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Wood ants (Formicidae, Insecta) at the alpine tree-line ecotone: negative and positive associations with other arthropods

Abstract

Wood ants are dominant insects in coniferous forests that interact with many other organisms, thereby significantly shaping the presence and behavior of other species. These interactions can be either positive, like in the case of trophobiotic mutualisms, or negative in cases of competition or predation. We investigated associations of wood ant prevalence with ground beetles, spiders and harvestmen, and plant lice along a natural density gradient of wood ants over the elevational tree line ecotone in the southern Central Alps. Plant lice were found to be positively associated with wood ants (r = 0.38), in contrast to spiders and harvestmen that tended to occur at lower densities where wood ants were more prevalent (r = -0.45.). Ground beetle individual numbers showed no pattern in relation to wood ants, but their community composition displayed an interesting geographic segregation. Both ground beetles and spiders showed no significant reaction to the wood ant density regarding their community composition.

Keywords: biotic interaction, trophobiosis, wood ants, ground beetles, spiders, plant lice.

Zusammenfassung

Rote Waldameisen sind dominante Insekten borealer und montaner Wälder, die das Vorkommen vieler weiterer Arten stark prägen. Diese Interaktionen können einerseits positiv sein, wie im Falle mutualistischer Trophobiosen, oder negativ ausfallen, etwa in Form von Konkurrenz oder Prädation. Wir berichten hier über Assoziationen Roter Waldameisen mit Laufkäfern, Spinnen und Weberknechten sowie mit Pflanzenläusen entlang eines natürlichen Dichtegradienten der Waldameisen im Bereich der alpinen Waldgrenze an fünf verschiedenen Standorten in Südtirol. Das Auftreten von Pflanzenläusen war positiv mit der Prävalenz Roter Waldameisen assoziiert (r = 0.38), wohingegen Spinnen und Weberknechte eine negative Assoziation zeigten (r = -0.45). Zwischen dem Auftreten von Laufkäfern und der Waldameisendichte bestand hingegen kein Zusammenhang. Die Laufkäfer wiesen jedoch eine interessante geographische Auftrennung zwischen zwei Teilgebieten auf. Sowohl die Gemeinschaftszusammensetzung der Laufkäfer als auch der Spinnen wurde nicht signifikant von der Dichte der Roten Waldameisen beeinflusst.

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eingereicht: 11.09.2018
angenommen: 17.09.2018

Introduction

Biotic interactions are increasingly recognized as essential drivers of community composition (Araújo & Luoto 2007, Schemske et al. 2009). However, compared to mere biodiversity inventories, information about interactions is often still sparse. Only during the last decade the analysis of biotic networks has received revived attention, fostered by the development of novel statistical tools (e.g. Blüthgen 2010, Dyer et al. 2010). Research on interactions and on their significance for ecosystem functioning also becomes urgent in the face of climate change, which might increase the likelihood of co-extinction events, but may also leads to the formation of novel interaction networks (e.g. Blois et al. 2013, Preston et al. 2008).

Ants are widely recognized as ecosystem engineers with a broad impact at multiple ecosystem levels (Hölldobler & Wilson 1990, Lach et al. 2010). Only at very high elevations or latitudes the impact of ants is more limited. In boreal forests as well as in montane to subalpine forests in the Northern Hemisphere, mound-building red wood ants (subgenus *Formica* s. str.) are a dominant group of terrestrial arthropods (Stockan & Robinson 2016). These ants form huge (super-) colonies (hundreds of thousands to millions of workers) which are long lived, may persist for decades, and defend vast areas (up to >2.5 km^2) against competing ant colonies (Stockan et al. 2016). Wood ants reach highest densities in the coniferous forests of the boreal and temperate biome, with often 5-10 (and sometimes even more) mounds per hectare. They contribute to soil perturbation, nutrient accumulation or seed dispersal and act as key predators. Through trophobiotic associations with plant-sucking insects, wood ants even partially take the role of functional herbivores (Stockan & Robinson 2016).

Wood ants are known to affect the occurrence and abundance of less dominant ant species (e.g. in the subgenera *Serviformica* and *Coptoformica*, or the genera *Myrmica* and *Lasius*: Johansson & Gibb 2016). Beyond their influence on ant communities, wood ants also affect densities and assemblage composition of their competitors (like birds, ground beetles and spiders: Haemig 1994, Hawes et al. 2002, Cherix & Bourne 1980, Robinson et al. 2016 and citations therein). On the other hand, many plants or arthropods are positively associated with wood ants, indicating cases of facilitation or mutualism (Robinson et al. 2016, Stadler & Dixon 2008). Several studies focused on interactions between ground beetles and wood ants (Hawes et al. 2002, Reznikova & Dorosheva 2004, Dorosheva & Reznikova 2006) and came to the general conclusion that wood ants limit the presence and abundance of ground beetles through negative interference rather than predation (Reznikova & Dorosheva 2004, Haves et al. 2013). Evidence is more mixed with regard to relationships between ground active spiders and wood ant densities, though most studies also indicate a negative relation (Moldenke 1997, Laakso 1999, Zmihorski 2011). Other authors, however, argued that habitat structure and abiotic conditions are more important in shaping communities of both spiders and ground beetles than is the density of wood ants (Koivula et al. 1999, Punttila et al. 2004, Neuvonen et al. 2012, Woodcock et al. 2010).

Organisms that are able to coexist with wood ants, or even engage in beneficial associations with this aggressive and dominant ant group, enjoy a reduced pressure from predators and parasites and gain a significant evolutionary advantage (Stadler & Dixon 2008). The most classic example in this respect is the trophobiotic mutualism with plant sucking insects that provide to the ants a nearly direct access to plant produced carbohydrates. Carbohydrates are the prime energy source for ants and since a wood ant colony may comprise several hundred thousand workers, the required energy supply is very high. Wood ants cover most of their carbohydrate demand by attending aphids, especially from the genus *Cinara* (Domisch et al. 2016). This aphid genus feeds on conifers of the northern hemisphere, where most wood ants occur, and often big aphid colonies are formed on their host trees. The presence of aphids is an essential requisite for the survival of bigger wood ant colonies. For example, forest clear-cutting leads to the loss of trees and *Cinara* aphids and thereby triggers a decline in wood ant density and colony sizes (Zmihorski 2011).

In the present study we chose habitats situated around the alpine tree-line ecotone in the southern Alps, which are especially suited to assess contingencies between the

densities of wood ants and other arthropods. Here, wood ant densities change particularly sharply over short distances. The tree-line ecotone is characterized by a natural change in multiple factors. Above the tree-line, an abrupt reduction of the primary production and of the structural complexity of the ecosystem comes with an increase in insolation and daily temperature amplitudes (Körner et al. 2012). This natural steep gradient is especially well suited to study relationships with wood ants because their abundance is expected to be dramatically reduced by the absence of trees, along with their ecological impact. The ecological role of wood ants is often supposed to be covered by other taxa, like ground beetles and ground active spiders, in habitats where wood ants are rare or absent (Johansson & Gibb 2016 and citations therein). On the other hand, plant sucking insects are known to reduce their investment in interactions with ants at higher altitudes, where coping with increased abiotic pressures becomes more important than being protected (against biotic factors) by ants (Stadler et al. 2003).
We here use intense surveys of ant assemblages, pitfall trap by-catches of ground beetles and epigaeic spiders, and records of trophobiotic associations between aphids and wood ants to test the following hypotheses: 1. Densities of ground beetles and ground dwelling spiders are both negatively associated with wood ants. 2. Trophobionts are positively associated with wood ants. 3. Species composition of both groups of predacious arthropods, viz. ground beetles and spiders, is significantly shaped by the local prevalence of wood ants.

Methods

Study plots:
Sampling was conducted around the tree line on five slopes in South Tyrol (Italy). To facilitate comparisons between plots, only south facing slopes on silicate bedrock were chosen. Two slopes were situated within the nature reserve Texelgruppe and three within the National Park Stilfserjoch / Parco Nazionale dello Stelvio (Fig. 1). Restriction of sampling to nature reserves or national parks aimed to minimize effects of human land use activities (e.g. pasturing and forestry) as far as possible.

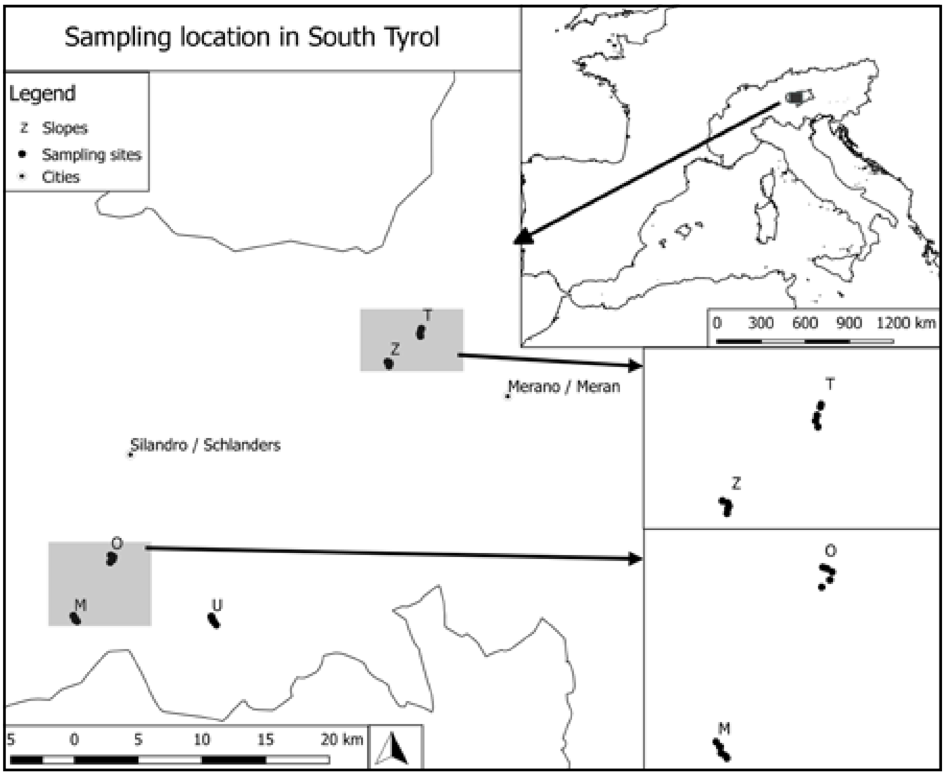


Fig. 1: Schematic map of the study plots. The three slopes denominated O, M and U are located within the National Park Stilfserjoch, the other two, denominated Z and T, are situated in the nature reserve Texelgruppe.

Each selected slope revealed a gradient of vegetation from subalpine woodland to open alpine grassland interspersed with shrubs. The tree line itself was in most cases rather clearly defined because of management that occurred over centuries in the past and still persists in the form of extensive summer pasturing by cattle (Tasser et al. 2001). On each slope five plots of 800 m^2 area (40 m x 20 m rectangular subplots, set orthogonal to the slope) were delimited and sampled. The subplots were selected in reference to the tree line with one situated on the ecotone itself, two in the alpine zone above, and two in the forest below, spaced by 50 elevation meters from each other. This way, the subplots at each plot covered roughly 200 meters of elevation per slope, but 470 meters if integrated over all slopes, from 1935 m (the lowest plots) to 2405 m (the highest plots). All in all, data were collected on 25 plots, five of which were situated in the ecotone, 10 above the tree-line within the alpine environment, and 10 below the tree-line within upper montane to subalpine coniferous forest. Sampling took place in July and August 2016 and 2017. At each plot we recorded the plant species and the mean indicator values for temperature, light, humidity and humus following Landolt (1977) were calculated and used for further analyses (Tab. 1). For further recorded factors and more details see Guariento (2018).

Tab. 1: Synopsis of sampling plot characteristics. “Basal area” refers to the sum of stem area calculated from the diameter of all trees with a diameter at breast height greater than 10 cm found in a 100 m^2 area. The different cover values (in %) refer to the whole sampling area of 800 m^2 on each plot. Light, humidity and soil humus values refer to the average indicator values of all plant species on a plot taken from Landolt (1977). Finally, the reference number from Wallnöfer et al. (2007) refers to the main habitat classification and in brackets to less prominent habitat characteristics within the sampling plot.

Plot code	Slope	Habitat	Date of sampling in summer 2016 and 2017	Longitude	Latitude	Exposition	Elevation (m a.s.l.)	Steepness (in %)	Basal area	N trees (d>10cm)	Tree cover (%)	Shrubs cover (%)	Rock/stone (%)	Bare soil (%)	Dead wood (%)	Low veg cover (%)	Temperature value	Light value	Humidity value	Humus value	Wallnöfer et al. Liste Nr.
Z 1	Zielspitz	alpine	15.07.2016 / 13.08.17	N46°41.359’	E011°01.829’	SSO	2239	62.12	0	0	0	10	10	2	0	80	2.21	3.65	2.79	3.61	41200
Z 2	Zielspitz	alpine	15.07.2016 / 13.08.17	N46°41.331’	E011°01.942’	SO	2186	63.62	0	0	0	7.5	12.5	5	0	75	2.28	3.69	2.78	3.62	41200 (5200-3-4)
Z 3	Zielspitz	tree line	15.07.2016 / 13.08.17	N46°41.283’	E011°01.968’	S	2130	58.5	4392	15	27.5	15	10	2.5	1	62.5	2.35	3.47	2.77	3.60	45210 (62122)
Z 4	Zielspitz	forests	16.07.2016 / 15.07.17	N46°41.241’	E001°01.941’	SSW	2082	91	7040	12	62.5	20	3	15.5	3	45	2.35	3.25	2.79	3.60	62112-22
Z 5	Zielspitz	forests	16.07.2016 / 15.07.17	N46°41.179’	E001°01.926’	SSW	2015	75	4660	9	45	22.5	10	10	3	35	2.19	3.37	2.82	3.84	62113
O 1	Orgelspitz	alpine	19.07.2016 / 29.07.17	N46°33.218’	E010°44.864’	SO	2393	62	0	0	0	42.5	11	1.5	0	45	2.20	3.72	2.78	3.44	5200-4
O 2	Orgelspitz	alpine	20.07.2016 / 29.07.17	N46°33.201’	E010°44.944’	SO	2339	66.5	0	0	0	55	7.5	3.5	0	35	2.13	3.69	2.74	3.55	5200-4
O 3	Orgelspitz	tree line	20.07.2016 / 29.07.17	N46°33.149’	E010°45.060	SSO	2270	49.25	2022	12	30	55	6	4	2.5	30	2,20	3.58	2.77	3.75	5200-4 (62310-30)
O 4	Orgelspitz	forests	20.07.2016 / 29.07.17	N46°33.033’	E010°45.013’	SSO	2210	55.5	10413	12	60	12.5	15	11	6	52.5	2.48	3.21	2.75	4.00	62310-122
O 5	Orgelspitz	forests	21.07.2016 / 29.07.17	N46°32.926	E010°44.839’	SSO	2166	58.5	7550	22	50	20	17.5	20	5	35	2.29	3.12	3.00	4.06	62310-123
U 1	Ulten	alpine	02.08.2016 / 22.08.17	N46°30.630’	E010°51.043’	S	2352	57.25	0	0	0	45	11	4	0.5	42.5	1.92	4.00	2.71	3.57	42100 (5200-3-4)
U 2	Ulten	alpine	02.08.2016 / 22.08.17	N46°30.519’	E010°51.103’	S	2280	46.25	0	0	0	42.5	5.5	4.5	0.5	50	2.08	3.74	2.76	3.63	42100 (52400)
U 3	Ulten	tree line	03.08.2016 / 22.08.17	N46°30.440’	E010°51.168’	SSO	2230	30.25	4243	10	25	35	6	7.5	2	40	2.18	3.60	2.80	3.80	56400 (62310)
U 4	Ulten	forests	03.08.2016 / 22.08.17	N46°30.374’	E010°51.235’	SO	2186	44.5	10453	16	65	30	3	8.5	6	55	2.21	3.17	2.96	4.04	62310
U 5	Ulten	forests	04.08.2016 / 22.08.17	N46°30.279’	E010°51.354’	SSO	2111	57.5	20219	33	62.5	10	5	35	7.5	35	2.34	3.26	2.78	3.89	62310
T 1	Tschigat	alpine	08.08.2016 / 02.07.17	N46°42.757’	E011°03.916’	S	2231	83.5	0	0	0	0	5	0	0	95	2.34	3.52	2.78	3.52	45220
T 2	Tschigat	alpine	08.08.2016 / 02.07.17	N46°42.719’	E011°03.900’	S	2180	68	0	0	0	12.5	25	0	0	62.5	2.29	3.60	2.78	3.40	56200 (45220)
T 3	Tschigat	tree line	11.08.2016 / 03.07.17	N46°42.598’	E011°03.833’	SSW	2090	80.5	2547	12	37.5	40	10	10	1	45	2.26	3.28	2.97	3.78	62122 (56200)
T 4	Tschigat	forests	18.08.2016 / 03.07.17	N46°42.521’	E011°03.802’	SSW	1987	53.87	9666	23	62.5	12.5	15	3.5	1.5	45	2.43	2.87	3.06	4.37	62112-22 (45120)
T 5	Tschigat	forests	18.08.2016 / 03.07.17	N46°42.433’	E011°03.851’	S	1935	72.25	13955	7	70	10	10	20	5	55	2.42	2.79	3.07	4.43	62112
M 1	Martell	alpine	22.08.2016 / 15.08.17	N46°30.662’	E010°42.589’	SSO	2405	48.75	0	0	0	50	7.5	5	0.5	40	1.86	3.95	2.76	3.53	41200 (56400-2)
M 2	Martell	alpine	22.08.2016 / 15.08.17	N46°30.588’	E010°42.673’	SSO	2349	40.75	0	0	0	40	7.5	3.5	0	52.5	1.91	3.97	2.69	3.26	56400
M 3	Martell	tree line	19.08.2016 / 15.08.17	N46°30.495’	E010°42.700’	SSO	2300	31.87	4861	8	40	45	3	6.5	4	42.5	2.18	3.50	2.73	3.75	56400 (62310)
M 4	Martell	forests	19.08.2016 / 15.08.17	N46°30.461’	E010°42.789’	SSO	2260	38.25	11763	12	55	15	12.5	15	10	50	2.32	3.29	2.86	3.86	62310
M 5	Martell	forests	25.08.2016 / 15.08.17	N46°30.423’	E010°42.820’	SSO	2205	64.5	7116	24	60	5	10	17.5	12.5	45	2.50	3.12	2.88	4.06	62310

Arthropod sampling design:

Baits with six different resources (carbohydrate in form of saturated sugar solution, amino acid in form of pure glutamine-water mixture, a 1:1 mixture of sugar and glutamine, natrium in form of table salt saturated solution, lipids in form of pure olive oil and tap water) following a well-established protocol (Fowler et al., 2014; Kaspari et al., 2012; Peters et al., 2014; Spotti et al., 2015) were exposed at the ground for at least 3 hours. All ants visiting the baits were counted after three hours and voucher specimens were taken for further species determination. Pitfall traps are one of the main methods for surveying ground active ant communities (Bestelmeyer et al. 2000, Tista & Fiedler 2011) but also generally for ground active arthropods (Prasifka et al. 2007, Work et al. 2002). Ten pitfall traps (plastic tubes with 3 cm diameter opening and 7 cm deep) were placed at each plot, spaced by ca. 10 meters from another and exposed for three days. They were placed in a way that the soil surface and the trap edge were evenly connected. A metal net (mesh width 1.5 cm) was placed on top and fixed in the soil to prevent bigger animals or debris from falling into the traps. A tiny plastic roof was also fixed on top to shed traps from possible rain. Since the primary taxon of interest in this study were ants, the traps were filled with a baiting liquid composed of 1:1 mixture of rum and honey and few drops of a detergent to reduce surface tension (demonstrated to be effective in Tista & Fiedler (2011)). This baiting liquid is especially suitable for sampling the ant community, but might be less adequate for other taxa, because of uncontrolled attractive or repelling effects of the baiting liquid.

Sampling of trophobiotic associations took place in the summer 2017, always within the same sampling plots as for all other methods and taxa. Single animals and entire aphid aggregates were searched on three subplots (10 m x 2 m in size) within each plot. Leaves and branches of the vegetation up to 2 m above ground were carefully inspected for ca. 15 min per subplot. Within the forest plots only vegetation that could be reached from the ground was checked, but for each tree we recorded if there was ant visitation on it, indicating the existence of ant-attended homopterans higher up in the canopy that could not be reached from the ground.

The determination of the wood ants was performed using the key of Seifert (2007) and a stereoscope with 90x magnification. The species identification of the plant lice was performed with the same stereoscope and the key of Hannemann et al. (2000). The spider identification was performed using the World Spider Catalog (2018) and Carabids were identified by using the identification keys of Trautner & Geigenmüller (1987) and Müller-Motzfeld (2004).

Statistics:

Variation in community composition across the plots for ground beetles and ground-dwelling spiders was expressed as Bray-Curtis dissimilarities, using the function *vegdist()* in the package *vegan* (Oksanen et al. 2017) implemented in the *R* environment (R Team 2017). For ground beetles (Carabidae) and spiders (Araneae, but excluding orb-building or ambush-style species that do not hunt on the soil surface) the sum of individuals found in the 10 pitfall traps per plot served as a proxy of abundance. Harvestmen were added to the ground-hunting spiders since their active life style and interaction with wood ants resembles the vagant spiders (Johansson & Gibb 2016). With these similarity/dissimilarity values for each plot a non-metric multidimensional scaling (NMDS; function *metaMDS()* in the package *vegan*) was performed as unconstrained ordination, to visualise the patterns in species composition. Further environmental variables were plotted *ex post* on the ordination diagrams (using function *envfit()* in *vegan*) to facilitate interpretation.

To test the effect of the wood ant density on the community composition of the competing taxa a constrained ordination (function *capscale()* in the package *vegan*) was performed using wood ant density and the absolute elevation (in meters a.s.l.) as fixed factors and slope identity as random factor.

A Mantel test (function *mantel()* implemented in the *vegan* package, 10000 permutations) was computed to investigate possible contingencies between the community patterns of ground beetles and spiders. We used linear mixed models to assess possible effects of wood ant densities on the abundance of spiders, ground beetles and plant lice colonies, using slope identity as random factor to account for spatial autocorrelation and uncontrolled variation between the studied mountains. Also the variation in wood ant density across the sites was analysed similarly with absolute elevation as fixed and slope identity as random factors.

For each plot, the abundance of wood ants was scored as the sum of incidences on all pitfall traps and baits exposed on a plot divided by the total amount of traps and baits. In total 35 baits and 10 pitfall traps per plot were exposed making up 1225 trap data points in total. The number of all beetle and spider individuals per plot was square root transformed prior to analysis to meet the assumptions of linearity, because of few species being very dominant in both communities. The number of plant lice colonies was estimated for each plot by summing up the number of colonies directly found and adding two further colonies per ant-visited tree in the forest, where the colonies themselves were placed too far up in the canopy to be reached from the ground. Adding two colonies is a conservative estimate of aphid colony number per visited tree, because up to five colonies were found even on smaller trees directly at the treeline.

Since not in all plots active hunting spiders or harvestmen and aphid species were recorded, a dummy species coding 1 in abundance on each plot was added to allow computation of Bray-Curtis matrices for sparse data sets (Clarke et al. 2006)

Results

204 individuals belonging to 18 species of epigaeic spiders and four harvestman species with 21 individuals were found. 42 spiders were juveniles and could not be determined to species level. These were only included in the linear mixed model on spider abundance. Four observed spider species do not hunt on the ground and were thus also excluded, but listed in Appendix (Tab. C). We further recorded 222 individuals of ground beetles representing 13 species (Appendix Tab. A) in the pitfall traps. 77 observed aphid colonies (comprising from 1 to >150 individuals) belonged to 13 species (nine species were observed in trophobiotic interactions with ants; Appendix Tab. B). Three species of red wood ants were found, viz. *F. lugubris, F. aquilonia* and *F. rufa*. The first was present on 19 plots and in all habitat types and is presumably responsible for the proportionally largest ecological impact. The second wood ant species was found on just four sites within the forest (yet on two locations being very abundant), while the last only occurred on one plot in very low abundance.

Cumulative wood ant density was found to increase drastically from the alpine plots (where 27.6% of the traps contained wood ants) to the forest (where 85.6% of the traps contained wood ants; Fig. 2). The tree line plots scored intermediate (with 45.6% of the traps containing wood ants). In a linear mixed model of wood ant density against elevation with slope identity modelled as random factor) the result was highly significant (Likelihood ratio test: $\text{Chi}^2 = 11.68$, $p < 0.001$***).

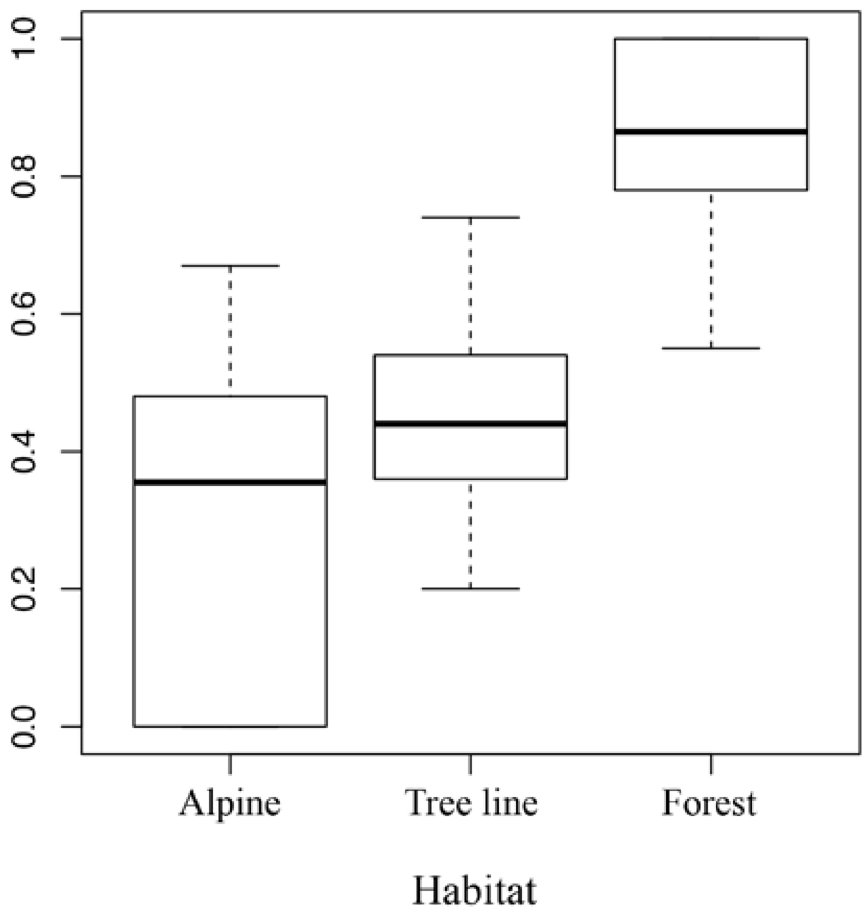
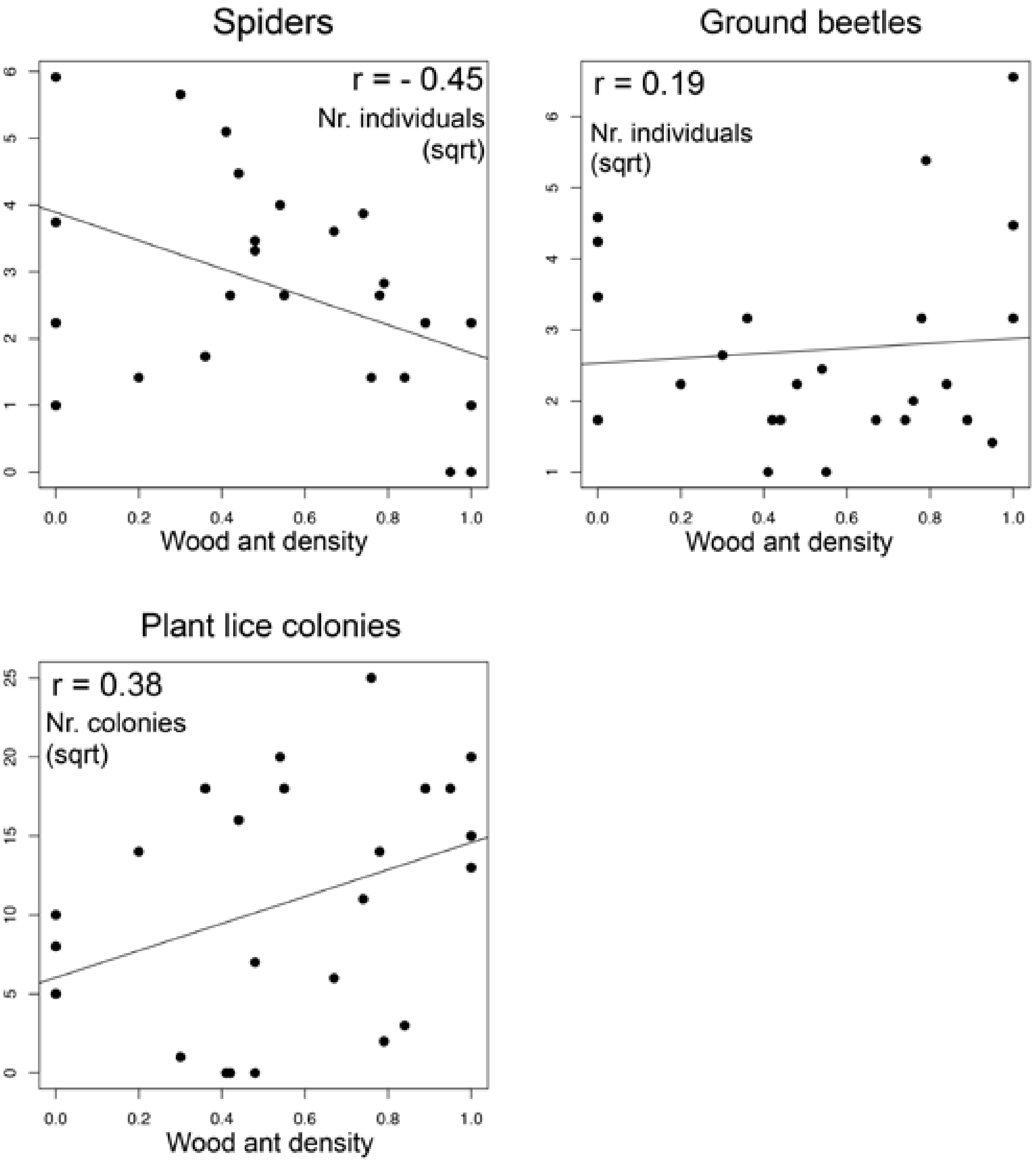


Fig. 2: Boxplot of the relative abundance of all red wood ants (*F. lugubris, F. aquilonia and F. rufa* summed together) across the different habitats, computed from the summed incidences of wood ants on baits and in pitfall traps, divided by the total trap number per plot.

Linear mixed models delivered a significant negative relationship between the abundance of wood ants and spiders and a less strong positive association between plant lice colonies and red wood ants, whereas no association was confirmed for the numbers of ground beetles (Tab. 2; Fig. 3). The significant intercept in all taxa shows that there were also significant differences in wood ant density between the five different mountain slopes.

Fig. 3: Ordinary least squares regression of the number of individuals (square root transformed) of spiders (A), ground beetles (B) and colonies of plant lice (C) on the cumulative density of red wood ants.



Tab. 2: Results of linear mixed models (LMM) relating the numbers of spiders and ground beetles found in pitfall traps, and the numbers of plant lice colonies in the searched vegetation subplots, to the relative abundance of red wood ants. Slope identity was modelled as random factor. ***: significant at p<0.001; * significant at p<0.05.

Taxon	Factor	Estimate	Standard Error	t value	p
Spiders	Intercept	3.956	0.69	5.69	< 0.001 ***
	Wood ants	- 2.93	0.66	- 4.46	< 0.001 ***
Ground beetles	Intercept	22.53	0.55	4.58	< 0.001 ***
	Wood ants	0.35	0.87	0.40	0.68
Plant lice colonies	Intercept	6.03	2.64	2.29	0.02 *
	Wood ants	8.54	4.16	2.05	0.04 *

An unconstrained ordination was computed for each taxon. Inspection of the ordination diagrams revealed that community composition of arthropods varied along with geographical position and habitat of the sites. Ground beetle communities mostly differed between the national park and the nature reserve, whereas wood ant density as well as habitat affiliation of sites played only a minor role (Fig. 4). Spiders showed no clear segregation on habitat or region (Fig. 4). Plant lice showed interestingly a differentiation according to both, habitat (i.e. elevation) and park type (Fig. 4). The elevational differentiation is clearly due to the lack of trees in the alpine environment, so that treeline plots clustered together with the forest plots. The differentiation between the two conservation areas is however a result of more tree species present in the national park (*Pinus cembra* and more often *Larix decidua*; Appendix Tab. B) than in the nature reserve.

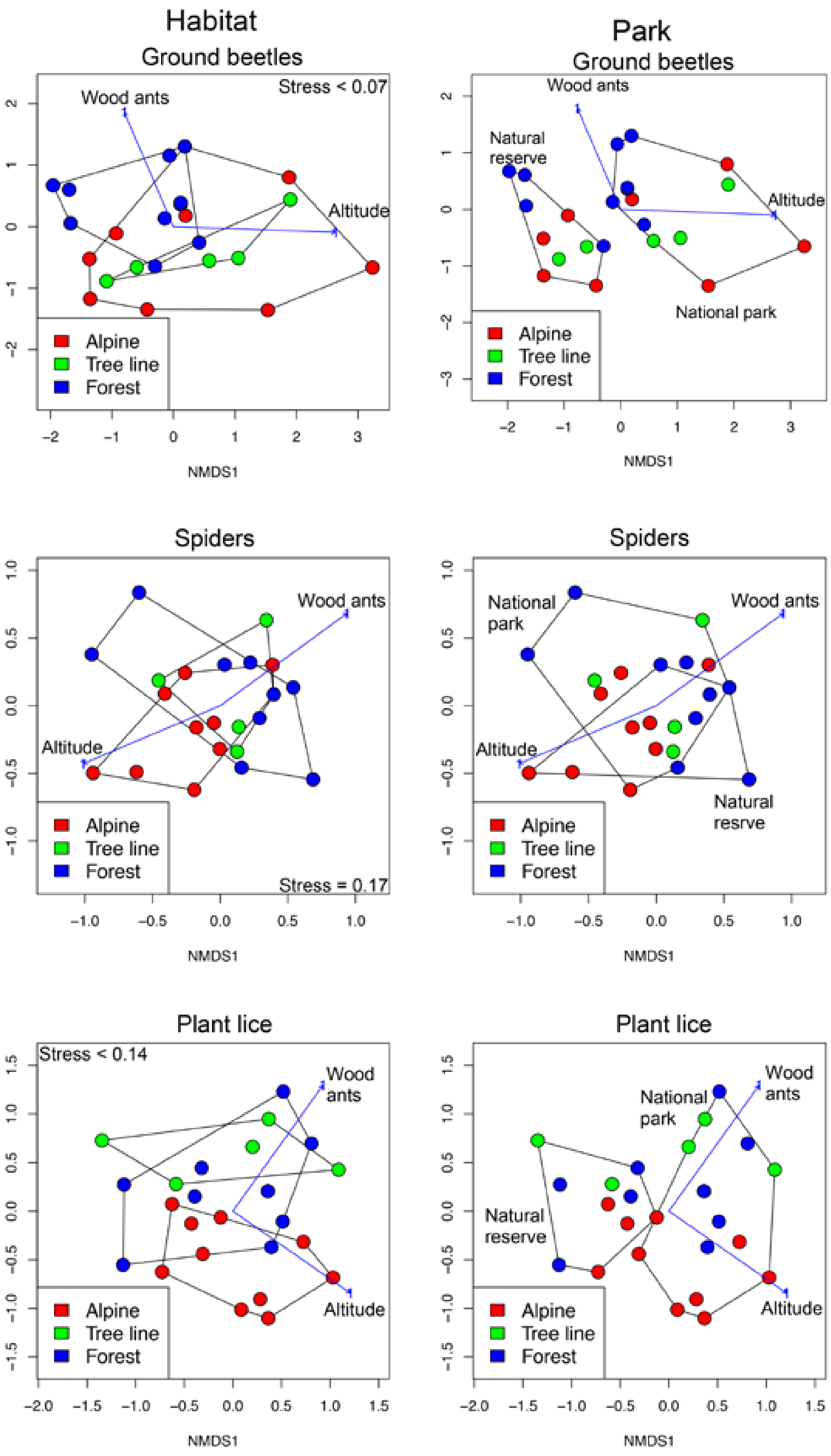


Fig. 4: NMDS of the communities, showing compositional differences of ground beetles (1st row of panels), spiders (2nd row), and plant lice (3rd row). For all animal taxa Bray-Curtis dissimilarities were used. In the left column of charts, local communities are segregated according to habitat type, and in the right panel according to the two conservation areas. Variables overlaid as vectors were *z* transformed prior to implementation.

To investigate the possible concomitant change of the ground beetle community with the spider community, a Mantel correlation test was performed showing that both communities had largely unrelated patterns (R = – 0.082; $p = 0.88$).

In order to finally test the effect of wood ant density on community composition of the two potentially competing taxa of epigaeic arthropods, a constrained ordination was performed which found no significant effect of the wood ants (Tab. 3).

Tab. 3: Results of constrained ordinations of ground beetle and spider communities against elevation and wood ant density. Both fixed factors explained little variance with only elevation for spiders scoring nearly significant (significance set at AIC<2). AICc refers to the Akaike Information criterion corrected, *w* to Akaike weight (Wagenmakers & Farrell 2004) and R^2 defines the explained variance.

Model	Fixed factors	Variable omitted	N variables	AIC	AICc	Diff to best model	w	R^2
Ground Beetles								
Full Model	All	-	2	54.33	54.88	0.60	0.21	0.10
2	Wood ants	Elevation	1	54.45	54.62	0.34	0.24	0.07
3	Elevation	Wood ants	1	54.21	54.38	0.10	0.27	0.05
Null Model	-			54.28	54.28	0.00	0.28	0.00
Spiders								
Full Model	All	-	2	47.08	47.63	1.20	0.22	0.15
2	Wood ants	Elevation	1	47.36	47.53	1.11	0.23	0.09
3	Elevation	Wood ants	1	46.25	46.42	0.00	0.40	0.12
Null Model	-		0	48.35	48.35	1.93	0.15	0.00

Homopterans and trophobiotic associations

The sampling of plant lice delivered a highly heterogeneous data set. At some plots or slopes many aphid-ant associations were observed, while at others there were none recorded directly. Probably the sampling on just one day per plot was not exhaustive enough to reliably quantify the number of trophobiotic interactions. The alpine slave ant (*Formica lemani*) and red wood ants (mainly *Formica lugubris* but also *Formica aquilonia*) were responsible for nearly all these interactions (Fig. 5). On the other side, the aphid genus *Cinara* was the predominant homopteran partner. The exceptions were *Adelges laricis* interacting with the alpine slave ant and *Manica rubida* and the alpine slave ant interacting with the mealybug *Planococcus* cf. *vovae* on low branches of *Juniperus communis* subsp. *nana* that were covered by dead organic material (Fig. 5; Tab. 4).

Tab. 4: Numbers and proportions of trophobiotic interactions, split between the alpine slave ant (*Formica lemani*) and red wood ants (*Formica lugubris* and *aquilonia*). Also, the number and proportion (relative to the total number of trees present) of visited trees were noted where ant visitation occurred.

Number transects	Habitat	% colonies visited by slave ants	Number of trees visited by slave ants	% colonies visited by wood ants	Number of trees visited by wood ants	Homopteran species
30	Alpine	37	0	27 %	4	6
15	Tree line	53 %	21	53 %	28	8
30	Forest	0 %	0	23 %	61	7

A tentative attempt to quantify the strength of the trophobiotic interactions is presented in Table 5. The proportion of ant-visited trees is given to visualise ant visitation that was observed but the homopteran aggregations were located too high up in the trees to be reached. It can be clearly seen that red wood ants were the dominant partners in these associations which further increased in their dominance at lower elevations, e.g. in forest. The alpine slave ant showed a higher visitation of trophobionts above the tree line compared to wood ants and a similar one directly at the tree line. Interestingly no interaction of the alpine slave ant with aphids was detected in the forest, suggesting an exclusion through competition by the wood ants (Savolainen 1991). The dominant interaction in the alpine zone was of *Cinara juniperi* on *Juniperus communis var. saxatilis* with both the slave ant (also on single aphid individuals) and the wood ants (only if the aggregation was bigger >2 aphids). Further treelets (*Pinus cembra* and *Picea abies*) if present were often highly colonised by *Cinara* (*C. cembrae* for the first and *C. piceicola* for the second tree species). These were mainly visited by the wood ant *F. lugubris* and rarely by the slave ants. The abundance of *Formica lugubris* above the tree line was found to highly correlate ($r = 0.80$) with the cover of dwarf shrubs (*Juniperus communis* and *Rhododendron ferrugineum*, no plant lice were found on the latter) suggesting that wood ants change to foraging for trophobionts on shrubs where no trees are available. Directly at the tree line 74.7% of the trees had ant visitation on them, whereas in the forest only 52.3% of trees were visited by ants.

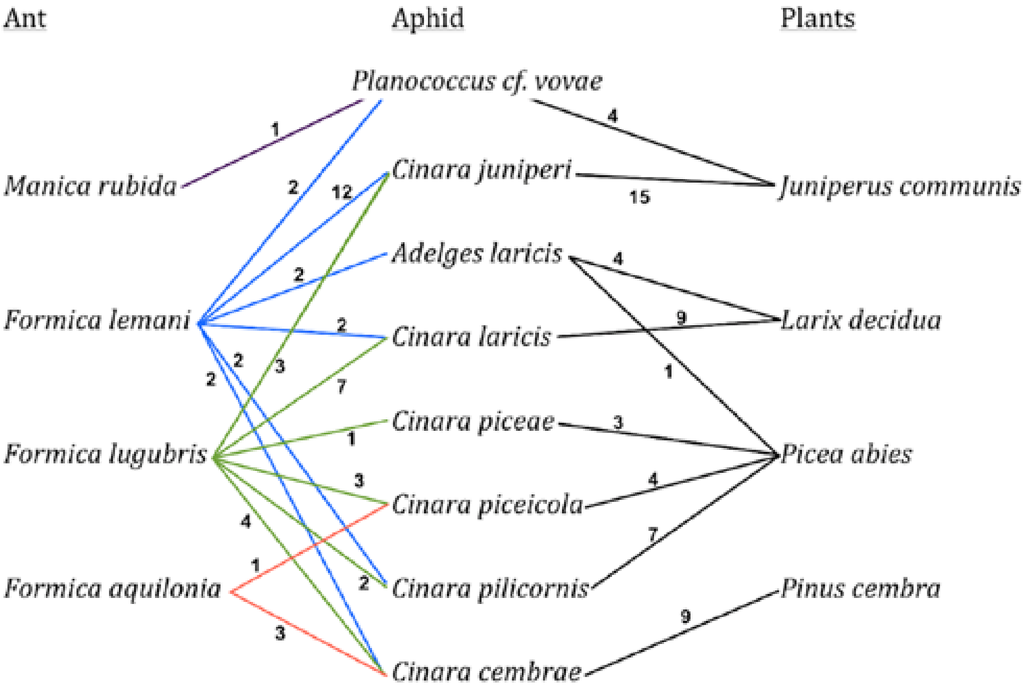


Fig. 5: Interaction network between ants, plant lice, and plants. The numbers above the lines indicate the number of subplots (three within each plot) on which these interactions were found. Coloured lines define to which ant species the interaction belongs.

Discussion

The expectation that wood ants influence the abundance of multiple other arthropod taxa was only partially met in our study at the alpine tree line, despite the presence of a strong gradient in the local prevalence of red wood ants. As predicted, the abundance of trophobionts (mostly *Cinara* aphids) was higher where also wood ants were found in high densities, especially inside the subalpine coniferous forest. These two groups of organisms maintain mutualistic associations that reciprocally buffer the existence of each other by providing protection (ants for the plant lice) and a highly valuable food source (plant lice for the ants). This mutualism is essential for both players and depends on the presence of a third network partner to be effective, viz. coniferous trees on which the *Cinara* aphids live (Stadler & Dixon 2008). Above the tree line, spruce, larch and pine were rare, only occurring as small treelets. Here, most of the trophobiotic homopterans were living on the shrub *Juniperus communis* var. *saxatilis*. This small coniferous plant probably cannot sustain big colonies of *Cinara juniperi* (the aphid species found on this plant), that were occurring either individually or in very small colonies (comprising just 2 to 6 individuals). This low number of trophobionts can hardly provide enough carbohydrate resources to sustain big wood ant colonies. In fact, every "bigger" aggregation (2 individuals) of this aphid species was visited by wood ants (or by slave ants, subgenus *Serviformica*) in the alpine zone. Within the alpine zone, the relative abundance of red wood ants was highly correlated ($r = 0.80$) with the density of shrubs, suggesting that in this environment shrubs play a similar role as trees in the forest by harbouring trophobionts. These results indicate that the presence of trees (or shrubs) is of major importance to support higher densities of both wood ants and their trophobionts (e.g. Risch et al. 2016). However, species composition of the aphid community was not further analysed. Rather, homopteran species composition seemed to be influenced by the presence of trees (alpine plots vs tree line and forest plots in the NMDS; Fig. 4) and the presence of different tree species in the two study areas. Only few frequent species of ants (3) interacted with several (7) species of plant lice in a consistent manner. Moreover, only two ant species other than red wood ants were found at all interacting with homopterans, suggesting that *Formica* s. str. (and to a lesser extent *F. lemani*) effectively monopolize trophobionts against most of the less dominant ant species that co-occurred at the tree-line ecotone and in adjacent habitats. Most trophobiotic interactions found here were already known in the pertinent literature (e.g. Domisch et al. 2016). Only the interaction between *Planococcus* cf. *vovae* with the alpine slave ant and with *Manica rubida* could, if the identification of the mealybug will be confirmed, represent novel interaction recordings.

Elsewhere in the Alps, *Formica lugubris* extends regularly into the lower alpine zone up to 2400 m elevation (Seifert 2007, Wagner 2014). The low density and colony size of their trophobiotic partners above the tree line suggests that the feeding ecology of this wood ant species most probably changes from the forest to the alpine setting, relying on alternative carbohydrate sources or even shifting the proportions of used resources (see Guariento (2018) for more details).

For ground-dwelling predacious arthropods we expected that their abundance would be negatively associated with that of wood ants as a consequence of direct or indirect competition. Indeed, the case of numbers of spiders and harvestmen individuals this expectation was clearly met, as already found in several other studies (e.g. Frizzi et al. 2018, Halaj et al. 1997, Johansson & Gibb 2016 and citations therein). Wood ants could influence spiders by directly preying on them or indirectly by reducing the potential prey density (Haemig 1994, Moya-laraño & Wise 2010). The spider community at our study plots was dominated by one single species, the lycosid *Pardosa blanda*, which alone made up 63.2% of all captured spiders. This species abundantly occurred on all slopes and plots, thereby preventing any further geographic differentiation of spider assemblages according to habitat or study region in our data. The rather casual occurrence of all other species resulted in the lack of any significant effect of the wood ants on the community composition of spiders. The sampling method with small pitfall traps probably delivered a partially incomplete sampling of the spider community, with only two species from Linyphiidae, one Theridiidae and none of Philodromidae and Salticidae.

Nevertheless, five regionally rare species were found in the samples (e.g. *Gonatium rubens, Pardosa ferruginea, Agroeca proxima, Micaria silesiaca* and *Zelotes talpinus*).
Ground beetle numbers instead did not show any pattern in relation to the presence of *Formica* s. str. (Fig. 3) or to the habitat type. This result supports the finding of Neuvonen et al. (2012) who called into question the importance of wood ants for ground beetle community composition and abundance. This however stands in contrast with many other studies that reported negative relationships between these two groups of organisms (e.g. Johansson & Gibb 2016 and citations therein). In our study, the major differentiation of ground beetle assemblages was related to the geographic position of the two study regions. These are separated by a major valley (Vinschgau Valley) that does not allow a dispersion of alpine or montane species that are mostly wingless (as in most of the species found in our study). Only two species (*Pterostichus unctulatus* and *Calathus micropterus*) out of 13 occurred in both parks. The genus *Pterostichus* comprises several alpine-endemic and locally distributed species and represented 79.2% of the records. *P. multipunctatus* alone accounted for 46.3% of the records, a species of the Western Alps which reaches with the national park Stilfserjoch one of its eastern range limits (Müller-Motzfeld 2004). Eastwards it is replaced by similar sized species of the genus *Pterostichus* with similar ecological functions, like *P. jurinei*. The geographical distribution of *P. jurinei* is limited to the Eastern Alps and the Carpathians where it is often the dominant carabid species at the tree line (Schatz 1994). The species was represented by several individuals at both sites in the nature reserve Texelgruppe and demonstrates the impact of the Vinschgau valley as distribution boundary for flightless carabids. According to Hellrigl (1996) all carabid species found in our pitfall samples are abundant in South Tyrol except for *Amara lunicollis* and *Carabus problematicus* both apparently just occurring within the national park Stilfserjoch and coded as not frequent. Ground beetles were not influenced by wood ant density or altitude in both their individual numbers and in their community composition. This might potentially be attributed to the stronger sclerotization of beetles in comparison to spiders, which are possibly more susceptible to wood ant attacks. Carabids can also apply a species-specific set of behavioural tactics to avoid the contact with wood ants (Reznikova & Dorosheva 2004).

Furthermore, spider and ground beetle community composition showed no correlation to another, indicating that communities of both these groups of organisms vary in a completely unrelated manner to habitat characteristics. Additionally, the expected influence of red wood ants on shaping the community composition of the competing taxa was not met, neither for spiders nor for ground beetles.

Our sampling method (pitfall traps filled with baiting liquid) was specifically targeted at monitoring ants. Beetles and spiders therefore were rather represented as by-catches. The baiting liquid could have had an attractive (or repulsive?) effect on beetles or spiders, thus potentially distorting abundance patterns. In addition, the digging-in effect (e.g. Woodcock 2005) was not taken into account, but since sampling was performed in the same manner on all plots, we consider a comparison between trap catches legitimate.

In conclusion, we found partial support for the negative effect of wood ants on competing arthropod taxa in the case of spider individual numbers that were present with fewer individuals where wood ants occurred in high abundances. Spiders were also found in greater numbers in pitfall trap samples in the alpine setting where they probably cover part of the ecological role that ants play at lower elevations. For ground beetles, in contrast, there was no such effect exerted by wood ants or habitat type, suggesting that carabid species around the alpine tree line are well adapted to co-exist with wood ants. Furthermore, wood ant densities did not influence the community composition of neither of the competing taxa, limiting the negative effect of wood ants on competing taxa just on the numbers of spider individuals. Ground beetles showed no reaction to the habitat type or to the wood ant density, however their communities were geographically segregated because flightlessness constrains their dispersal capacities.

Trophobiotic homopterans are an essential resource for red wood ants, and the close association between these organisms was clearly confirmed. Yet, this co-occurrence was mainly contingent on the presence of trees and shrubs (in the alpine environment) that support sufficiently large homopteran colonies which deliver carbohydrates to wood ant colonies.

Acknowledgements:
This study was partially financed by funds from the Faculty of Life Sciences, University of Vienna. We gratefully thank Brigitte Gottsberger for providing DNA barcode sequences for some Homoptera. Further, we thank helpful hands in the field: Luciano Guariento, Emil Guariento, Paul Martini, Nikola Falk, Jan Martini, Cristina Giuliani and Martin Guariento. We finally thank Julia Seeber and Andreas Hilpold for reviewing the final version. The sampling permissions were thankfully granted by „28.4 Amt für Landschaftsökologie“ from the Province of Bozen, Italy.

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Appendix

Tab. A. Species list of ground beetles found on the 25 sampling locations. (Nomenclature according to www.fauna-eu.org). Species identification by Dominik Rabl.

Ground Beetles Species	Z1	Z2	Z3	Z4	Z5	O1	O2	O3	O4	O5	U1	U2	U3	U4	U5	T1	T2	T3	T4	T5	M1	M2	M3	M4	M5
Abax exaratus Dejean, 1828	X																								
Amara lunicollis Schiodte, 1837													X												
Calathus melanocephalus Linne, 1758											X		X									X	X		
Calathus micropterus Duftschmid, 1812			X	X	X					X				X		X	X	X	X					X	
Carabus germarii Sturm, 1815		X														X	X								
Carabus problematicus Herbst, 1786											X														
Cymindis vaporariorum Linne, 1758								X													X		X		
Pterostichus burmeisteri Heer, 1838	X	X	X													X	X	X	X						
Pterostichus jurinei Panzer, 1803		X		X	X											X	X			X					
Pterostichus multipunctatus Dejean, 1828						X	X	X	X	X		X	X	X	X							X		X	X
Pterostichus unctulatus Duftschmid, 1812	X					X		X	X	X				X	X	X	X	X	X				X		
Notiophilus biguttatus Fabricius, 1779															X										

Tab. B. Species occurrences of plant lice and plants and their interaction with ants and the plant on which they were found (Nomenclature according to www.fauna-eu.org). Species identification by E. Guariento.

Aphid species	Ant species	Plant species	Z1	Z2	Z3	Z4	Z5	O1	O2	O3	O4	O5	U1	U2	U3	U4	U5	T1	T2	T3	T4	T5	M1	M2	M3	M4	M5
Adelges laricis Vallot, 1836	*Formica lemani*	*Larix decidua, Picea abies*					X			X	X					X									X		
Cinara cembrae Seitner, 1936	*Formica lemani,* *Formica lugubris,* *Formica aquilonia*	*Pinus cembra*							X	X	X		X	X	X	X											
Cinara cuneo-maculata Del Guercio, 1909	*Formica lugubris*	*Larix decidua*															X										
Cinara juniperi De Geer, 1773	*Formica lemani,* *Formica lugubris*	*Juniperus communis*						X	X				X	X	X								X				
Cinara laricis Hartig, 1839	*Formica lemani,* *Formica lugubris*	*Larix decidua*								X					X	X									X		
Cinara piceae Panzer, 1800	*Formica lugubris*	*Picea abies*																X	X		X						
Cinara piceicola Cholodkovsky, 1896	*Formica lugubris* *Formica aquilonia*	*Picea abies*		X	X																	X					
Cinara pilicornis Hartig, 1841	*Formica lemani,* *Formica lugubris*	*Picea abies*																	X	X	X	X					
Coccidea	*Manica rubida* *Formica lemani*	*Juniperus communis*											X	X	X												
Macrosiphum rosae Linnaeus, 1758	-	*Rosa pendulina*																		X							
Physokermes sp.	*Formica lugubris* NOT clear interaction	*Picea abies*			X															X							
Trioza sp	-	*Hieracium sp.*																						X			
Uroleucon sp. 1	-	*Solidago virgaurea*						X																			X
Uroleucon sp. 2	-	*Campanula scheuchzeri*											X														

Tab. C. Species list of spiders and harvestmen found on the 25 sampling locations. Marked in grey are species which do not hunt on the ground and therefore were omitted from statistical analyses. (Nomenclature according to www.fauna-eu.org) Species identification by Simone Ballini.

Spiders	**Z1**	**Z2**	**Z3**	**Z4**	**Z5**	**O1**	**O2**	**O3**	**O4**	**O5**	**U1**	**U2**	**U3**	**U4**	**U5**	**T1**	**T2**	**T3**	**T4**	**T5**	**M1**	**M2**	**M3**	**M4**	**M5**
Aranea																									
Robertus truncorum C.L. Koch, 1872																								X	X
Centromerus pabulator O. P.-Cambridge, 1875																			X					X	X
Gonatium rubens Blackwall, 1833														X				X							
Alopecosa pulverulenta Clerck, 1757			X	X				X																	
Alopecosa taeniata C.L. Koch, 1835				X																					
Alopecosa sp. juv. Simon, 1885																						X	X		
Arctosa renidescens Buchar & Thaler, 1995										X		X													
Pardosa blanda C.L. Koch, 1833	X	X	X		X	X	X	X	X		X	X	X					X			X		X	X	X
Pardosa ferruginea L. Koch, 1870										X															
Pardosa oreophila Simon, 1937	X	X														X								X	
Pardosa riparia C.L. Koch, 1833		X														X									
Pardosa sp. juv. C.L. Koch, 1847									X														X		X
Cybaeus minor Chyzer, 1897						X	X	X	X																X
Amaurobius fenestralis Ström, 1768											X														
Agroeca proxima O. P.-Cambridge, 1871																									X
Cheiracanthium sp. juv. C.L. Koch, 1839							X				X	X									X		X		
Drassodes pubescens Thorell, 1856		X	X			X																			
Gnaphosa badia L. Koch, 1866										X															
Gnaphosidae sp. juv										X											X		X	X	
Haplodrassus signifer C.L. Koch, 1839													X												
Micaria alpina L. Koch, 1872													X												
Micaria silesiaca L. Koch, 1875											X														
Zelotes talpinus L. Koch, 1872												X										X			
Ozyptila trux Blackwall, 1846																X									
Xysticus audax Schrank, 1803										X															
Opiliones																									
Histricostoma dentipalpe Ausserer, 1867					X					X															
Paranemastoma quadripunctatum Perty, 1833				X																					
Mitopus morio Fabricius, 1799					X							X			X						X		X	X	
Platybunus bucephalus C.L.Koch, 1835																X									