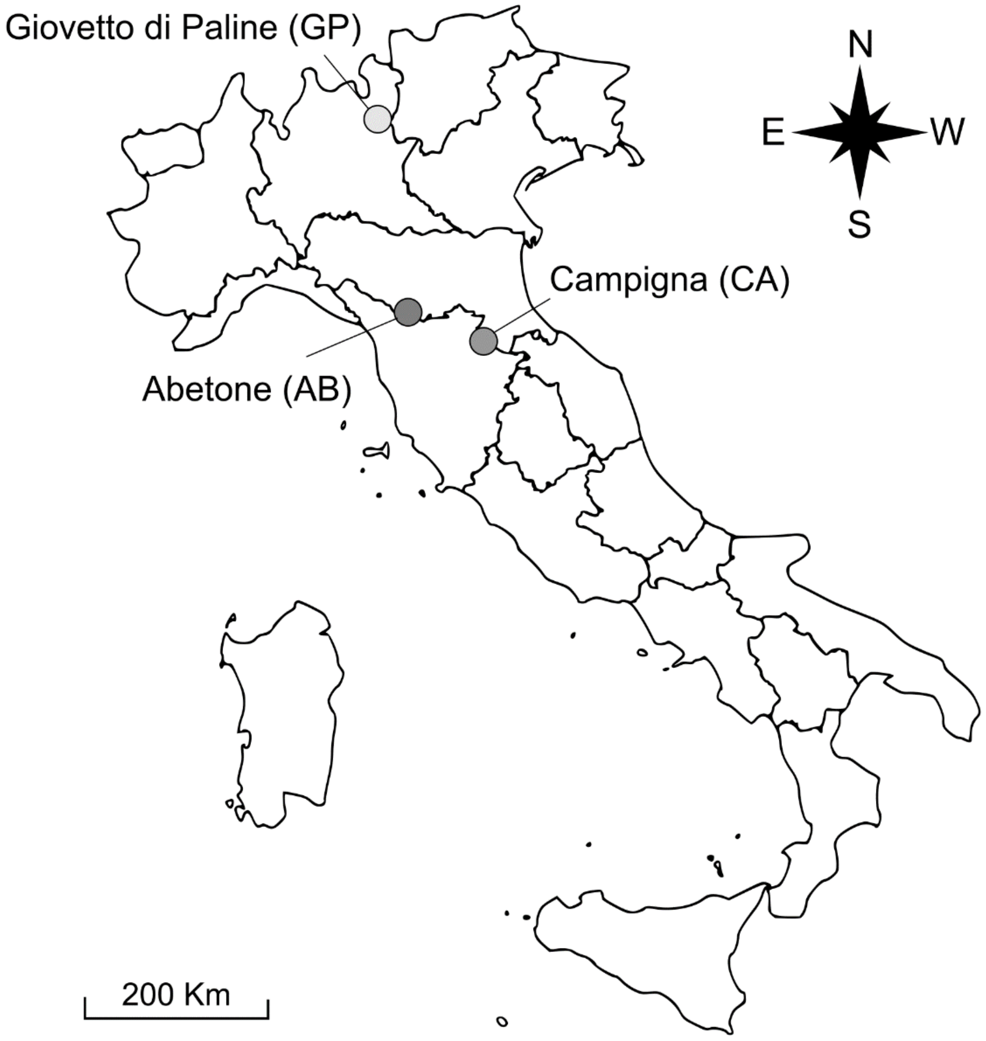
Giovetto di Paline (GP)
N
E
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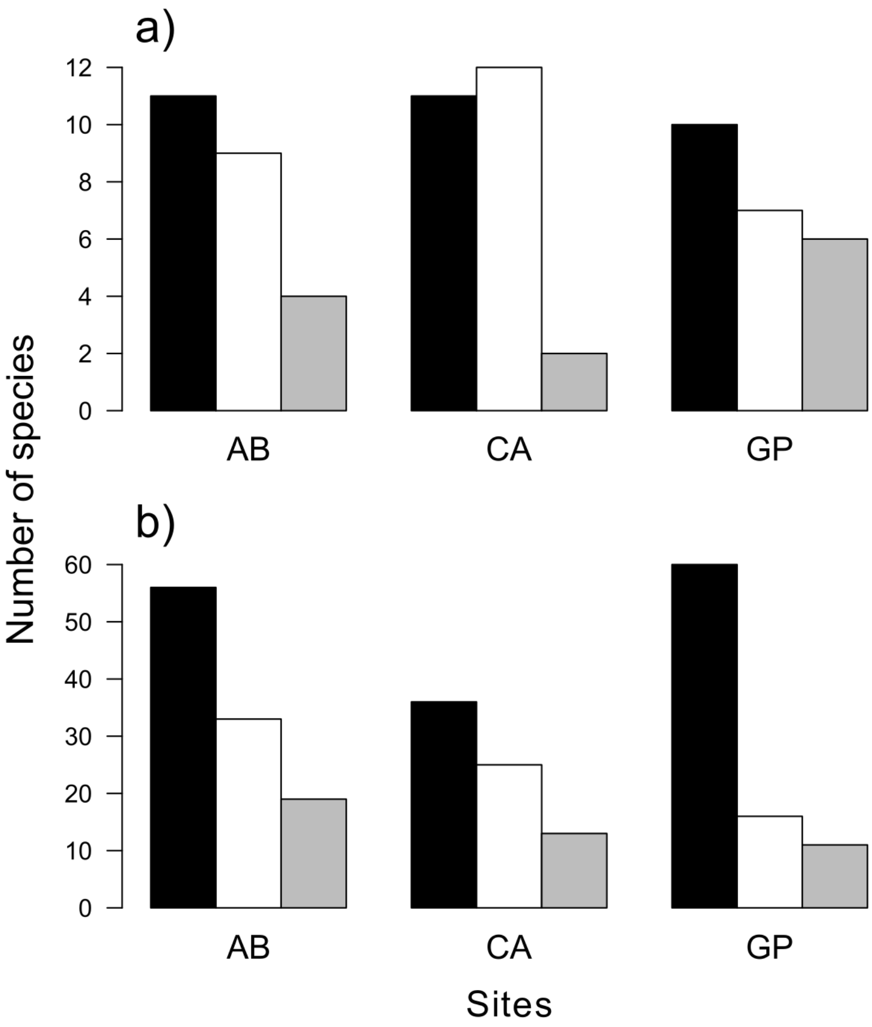
S
Campigna (CA)
Abetone (AB)
200 Km


a)
12
10
8
6
4
2
0
AB
CA
GP
Number of species
b)
60
50
40
30
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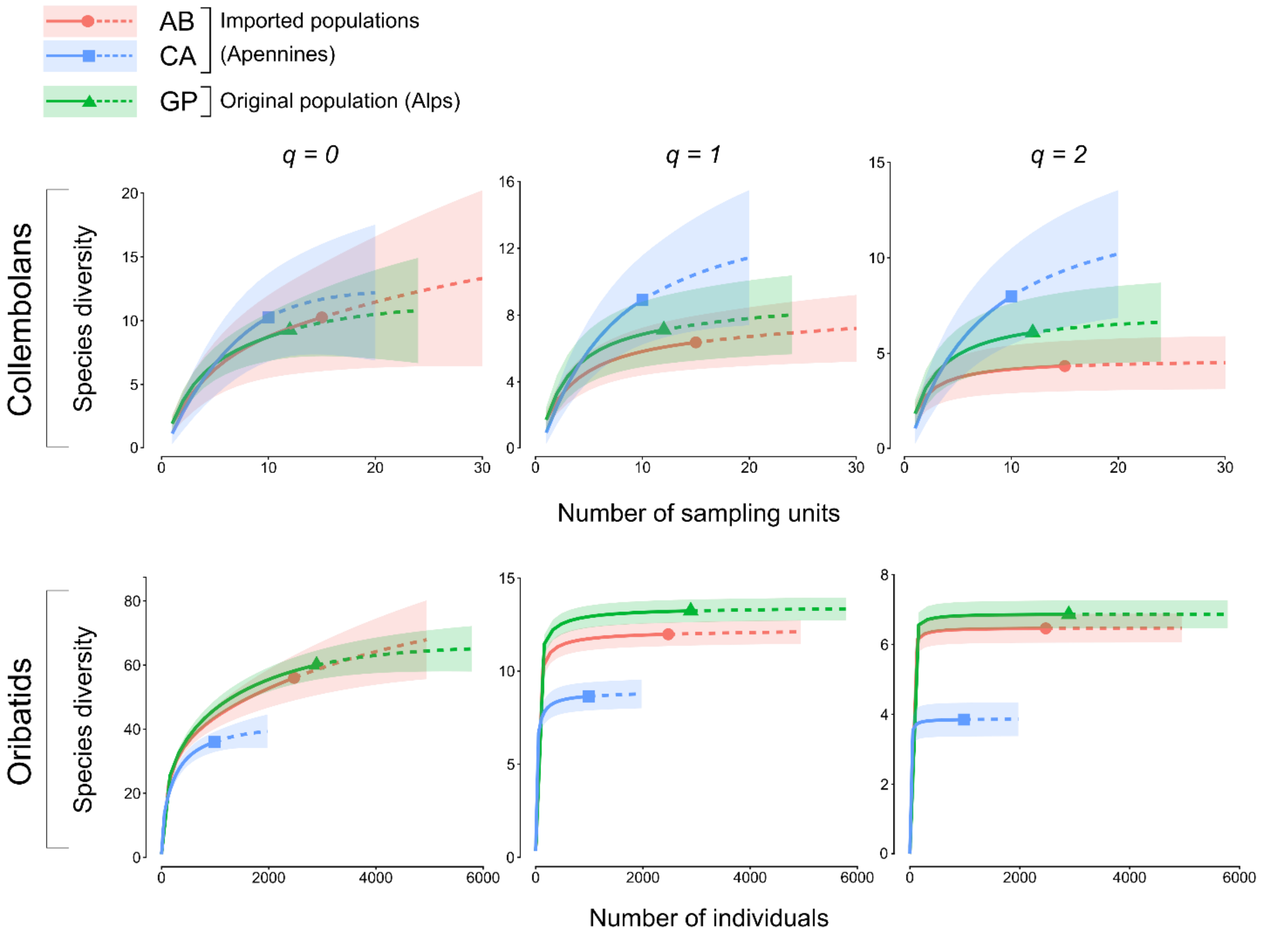
GP
Sites


AB
CA
Imported populations
(Apennines)
GP
Original population (Alps)
q = 0
q = 1
q = 2
Collembolans
Species diversity
Number of sampling units
Oribatids
Species diversity
Number of individuals
0
5
10
15
20
0
4
8
12
16
0
5
10
15
0
10
20
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4000
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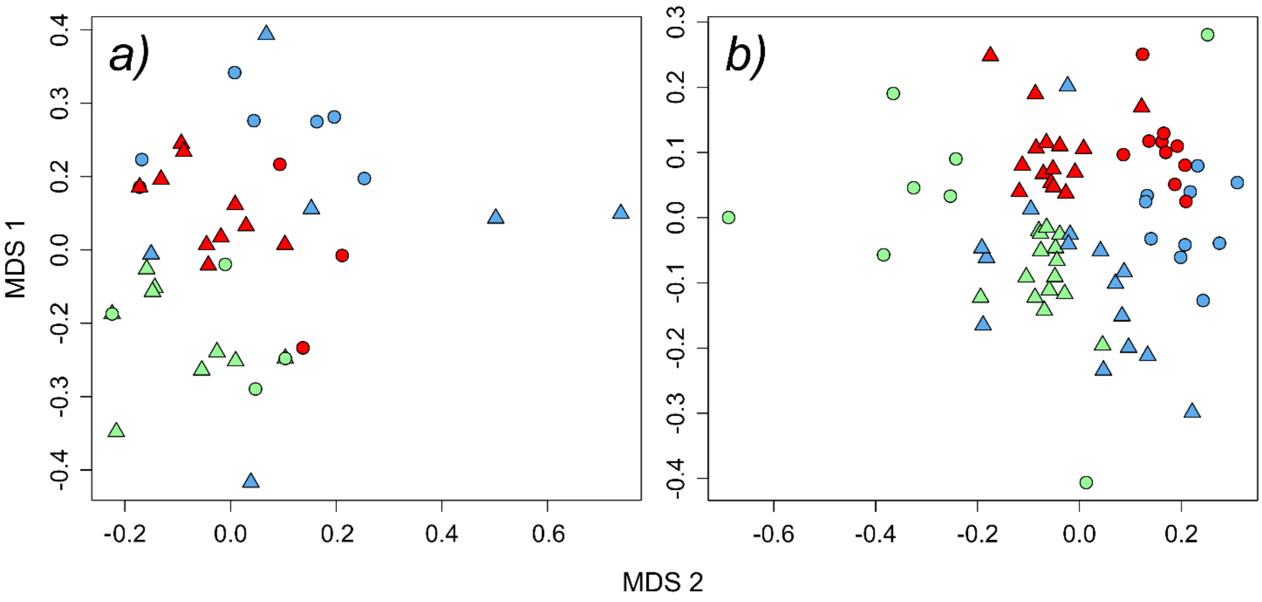
a)
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MDS 1
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0.4
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0.0
0.2
0.4
0.6
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.6
-0.4
-0.2
0.0
0.2

Table 1

Species of springtails and oribatids collected, with their abundance and the estimated preference for nest or soil according to results of models. Pref = preference. Sites: AB = Abetone (Apennines), CA = Campigna (Apennines), GP = Giovetto di Paline (Alps).

Springtails	AB		CA		GP		
Species	Nest	Soil	Nest	Soil	Nest	Soil	Pref
Anurophorus atlanticus	1	-	-	-	-	-	
Ceratophysella armata	-	2	-	10	-	-	
Cyphoderus albinus	2277	-	24	-	438	2	Nest
Desoria sp.	1	-	9	1	-	-	
Entomobrya nivalis	-	-	-	-	4	-	
Entomobrya sp.	3	2	1	-	-	-	
Folsomia manolachei	6	-	-	12	-	-	
Folsomia penicula	5	39	-	-	32	25	Soil
Folsomia sp.	-	-	-	3	-	-	
Friesea mirabilis	24	-	6	-	-	-	
Hypogastrura viatica	-	-	-	-	1	-	
Isotomurus sp.	-	-	-	3	-	-	
Lathriopyga longiseta	-	-	3	-	-	-	
Lepidocyrtus violaceus	-	-	9	-	-	-	
Lepidocyrtus cyaneus	8	-	21	-	56	1	Nest
Lepidocyrtus lanuginosus	-	-	-	-	1	-	
Lepidocyrtus lignorum	-	-	-	-	1	1	
Mesaphorura sp.	-	-	-	-	-	1	
Paratullbergia callipygos	-	1	1	-	-	-	

Parisotoma notabilis	18	1	-	-	6	1	
Protaphorura armata	-	1	1	1	-	-	
Protaphorura campata	-	1	-	-	-	-	
Protaphorura cancellata	-	-	2	-	6	1	
Pseudachorutes dubius	-	-	-	2	-	-	
Pseudachorutes sp.	-	-	-	1	-	-	
Pseudosinella alba	-	-	-	1	-	-	
Pseudosinella apuanica	6	13	-	1	-	-	Soil
Tetracanthella pilosa	-	-	-	2	-	-	
Tomocerus minor	-	2	-	-	-	-	
Vertagopus arborea	-	-	2	-	-	-	
Xenylla maritima	-	-	-	-	4	-	
Xenylla schillei	29	-	-	1	-	-	

Oribatids	AB		CA		GP		
Species	Nest	Soil	Nest	Soil	Nest	Soil	Pref
Achipteria coleoptrata	-	-	25	7	19	-	
Achipteria italica	-	-	6	2	-	-	
Acrogalumna longipluma	55	-	32	-	-	-	Nest
Adoristes ovatus	19	-	64	2	111	1	Nest
Atropacarus clavigerus	-	-	-	-	19	-	
Atropacarus platakisi	-	-	-	-	3	-	
Banksinoma lanceolata	-	-	1	-	-	-	
Belba bartosi	-	-	-	-	1	-	
Berniniella (Berniniella) hauseri	3	-	-	-	-	-	
Berniniella bicarinata	7	1	-	14	-	-	
Berniniella coronata	-	-	-	-	-	1	
Berniniella (Hypogeoppia) dungeri	-	9	-	-	-	-	

Camisia horrida	-	-	-	-	2	-	
Camisia spinifer	4	-	-	-	-	-	
Carabodes areolatus	2	-	-	-	2	-	
Carabodes labyrinthicus	149	3	3	5	13	1	Nest
Carabodes manganoi	3	-	4	-	-	-	
Carabodes marginatus	-	-	4	-	5	-	
Carabodes ornatus	11	-	5	-	19	-	Nest
Carabodes palmifer	1	-	-	-	-	-	
Carabodes reticulatus	-	-	-	-	1	-	
Cepheus pegazzonae	1	-	-	-	-	-	
Cerachipteria minuscula	23	1	1	8	-	-	
Ceratozetes gracilis	-	-	59	21	2	-	
Ceratozetes minutissimus	-	-	-	-	2	-	
Ceratozetes peritus	2	13	-	-	-	-	Soil
Chamobates cuspidatus	-	1	-	-	1	-	
Chamobates pusillus	23	1	-	-	-	-	
Chamobates rastratus	-	-	-	-	271	-	
Chamobates voigsti	-	-	-	-	5	6	
Cymbaeremaeus cymba	9	-	3	-	1	3	
Damaeus selgae	-	-	-	-	60	-	
Dissorhina ornata peloponnesiaca	-	4	-	-	-	-	
Eniochthonius minutissimus	-	-	-	-	24	-	
Eremaeus cordiformis	-	-	4	-	5	-	
Eueremaeus oblongus	340	-	-	-	-	-	Nest
Eueremaeus silvestris	-	-	52	9	-	-	
Eueremaeus valkanovi	-	-	-	-	7	-	
Eulohmannia ribagai	-	-	-	1	-	-	

Eupelops acromios	3	-	-	-	3	-	
Eupelops affinis	1	-	-	-	-	-	
Eupelops torulosus	1	-	1	-	46	-	Nest
Euzetes globulus	-	1	-	-	-	-	
Fosseremus laciniatus	-	-	-	-	-	1	
Hemileius initialis	-	-	-	-	1	-	
Hermannia gibba	48	1	2	2	29	-	
Hypochthonius luteus	-	-	-	-	8	-	
Jugatala angulata	2	-	2	-	1	-	
Lepidozetes singularis	-	-	6	-	6	2	
Liacarus coracinus	30	1	-	-	197	3	Nest
Liacarus perezinigoi	-	-	-	-	1	-	
Liacarus subterraneus	-	-	4	-	-	-	
Liebstadia humerata	-	-	-	-	3	-	
Liebstadia longior	15	-	-	-	-	-	Nest
Medioppia pinsapi	-	-	-	-	-	2	
Metabelba parapulverosa	-	-	-	-	35	-	
Microppia minus	-	7	-	-	-	-	
Minunthozetes pseudofusiger	5	75	-	53	-	-	Soil
Multioppia glabra	-	-	-	-	5	-	
Nanhermannia nana	-	-	-	-	1	-	
Neotrichoppia (Confinoppia) confinis	20	9	-	3	84	1	
Nothrus anauniensis	-	1	-	1	-	-	
Nothrus silvestris	-	-	-	-	-	1	
Odontocepheus elongatus	11	-	-	-	2	-	
Ommatocepheus ocellatus	5	-	-	-	-	-	
Ophidiotrichus vindobonensis	-	-	-	-	3	-	

Oppiella (Moritzoppia) keilbachi	-	-	-	-	140	-	
Oppiella (Moritzoppia) unicarinata	-	-	37	-	4	-	
Oppiella (Oppiella) acuminata	96	-	-	-	-	-	
Oppiella (Oppiella) nova	30	39	-	10	25	-	
Oppiella (Rhinippia) fallax	1	2	-	-	-	-	
Oppiella (Rhinoppia) obsoleta	-	39	-	-	-	-	Soil
Oppiella (Rhinoppia) similifallax	-	1	-	-	-	-	
Oppiella (Rhinoppia) subpectinata	1	97	-	95	8	-	Soil
Oribatella brevipila	-	-	11	-	58	-	
Oribatella calcarata	-	-	-	-	4	-	
Oribatella euthricha	-	-	2	-	-	-	
Oribatella hungarica	15	-	-	-	-	-	
Oribatella quadricornuta	-	-	-	-	7	-	
Oribatella sexdentata	1	-	-	-	-	-	
Oribatula tibialis	4	-	8	3	2	1	
Pantelozetes paolii	-	1	-	-	2	-	
Parachipteria petiti	13	11	-	-	-	-	
Parachipteria punctata	1	-	-	-	-	-	
Pergalumna altera	39	-	4	-	63	-	Nest
Pergalumna nervosa	131	-	83	-	736	-	Nest
Phauloppia lucorum	17	-	-	-	-	-	Nest
Phauloppia rauschenensis	-	-	-	-	2	-	
Phthiracarus anonymus	1	-	-	-	8	-	
Phthiracarus clavatus	2	-	1	-	-	-	
Phthiracarus globosus	-	-	1	-	-	-	
Phthiracarus italicus	-	1	-	3	-	-	
Phthiracarus laevigatus	-	-	9	-	-	-	

Phthiracarus lentulus	1	1	-	-	-	-	
Phthiracarus nitens	1	2	5	1	-	-	
Phthiracarus peristomaticus	-	-	-	-	12	-	
Platynothrus peltifer	-	-	-	-	1	-	
Porobelba spinosa	551	-	121	-	-	-	Nest
Poroliodes farinosus	2	-	-	-	-	-	
Ramusella (Inscuptoppia) elliptica	1	22	-	-	-	-	Soil
Ramusella (Ramusella) assimilis	-	-	3	4	1	-	
Raphigneta numidiana	-	-	-	-	-	1	
Rhysotritia duplicata	-	-	10	1	109	1	Nest
Scheloribates laevigatus	1	-	-	-	-	-	
Scheloribates pallidulus	565	1	407	-	574	-	Nest
Scheloribates tuberculatus	-	-	-	-	108	3	
Serratoppia serrata	-	1	-	-	-	-	
Steganacarus (Steganacarus) applicatus	-	-	-	-	25	-	
Steganacarus (Steganacarus) donatoi	-	1	-	-	-	-	
Steganacarus (Steganacarus) hirsutus	19	1	-	-	-	-	Nest
Steganacarus (Tropacarus) carinatus	1	-	-	-	2	-	
Suctobelbella acutidens	-	1	-	-	-	-	
Suctobelbella alleonasuta	-	-	-	2	-	-	
Suctobelbella cf. *subcornigera*	1	-	-	-	-	-	
Suctobelbella opistodentata	-	-	-	2	-	-	
Suctobelbella sarekensis	-	1	-	2	-	-	
Tectocepheus sarekensis	9	1	-	5	1	1	
Tectocepheus velatus	10	-	2	1	2	-	
Xenillus clypeator	-	-	1	-	-	-	
Xenillus tegeocranus	22	-	-	-	-	-	Nest

Zygoribatula exilis	143	-	4	-	-	-	Nest
Zygoribatula propinqua	1	-	-	-	-	-	

Table 2

Number of species shared between sites, both for soils and nests. Sites: AB = Abetone (Apennines), CA = Campigna (Apennines), GP = Giovetto di Paline (Alps).

	Springtails				Oribatids			
	soil		nests		soil		nests	
Group	shared	total	shared	total	shared	total	shared	total
AB-CA	3	18	5	17	13	45	19	73
AB-GP	2	14	4	17	4	45	22	94
CA-GP	0	19	3	18	6	35	21	75
AB-CA-GP	0	23	2	22	3	54	12	102

Table 3

Results of PERMANOVA tests.

	Springtails				Oribatids			
Factor	df	SS	F	*P*	df	SS	F	*P*
Site	2	2.300	2.35	< 0.001***	2	3.669	4.04	< 0.0001***
Nest[Site]	12	5.864	3.12	< 0.0001***	12	5.451	2.24	< 0.0001***
Residuals	21	3.288			30	6.076		