SAN FRANCISCO DE QUITO UNIVERSITY

Effects Of The Presence Of *Myrmelachista Schumanni* Ants On The Abundance And Diversity Of Edaphic Macro Invertebrates Within 'Devil's Gardens'.

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Degree Thesis Requirement For Obtaining The Degree In Applied Ecology

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Agosto 2012

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APPROVAL OF THESIS

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ACKNOWLEDGMENTS

I thank the Tiputini Biodiversity Station staff both in Quito and Tiputini; David Romo, my Thesis Director; Stella de la Torre, Dean of College of Biological and Environmental Sciences; Carlos Valle and Diego Cisneros for their guidance and constructive reviews that improved the thesis and the staff of the Aquatic Ecology Laboratory for facilitating the use of their equipment and laboratory. I would like to thank also to the Scholarship Committee of the USFQ, to my partners and my mother.

ABSTRACT

‘Devil’s gardens’ are created by *Myrmelachista schumanni* ants, which nest in the hollow, swollen stems of *Duroia hirsuta*, and create these areas devoid of vegetation by poisoning all plants, with the exception their host plants, with formic acid. In this study I investigated if in addition to killing encroaching vegetation around their host plants, *M. schumanni* workers also compete or interfere with the abundance and diversity of edaphic macro invertebrates within ‘devil’s gardens’. The study was carried out at Tiputini Biodiversity Station in the province of Orellana, Ecuador, where twelve ‘devil’s gardens’ were located and soil samples were collected. The abundance and diversity of macro invertebrates of each sample was measured and compared between controls, soil within ‘devil’s gardens’, and soil outside ‘devil’s gardens’. The results of this study suggested that the presence of *M. schumanni* has no effects on the abundance nor on the diversity of edaphic macro invertebrates within ‘devil’s gardens’.

RESUMEN

Las "Chacras del diablo" son creadas por las hormigas *Myrmelachista schumanni*, que anidan en los troncos huecos y abultados de los árboles *Duroia hirsuta*, y crean estas áreas desprovistas de vegetación al inhibir el crecimiento de todas las plantas excepto sus plantas hospederas con ácido fórmico. En este estudio se investigó si, además de matar a la vegetación alrededor de sus plantas hospederas, las obreras *M. schumanni* también compiten o interfieren en la abundancia y diversidad de macroinvertebrados edáficos en las "Chacras del diablo". El estudio se llevó a cabo en la Estación Biológica Tiputini en la provincia del Napo, Ecuador, donde doce "chacras del diablo" fueron localizadas y se recogió muestras del suelo de cada una de ellas. La abundancia y diversidad de macroinvertebrados de cada muestra se midió y se comparó con los controles dentro y fuera de las chacras. De acuerdo con los resultados de este estudio, la presencia de *M. schumanni* no tiene efectos en la abundancia o en la diversidad de macroinvertebrados edáficos en las "chacras del diablo".

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1. INTRODUCTION

'Devil's gardens' are areas in the Amazon rainforest that consist almost entirely of a single species of trees, *Duroia hirsuta* (Rubiaceae), and according to a local legend, are cultivated by an evil forest spirit (Frederickson et al. 2005; Edwards et al. 2009). It has been determined that devil's gardens are created by *Myrmelachista schumanni* ants, and not by allelopathy of *D. hirsuta* (Frederickson et al. 2005). The ant *M. schumanni*, which nests in the hollow, swollen stems of *D. hirsuta*, creates devil's gardens by poisoning all plants, with the exception of its host plants, with formic acid (Frederickson et al. 2005). When attacking non-host plants, a worker *M. schumanni* ant bites a small hole in the leaf tissue, inserts the tip of its abdomen into the hole and releases formic acid. As a result, affected leaves develop necrosis along primary veins within hours of the attack (Frederickson 2005). By killing plants of other species, the ant promotes the growth and establishment of *D. hirsuta*, thereby gaining more nest sites (Frederickson 2005).

For this reason, *M. schumanni* ants are known to interfere with the establishment and development of vegetation, except that of *D.hirsuta* (and a few other species) (Frederickson et al 2005; Edwards et al 2009). However, it is also possible that *M. schumanni* ants compete with other invertebrate species in two ways: by an exploitative competition, where interactions between species arise from the use of a common resource (Case et al. 1974) and each consumer affects others by reducing resource abundance (Vance 1984); or by interference competition, where interactions arise from territoriality, overgrowth, undercutting, predation or chemical competition (Schoener 1983) and each consumer alters the others' ability to exploit the resource at any level of abundance (Vance 1984).

In addition to killing encroaching vegetation around their host plants, *M. schumanni* workers also protect their host plants against insects and vertebrate herbivores, significantly reducing leaf herbivory (Frederickson 2005, Rosumek 2009). However, *D. hirsuta* located within devil's gardens with *M. schumanni* ants suffers higher herbivory than *D. hirsuta* outside of devil's gardens, even though the ants defend their host plants against herbivores (Frederickson and Gordon 2007). The changing environment in devil's gardens attracts more herbivores and increased herbivory in turn increases as the number of *D. hirsuta* trees in a devil's garden (Frederickson and Gordon 2007). Furthermore, there are other effects of ants in the ecosystems they inhabit; it is known that the presence of nests of other Formicidae ants in the soil affects many soil properties (Jilkova et al. 2010) and that ants are considered ecosystem engineers because they either directly or indirectly modulate the availability of resources to other species (Jouquet et al. 2006). That being said, it is still unknown if the presence of ants has an effect on the invertebrates colonies of "devil gardens".

GENERAL GOAL

The aim of this study is to investigate if, besides the effects on surrounding vegetation and in the herbivory in ‘devil’s gardens’, the presence of *M. schumanni* ants has an effect on the abundance and diversity of the communities of edaphic macro-invertebrates in the soil of ‘devil’s gardens’. Evaluating the occurrence of soil fauna in ‘devil’s gardens’, as in every terrestrial ecosystem, is important because it exerts an important effect on mineralization rates of detritus (Reichle 1977), it increases nutrient release by fragmentation of litter, grazing of microflora and improvement of soil structure (Reichle 1977) and therefore implies a direct effect on *D. hirsuta* fitness.

SPECIFIC OBJECTIVES

- Determine the abundance, diversity and species composition of edaphic macro-invertebrates inside ¨devil gardens¨.
- Identify these macro-invertebrates up to their taxonomic order.
- Compare the parameters of diversity and abundance of edaphic macro-invertebrates inside and outside ¨devil gardens¨ and with several control groups by means of statistical analysis.

2. METHODS

Study Area:

This study was carried out over seven days in May of 2010 at the Universidad San Francisco de Quito's Tiputini Biodiversity Station (76°04'W, 00°38'S), altitude approximately 200 m.a.s.l., Province of Orellana, Ecuador, on the north bank of the Tiputini River (a tributary of the Napo River) in Eastern Ecuador. Twelve 'devil's gardens' located near the well-marked trails around the camp were sampled. For purposes of this publication, I define a 'devil's garden' as one or more trees of *D. hirsuta* occupied by *M. schumanni* and clustered together in an area that is largely devoid of other plants. While at the study area there is an abundance of primary *terra firme* (upland) forest and varzea (seasonally-flooded) forest, all 'devil's gardens' I selected were located in terra firma forests.

For each 'devil's garden' encountered, a number was assigned and the following variables were recorded: location (name of the trail and distance from the station), total number of *D. hirsuta* trees, distance between the two most distant trees and shape of the 'devil's garden' (an outline of the arrangement of the trees in the area was drawn to estimate a central point of the 'devil's garden'). A hole fifteen centimeters deep and fifteen centimeters in diameter, was dug in the ground at the center point (area devoid of vegetation) of each 'devil's garden'. Another hole was dug at a point located at a distance of four meters from the edge of each 'devil's garden' (area with vegetation). Soil samples were placed in plastic containers appropriately labeled and carried to the station lab for further analyses.

Also, eight control locations were established to discern any potential effect of the 'devil's gardens' from those that may have resulted from lack of vegetation in the abundance of edaphic macro-invertebrates. Controls were located on *terra firme* forests, in areas devoid of vegetation, close to the 'devil's gardens' to maintain similar environmental conditions but free from the effects of the communities of *M. schumanni* ants. A soil sample from the middle of each control zone was collected and analyzed.

The abundance (number) of macro-invertebrates in each sample was assessed through a 20-minutes visual search per sample while the soil was manually mixed to locate the visible macro-invertebrates. Macro-invertebrates collected were placed in 70-degree alcohol for preservation and subsequent identification. Collected macro-invertebrates were counted and identified down to their taxonomic order using a stereo microscope. Abundance, diversity (Simpson index) and species composition (Margalef index and Menhinik index) of macro invertebrates at the level of taxonomic orders were calculated and compared between the samples. Differences in abundance and diversity of macro invertebrates among the three groups (inside 'devil's gardens', outside 'devil's gardens' and controls) were analyzed using One Way ANOVA. Independent samples t-test were used to test for differences between 'devil's gardens' and controls and paired samples t-test for those between within 'devil's gardens' and outside 'devil's gardens'.

3. RESULTS

A total of 490 macro invertebrates were collected: 123 in soil samples of the control areas, 152 in soil samples inside 'devil's gardens' and 215 outside 'devil's gardens' (Table 1). Twenty different orders were identified; Collembola, Orthoptera, Dyctioptera, Isoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, Pulmonata, Oligochaeta, Diplopoda, Quilopoda, Isopoda and Araneae (14 orders) were present in the control areas. Thysanura, Diplura, Collembola, Dermaptera, Isoptera, Embioptera, Hemiptera, Coleoptera, Hymenoptera, Pulmonata, Oligochaeta, Diplopoda, Quilopoda, Isopoda and Acarina (15 orders) were present inside 'devil's gardens'. Thysanura, Diplura, Collembola, Orthoptera, Dyctioptera, Dermaptera, Isoptera, Hemiptera, Coleóptera, Diptera, Hymenoptera, Oligochaeta, Diplopoda, Quilopoda, Acarina, Pseudoescorpionida and Araneae (17 orders) were found outside 'devil's gardens'(Table 2).

When comparing the three groups: controls, within 'devil's gardens' and outside 'devil's gardens'; significant differences were not found in global abundance nor in diversity or species composition indexes of macro-invertebrates between the three groups (Figure 1, Table 3). No significant differences were found in the abundance of any taxonomic order between the three groups (Table 4).

When comparing the global abundance within 'devil's gardens' with the global abundance outside 'devil's gardens', no significant differences were found (Table 5). No significant differences were found in the diversity index or in species composition indexes of macro-invertebrates between the two groups (Table 5). No differences were found between the abundance of macro-invertebrates within 'devil's gardens' and the abundance of macro-invertebrates outside 'devil's gardens' to no taxonomic order except Araneae (paired samples t test, p=0.027, t=-2.548, df=11) (Table 6).

Significant differences were found when comparing the number of taxonomic orders within 'devil's gardens' with the number of taxonomic orders in controls (independent samples t-test, p=0.035, t= -2.28, df=18) (Table 7). Significant differences were also found between Simpson indexes within 'devil's gardens' and controls (independent samples t-test, p=0.035, t=-2.28, df=18) (Table 7). No differences were found between the abundance of macro invertebrates within 'devil's gardens' and the abundance of macro invertebrates in controls to no taxonomic order except with Diptera (independent samples t test, p=0.020, t=-2.546, df=18) (Table 8).

4. DISCUSSION

The results of this study indicated that the presence of *M. schumanni* has no effects in the abundance or in the diversity of edaphic macro invertebrates within ‘devil’s gardens’. Many plant species provide food or nest sites for ants in exchange for protection from herbivores and competition or for nutrient advantages (Beattie 1985 cit. in Davidson 1989). A lower diversity of invertebrates might not be beneficial for the community of trees of *D. hirsuta,* because the occurrence of soil fauna populations increases nutrient release by fragmentation of litter, grazing of microflora and improvement of soil structure (Reichle 1977). As plants utilize mineral nutrients in the inorganic form, and are dependent upon the rate at which mineralization occurs in the soil (Reichle 1977), the presence of soil fauna is not prejudicial for the population of *D. hirsuta.* In addition of a nesting place, *M. schumanni* could be receiving nutrition from their host plants, either directly in the form of food bodies and extrafloral nectar, or indirectly via homopteran coccoids (Frederickson 2005), therefore *M. shumanni* ants do not need to deter or prey upon insects and invertebrates except for those that decrease *D. hirsuta* fitness by means of herbivory.

A lower abundance and diversity was expected within ‘devil’s gardens’ than outside ‘devil’s gardens’ because species like *M. schumanni* ants, that use costly interference mechanisms (e.g. territoriality, over-growth or undercutting, allelopathy and other forms of chemical competition) should not be able to coexist unless they also engage in beneficial interference mechanisms (e.g. predation or parasitism) (Amarasekare 1974). However, the presence of *M. schumanni* within ‘devil’s gardens’ produces almost pure stands of *D. hirsuta,* generating different environmental conditions from those outside of ‘devil’s gardens’. These new conditions could have effects on herbivory (Rosumek 2009) and probably in the abundance and diversity of macro invertebrates in soil. For example, abundances of herbivores are often higher in pure stands than in mixed stands of plants (Davidson 1989). Compared with other ant species, Myrmelachista provides the least protection against leaf herbivory to Cordia and Duroia, which could suggest that *M. schumanni* do not interfere in the most effective way with other invertebrate species. Indeed, ants can increase herbivore loads on their host plants (Frederickson and Gordon 2007; Frederickson et al. 2012; Palmer et al. 2008). On the other hand, Myrmelachista ants provide better protection against encroaching vegetation, increasing canopy openness over their host plants (Frederickson 2005). *M. schumanni* ants provide the most light environment; plants occupied by *M. schumanni* have more open canopies above them than plants occupied by ants species like Allomerus or Azteca (Frederickson 2005). The differences in canopy openness and light availability could have an effect on the number and diversity of macro invertebrates living within 'devil's gardens'.

The results found when comparing the samples within 'devil's gardens' with the control samples suggest that when the other conditions are similar (areas devoid of vegetation, light availability, canopy openness), there are significant differences in the number of taxonomic orders and in the diversity of edaphic macro invertebrates. Nevertheless, it cannot be determined if the presence of *M. schumanni* ants or the presence of *D. hirsuta* trees cause of the differences. The cause for why the diversity and abundance of taxonomic orders in controls was higher than the diversity and abundance of taxonomic orders within 'devil's gardens' could be that species with costly interference mechanisms (like encroaching vegetation with chemical) are common in communities of low diversity and can coexist only with species that are immune to their interference (Amarasekare 1974).

5. CONCLUSIONS

M.schumanni ants do not compete or interfere with the communities of edaphic macro invertebrates. The colonies of *M. schumanni* have no effects on the abundance or on the diversity of edaphic macro invertebrates within 'devil's gardens'.

As ecosystem engineers, ants alter the ecosystem dynamics within devil gardens and cause a modification of the habitat and the environmental conditions, hence, the richness of edaphic fauna would be influenced by these new conditions and not directly by the presence of *M. schumanni* ants nor by the population of *D. hirsuta.*

M. schumanni ants provide defense against herbivores which is directly beneficial to *D. hirsuta* but according to this study they do not attack or prey on other arthropods that coexist near "devil gardens" areas at considerable levels because there is not a significant reduction of abundance of macro invertebrates in these areas. Soil fauna is not significantly reduced; if it were, it could represent an ecological cost for *M. schumanni* host plants as their fitness depends in part on the composition of the soil.

6. RECOMMENDATIONS

In this study, it should be pointed out that the macro invertebrates that were collected were identified down to the taxonomic order. Therefore, differences within and outside "devil gardens" at a species level could not be evaluated. That being said, a more detailed study which would take into account differences at the species level would have been necessary. I also recommend increasing the number of samples and the study area to confirm the results obtained in this investigation.

As soil fauna depends greatly on the properties of the soil, I consider it would be really informative to evaluate the effect, if it exists, of the presence of *M. schumanni* ants or *D. hirsuta* trees on the values of pH, water content, organic matter content and other chemical and microbiological properties of the soils of "devil gardens".

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8. TABLES AND FIGURES

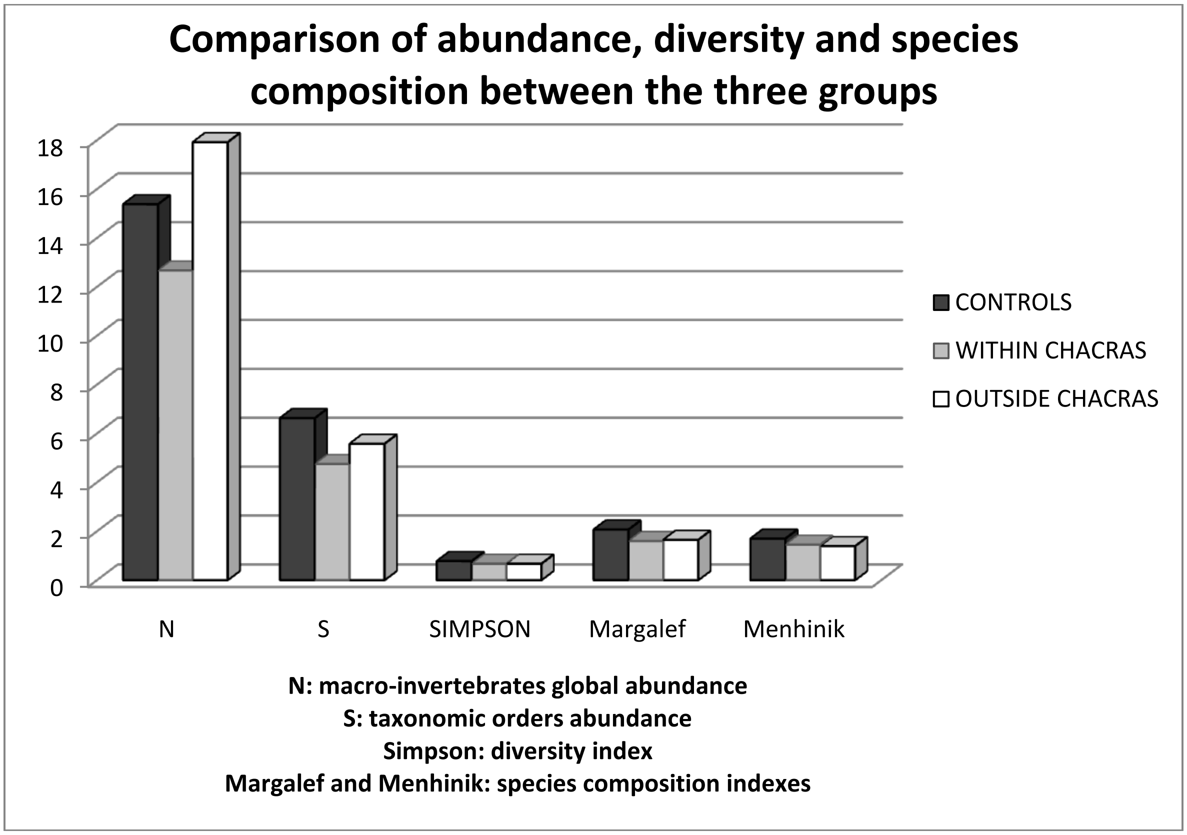

Figure 1. Comparison of abundance, diversity and species composition between the three groups (controls, within 'devil's gardens' and outside 'devil's gardens').

TABLE 1. Values of global abundance of macro-invertebrates (N), abundance of taxonomic orders (S) and diversity (Simpson index) and species composition (Margalef and Menhinik indexes) found within "devil gardens", outside "devil gardens" and in controls.

UBICACION1	N1	S1	MARGALEF1	MENHINIK1	D Si	Simpson1
CHACRA 1	16	3	0,72	0,75	0,43	0,57
CHACRA 2	8	6	2,40	2,12	0,22	0,78
CHACRA 3	34	5	1,13	0,86	0,49	0,51
CHACRA 4	15	6	1,85	1,55	0,23	0,77
CHACRA 5	4	2	0,72	1,00	0,63	0,38
CHACRA 6	10	4	1,30	1,26	0,28	0,72
CHACRA 7	7	3	1,03	1,13	0,39	0,61
CHACRA 8	24	8	2,20	1,63	0,34	0,66
CHACRA 9	3	3	1,82	1,73	0,33	0,67
CHACRA 10	10	5	1,74	1,58	0,24	0,76
CHACRA 11	10	7	2,61	2,21	0,16	0,84
CHACRA 12	11	5	1,67	1,51	0,26	0,74
	12,67	4,75	1,60	1,45	0,33	0,67
UBICACION2	**N2**	**S2**	**MARGALEF2**	**MENHINIK2**	**D Si**	**Simpson2**
NO CHACRA 1	24	5	1,26	1,02	0,36	0,64
NO CHACRA 2	9	5	1,82	1,67	0,23	0,77
NO CHACRA 3	18	8	2,42	1,89	0,23	0,77
NO CHACRA 4	8	5	1,92	1,77	0,25	0,75
NO CHACRA 5	16	6	1,80	1,50	0,27	0,73
NO CHACRA 6	30	6	1,47	1,10	0,60	0,40
NO CHACRA 7	23	3	0,64	0,63	0,43	0,57
NO CHACRA 8	17	7	2,12	1,70	0,32	0,68
NO CHACRA 9	14	5	1,52	1,34	0,35	0,65
NO CHACRA 10	19	9	2,72	2,06	0,18	0,82
NO CHACRA 11	14	5	1,52	1,34	0,35	0,65
NO CHACRA 12	23	3	0,64	0,63	0,43	0,57
	17,92	5,58	1,65	1,39	0,33	0,67
UBICACION3	**N2**	**S2**	**MARGALEF2**	**MENHINIK2**	**D Si**	**Simpson2**
CONTROL 1	10	7	2,61	2,21	0,16	0,84
CONTROL 2	22	10	2,91	2,13	0,14	0,86
CONTROL 3	14	5	1,52	1,34	0,33	0,67
CONTROL 4	15	5	1,48	1,29	0,23	0,77
CONTROL 5	19	8	2,38	1,84	0,17	0,83
CONTROL 6	16	7	2,16	1,75	0,16	0,84
CONTROL 7	11	5	1,67	1,51	0,26	0,74
CONTROL 8	16	6	1,8	1,5	0,28	0,72
	15,38	6,63	2,07	1,70	0,22	0,78

TABLE 2. Identified taxonomic orders found in controls, within ‘devil’s gardens’ and outside ‘devil’s gardens’.

	Controles	Dentro	Fuera
Acarina		x	x
Araneae	x		x
Coleoptera	x	x	x
Collembola	x	x	x
Dermaptera		x	x
Diplopoda	x	x	x
Diplura		x	x
Diptera	x		x
Dyctioptera	x		x
Embioptera		x	
Hemiptera	x	x	x
Hymenoptera	x	x	x
Isopoda	x	x	
Isoptera	x	x	x
Oligochaeta	x	x	x
Orthoptera	x		x
Pseudoescorpionida			x
Pulmonata	x	x	
Quilopoda	x	x	x
Thysanura		x	x
	14	15	17

TABLE 3. ANOVA test results for the global abundance of macro-invertebrates (N), for the abundance of taxonomic orders (S), for the diversity (Simpson index) and for the species composition (Margalef and Menhinik indexes) in the three groups (controls, within 'devil's gardens' and outside 'devil's gardens').

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
N	Between Groups	165.417	2	82.708	1.709	.199
	Within Groups	1403.458	29	48.395		
	Total	1568.875	31			
S	Between Groups	16.927	2	8.464	2.638	.089
	Within Groups	93.042	29	3.208		
	Total	109.969	31			
MARGALEF	Between Groups	1.174	2	.587	1.595	.220
	Within Groups	10.672	29	.368		
	Total	11.846	31			
MENHINIK	Between Groups	.494	2	.247	1.272	.295
	Within Groups	5.627	29	.194		
	Total	6.120	31			
SIMPSON	Between Groups	.083	2	.041	3.214	.055
	Within Groups	.373	29	.013		
	Total	.456	31			

TABLE 4. ANOVA test results for the abundance of each taxonomic order in the three groups (controls, within 'devil's gardens' and outside 'devil's gardens').

ANOVA

		Suma de cuadrados	gl	Media cuadrática	F	Sig.
Thysanura	Inter-grupos	.333	2	.167	1.526	.234
	Intra-grupos	3.167	29	.109		
	Total	3.500	31			
Diplura	Inter-grupos	.167	2	.083	.453	.640
	Intra-grupos	5.333	29	.184		
	Total	5.500	31			
Collembola	Inter-grupos	.677	2	.339	.576	.568
	Intra-grupos	17.042	29	.588		
	Total	17.719	31			
Orthoptera	Inter-grupos	.375	2	.188	1.740	.193
	Intra-grupos	3.125	29	.108		
	Total	3.500	31			
Dictyoptera	Inter-grupos	.708	2	.354	2.143	.135
	Intra-grupos	4.792	29	.165		
	Total	5.500	31			
Dermaptera	Inter-grupos	.167	2	.083	.725	.493
	Intra-grupos	3.333	29	.115		
	Total	3.500	31			
Isoptera	Inter-grupos	49.885	2	24.943	.658	.525
	Intra-grupos	1098.583	29	37.882		
	Total	1148.469	31			
Embioptera	Inter-grupos	.052	2	.026	.824	.449
	Intra-grupos	.917	29	.032		
	Total	.969	31			
Hemiptera	Inter-grupos	.135	2	.068	.481	.623
	Intra-grupos	4.083	29	.141		
	Total	4.219	31			
Coleoptera	Inter-grupos	9.294	2	4.647	.557	.579
	Intra-grupos	233.803	28	8.350		
	Total	243.097	30			
Diptera	Inter-grupos	.782	2	.391	2.698	.085
	Intra-grupos	4.057	28	.145		
	Total	4.839	30			
Hymenoptera	Inter-grupos	4.417	2	2.208	.240	.788

	Intra-grupos	266.458	29	9.188		
	Total	270.875	31			
Pulmonata	Inter-grupos	.083	2	.042	.674	.517
	Intra-grupos	1.792	29	.062		
	Total	1.875	31			
Oligochaeta	Inter-grupos	2.833	2	1.417	.279	.758
	Intra-grupos	147.167	29	5.075		
	Total	150.000	31			
Diplopoda	Inter-grupos	3.542	2	1.771	.682	.514
	Intra-grupos	75.333	29	2.598		
	Total	78.875	31			
Quilopoda	Inter-grupos	.927	2	.464	.894	.420
	Intra-grupos	15.042	29	.519		
	Total	15.969	31			
Isopoda	Inter-grupos	.083	2	.042	.674	.517
	Intra-grupos	1.792	29	.062		
	Total	1.875	31			
Acarina	Inter-grupos	.333	2	.167	1.526	.234
	Intra-grupos	3.167	29	.109		
	Total	3.500	31			
Pseudoscorpionida	Inter-grupos	.052	2	.026	.824	.449
	Intra-grupos	.917	29	.032		
	Total	.969	31			
Araneae	Inter-grupos	2.708	2	1.354	2.339	.114
	Intra-grupos	16.792	29	.579		
	Total	19.500	31			

TABLE 5. Paired t-test results for the global abundance of macro-invertebrates (N), for the abundance of taxonomic orders (S), for the diversity (Simpson index) and for the species composition (Margalef and Menhinik indexes) between samples within 'devil's gardens'(group 1) and outside 'devil's gardens'(group 2).

Paired Samples Test

		Paired Differences					t	df	Sig. (2-tailed)
					95% Confidence Interval of the Difference				
		Mean	Std. Deviation	Std. Error Mean	Lower	Upper			
Pair 1	N1 - N2	-5.250	10.661	3.078	-12.024	1.524	-1.706	11	.116
Pair 2	S1 - S2	-.833	2.250	.649	-2.263	.596	-1.283	11	.226
Pair 3	MARGALEF1 - MARGALEF2	-.0539262	.7931032	.2289492	-.5578400	.4499875	-.236	11	.818
Pair 4	MENHINIK1 - MENHINIK2	.0601531	.5893556	.1701323	-.3143056	.4346118	.354	11	.730
Pair 5	Simpson1 - Simpson2	.0013048	.1851439	.0534464	-.1163300	.1189396	.024	11	.981

TABLE 6. Paired t-test results for the abundance of each taxonomic order between the two groups (within 'devil's gardens' (1) and outside 'devil's gardens' (2)).

Paired Samples Test

		Paired Differences							
					95% Confidence Interval of the Difference				
		Mean	Std. Deviation	Std. Error Mean	Lower	Upper	t	Df	Sig. (2-tailed)
Pair 1	Thysanura1 - Thysanura2	-.167	.389	.112	-.414	.081	-1.483	11	.166
Pair 2	Diplura1 - Diplura2	.000	.739	.213	-.469	.469	.000	11	1.000
Pair 3	Collembola1 - Collembola2	.167	1.115	.322	-.542	.875	.518	11	.615
Pair 4	Orthoptera1 - Orthoptera2	-.250	.452	.131	-.537	.037	-1.915	11	.082
Pair 5	Dictyoptera1 - Dictyoptera2	-.083	.289	.083	-.267	.100	-1.000	11	.339
Pair 6	Dermaptera1 - Dermaptera2	.000	.603	.174	-.383	.383	.000	11	1.000
Pair 7	Isoptera1 - Isoptera2	-1.750	10.593	3.058	-8.480	4.980	-.572	11	.579
Pair 8	Embioptera1 - Embioptera2	.083	.289	.083	-.100	.267	1.000	11	.339
Pair 9	Hemiptera1 - Hemiptera2	.083	.515	.149	-.244	.411	.561	11	.586
Pair 10	Coleoptera1 - Coleoptera2	-.818	2.401	.724	-2.431	.795	-1.130	10	.285
Pair 11	Diptera1 - Diptera2	-.273	.467	.141	-.587	.041	-1.936	10	.082
Pair 12	Hymenoptera1 - Hymenoptera2	-.750	3.980	1.149	-3.279	1.779	-.653	11	.527
Pair 13	Pulmonata1 - Pulmonata2	.083	.289	.083	-.100	.267	1.000	11	.339
Pair 14	Oligochaeta1 - Oligochaeta2	-.167	2.691	.777	-1.877	1.543	-.215	11	.834
Pair 15	Diplopoda1 - Diplopoda2	.167	1.899	.548	-1.040	1.373	.304	11	.767
Pair 16	Quilopoda1 - Quilopoda2	-.333	1.073	.310	-1.015	.348	-1.076	11	.305
Pair 17	Isopoda1 - Isopoda2	.083	.289	.083	-.100	.267	1.000	11	.339

Pair 18	Acarina1 - Acarina2	-.167	.577	.167	-.533	.200	-1.000	11	.339
Pair 19	Pseudoscorpionida1 - Pseudoscorpionida2	-.083	.289	.083	-.267	.100	-1.000	11	.339
Pair 20	Araneae1 - Araneae2	-.583	.793	.229	-1.087	-.080	-2.548	11	.027

TABLE 7. Independent samples t-test for the global abundance of macro-invertebrates (N), for the abundance of taxonomic orders (S), for the diversity (Simpson index) and for the species composition (Margalef and Menhinik indexes) between samples within 'devil's gardens' and controls.

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference Lower	Upper
N	Equal variances assumed	2.676	.119	-.815	18	.426	-2.708	3.324	-9.691	4.275
	Equal variances not assumed			-.938	16.290	.362	-2.708	2.888	-8.822	3.405
S	Equal variances assumed	.034	.855	-2.286	18	.035	-1.875	.820	-3.598	-.152
	Equal variances not assumed			-2.299	15.445	.036	-1.875	.816	-3.609	-.141
MARGALEF	Equal variances assumed	.244	.628	-1.723	18	.102	-.4659945	.2704855	-1.0342635	.1022745
	Equal variances not assumed			-1.782	16.787	.093	-.4659945	.2614338	-1.0181043	.0861153
MENHINIK	Equal variances assumed	.662	.426	-1.301	18	.210	-.2503777	.1925190	-.6548450	.1540897
	Equal variances not assumed			-1.379	17.635	.185	-.2503777	.1815902	-.6324516	.1316963
Simpson	Equal variances assumed	2.224	.153	-2.286	18	.035	-.1167781	.0510825	-.2240984	-.0094579
	Equal variances not assumed			-2.586	17.175	.019	-.1167781	.0451567	-.2119765	-.0215797

TABLE 8. Independent samples t-test results for the abundance of each taxonomic order between the two groups controls and samples within 'devil's gardens'.

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
									95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Thysanura	Equal variances assumed	3.168	.092	.809	18	.429	.083	.103	-.133	.300
	Equal variances not assumed			1.000	11.000	.339	.083	.083	-.100	.267
Diplura	Equal variances assumed	9.000	.008	1.200	18	.246	.167	.139	-.125	.458
	Equal variances not assumed			1.483	11.000	.166	.167	.112	-.081	.414
Collembola	Equal variances assumed	.655	.429	-.541	18	.595	-.208	.385	-1.017	.600
	Equal variances not assumed			-.525	13.583	.608	-.208	.397	-1.061	.645
Orthoptera	Equal variances assumed	8.400	.010	-1.242	18	.230	-.125	.101	-.336	.086
	Equal variances not assumed			-1.000	7.000	.351	-.125	.125	-.421	.171
Dictyoptera	Equal variances assumed	20.344	.000	-1.771	18	.094	-.375	.212	-.820	.070
	Equal variances not assumed			-1.426	7.000	.197	-.375	.263	-.997	.247
Dermaptera	Equal variances assumed	9.000	.008	1.200	18	.246	.167	.139	-.125	.458
	Equal variances not assumed			1.483	11.000	.166	.167	.112	-.081	.414
Isoptera	Equal variances assumed	1.520	.233	.598	18	.557	1.417	2.369	-3.561	6.394
	Equal variances not assumed			.725	12.499	.482	1.417	1.954	-2.822	5.655
Embioptera	Equal variances assumed	3.168	.092	.809	18	.429	.083	.103	-.133	.300

	Equal variances not assumed			1.000	11.000	.339	.083	.083	-.100	.267
Hemiptera	Equal variances assumed	.732	.403	-.435	18	.669	-.083	.191	-.486	.319
	Equal variances not assumed			-.420	13.277	.681	-.083	.199	-.511	.345
Coleoptera	Equal variances assumed	2.043	.171	-.075	17	.941	-.068	.910	-1.987	1.851
	Equal variances not assumed			-.086	12.139	.933	-.068	.789	-1.786	1.649
Diptera	Equal variances assumed	162.000	.000	-2.546	18	.020	-.375	.147	-.684	-.066
	Equal variances not assumed			-2.049	7.000	.080	-.375	.183	-.808	.058
Hymenoptera	Equal variances assumed	.640	.434	-.575	18	.572	-.792	1.376	-3.682	2.099
	Equal variances not assumed			-.650	17.250	.524	-.792	1.218	-3.359	1.776
Pulmonata	Equal variances assumed	.333	.571	-.289	18	.776	-.042	.144	-.344	.261
	Equal variances not assumed			-.277	12.974	.786	-.042	.150	-.366	.283
Oligochaeta	Equal variances assumed	.009	.923	-1.073	18	.298	-.750	.699	-2.219	.719
	Equal variances not assumed			-1.055	14.313	.309	-.750	.711	-2.271	.771
Diplopoda	Equal variances assumed	.539	.472	-.891	18	.385	-.667	.749	-2.239	.906
	Equal variances not assumed			-.827	11.485	.425	-.667	.806	-2.431	1.098
Quilopoda	Equal variances assumed	4.114	.058	-1.408	18	.176	-.375	.266	-.934	.184
	Equal variances not assumed			-1.277	10.469	.229	-.375	.294	-1.025	.275
Isopoda	Equal variances assumed	.333	.571	-.289	18	.776	-.042	.144	-.344	.261
	Equal variances not assumed			-.277	12.974	.786	-.042	.150	-.366	.283
Acarina	Equal variances assumed	3.168	.092	.809	18	.429	.083	.103	-.133	.300

	Equal variances not assumed			1.000	11.000	.339	.083	.083	-.100	.267
Araneae	Equal variances assumed	26.703	.000	-1.849	18	.081	-.625	.338	-1.335	.085
	Equal variances not assumed			-1.488	7.000	.180	-.625	.420	-1.618	.368