Original article

Species diversity and community structure in trap-nesting bees in Southern Brazil¹

Maria Luisa Tunes BUSCHINI*

Departamento de Biologia, Universidade Estadual do Centro Oeste, Rua Presidente Zacarias 875, Guarapuava (PR), 85010990, Brazil

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Abstract – The species diversity and community structure of trap-nesting bees in the Parque Municipal das Araucárias in Southern Brazil was studied during 2 years. Three different habitats (Araucaria forest, swamp and grassland) were investigated in terms of abundance, richness, diversity and similarity of bee communicites. A total of 120 nests of 11 species were collected. The largest abundance of individuals and species richness was found for the family Megachilidae. The most abundant species were *Centris tarsata, Megachile brasiliensis* and *Colletes* sp. Intermediate species were *C. tarsata, M. brasiliensis, Colletes* sp, *Epanthidium nectarinioides, Megachile* (*Dactylomegachile*) sp₁, *Anthodioctes claudii, Megachile* sp₁ and *Megachile* sp₂. *Megachile* (*Austramegamegachile*) fiebrigi, *Xylocopa* (*Neoxylocopa*) augusti and *Megachile* (*Moureapis*) sp₁ were the rare species. Swamp habitat yielded the greatest abundance and diversity of bee species. The similarity between this habitat and grassland, in relation to their species abundance and also to their species presence-absence, was the greatest.

solitary bees / community / biocenosis / species diversity / trap-nest / Apoidea

1. INTRODUCTION

Studies of tropical forest systems have made important contributions to understanding patterns of species diversity and community structure (Ricklefs and Schluter, 1993). Due to increasing global habitat destruction modern studies of diversity are of vital importance for understanding biological communities and their conservation (Purvis and Hector, 2000).

The nature of land-use change in recent decades has not only resulted in a dramatic decrease in total forest cover, but also in an increasingly skewed size-distribution of forest remnants. Forest fragmentation is an important process contributing to the present-day concern over the loss of biodiversity and species extinction rates (Didham et al., 1996; Tscharntke et al., 1998; Steffan-Dewenter et al., 2002). Some recent studies have shown that the diversity and abundance of several animal taxa in agricultural landscapes decline significantly with increasing distance from native habitats (Klein et al., 2002; Steffan-Dewenter, 2002, 2003; Ricketts, 2004; Schulze et al., 2004). Although these declines might be intuitive and expected from theory (MacArthur and Wilson, 1967), the degree of decline differs widely among taxa (Ricketts et al., 2001).

Several countries such as Brazil, Britain, Canada, S. Africa, and the United States have recently developed initiatives to conserve and protect pollinators, which are declining in many parts of the world (Stubbs and Drumond, 2001). Fragmentation-induced changes in the structure of the pollinator guild may have far-reaching consequences for gene flow in plant populations and for plant and animal community

^{*} Corresponding author: isatunes@yahoo.com.br

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dynamics (Didham et al., 1996). Bees are probably the most important pollinator group in both number and diversity of pollinated plant species (Didham et al., 1996). It is estimated that there are over sixteen thousand species of bees throughout the world (Michener, 2000). Of these, approximately eighty five percent are solitary and some build their nests in preexisting cavities. Thus, wooden trap nests have been used by biologists for years to lure bees and wasps to make their nests, where they can be easily studied (Krombein, 1967).

More recently, trap nests have also been used to monitor selected bee species through time in several sites to record possible frequency changes and constancy in different habitat type (Frankie et al., 1993; Strickler et al., 1996). These insects can be expected to reflect ecological change through their species richness and related parameters, and ecological functions or interactions: pollination, predation, and mortality due to their natural enemies. In a comparison of habitat types (grasslands and field margins), species richness of trap-nest communities correlated to plant diversity, but percentage mortality, due to parasitism and predation, correlated only to field age (Tscharntke et al., 1998).

The purpose of this study was to monitor the solitary bee fauna caught in trap nests in three different habitats at the Parque Municipal das Araucárias. The main questions addressed in this paper are: Are there significant differences in bee species composition between habitats? Could environmental factors, such as air temperature and humidity, be related to these differences? What is the constancy of selected species in the habitats? Is there any association between the species? What type of association could occur between species?

2. MATERIALS AND METHODS

2.1. Study areas

This study was carried out at the Parque Municipal das Araucárias, in the municipality of Guarapuava, state of Paraná, southern Brazil (25°23'S– 51°27'W, 1.120 m of altitude (above sea level). This area is characterized by a wet, cool season, and during the warmest months the average temperature is less than 22 °C. Hoar frosts are common and severe in this region. The landscape in Guarapuava is composed mainly of araucaria forest and grasslands (Veloso et al., 1991). However the grasslands have suffered high anthropic interference and the araucaria forest has been reduced to approximately 5% of its original size, due to agriculture and wood exploration. The total area of the Parque Municipal das Araucarias is 104 ha, comprised of araucaria forest (43 ha), grassland (6.8 ha), swamp (11.1 ha), riparian forest (10.1 ha) and altered areas (33 ha).

Collections were carried out from December 2001 to December 2003 and were concentrated in a very heterogeneous site which included araucaria forests, swamps and grasslands. The grasslands are characterised physionomically by areas of low grasses and no bushes. Species of grasses from Ciperaceae, Fabaceae, Verbenaceae, Asteraceae and Apiaceae families are the main ones found in this habitat. Surrounded by the grasslands are the araucaria forests, in which there is a predominance of *Araucaria angustifolia* (Coniferae; Araucariaceae). The swamps are located at the lowest regions of the park. These are composed mainly of grasses and Apiaceae.

2.2. Sampling program

Nests of solitary bees were obtained using trapnests made by blocks of wood (Araucaria angustifolia) $25 \times 20 \times 120$ mm, drilled longitudinally to a depth of 80 mm with the apertures 7.0, 10.0, and 13.0 mm in diameter. Before being drilled, the wood blocks were sawed in half longitudinally and then held together with adhesive tape to permit the examination of the cavities when opened. Each nest was placed 1.5 m above the ground and was inspected every two weeks. In each inspection, all completed nests were removed and immediately replaced with empty traps of the same diameter. The nests were then brought to the laboratory in order to investigate their contents. If eggs and/or larvae were present, the nest was closed to allow the completion of the lifecycle and the emergence of the adults.

Two areas were studied in each habitat, with 2 transects per area and 4 sampling stations per transect. Each sampling station included 12 trap nests, four for each opening diameter (7.0, 10.0 and 13.0 mm, respectively), totaling 576 traps.

Humidity and temperature in each habitat were measured using a digital thermohygrometer, every two weeks. The order in which the habitats were measured was randomized.

2.3. Statistical analyses

The species abundance data in the Parque Municipal das Araucarias was illustrated by plotting the number of specimens collected for each species in order of its rank, from greatest to least abundance, following Whittaker (1965). Species richness was then estimated by fitting the log-normal distribution (Krebs, 1989; Ludwig and Reynolds, 1988).

Species frequency of occurrence (FO) and species dominance (D) were calculated according to Palma (1975): FO = (Number of sampling with species i + Number of sampling) × 100. If FO \geq 50%, the species is termed a primary species; if 50% \geq FO \geq 25%, the species is termed a secondary species; if 25% \geq FO, the species is termed an incidental species. D = (Abundance of species i + total abundance) × 100. If D > 5% the species is termed a dominant species; if 2.5% < D < 5% the species is termed an accessory species; if D < 2.5% the species is termed an incidental species. Palma (1975) reported that these indices together can be used to group the species into three categories: common species, intermediate species, and rare species.

The association between species was also investigated, using Jaccard's index (Ludwig and Reynolds, 1988). Species diversity was calculated using three indices: species richness (Margalef's index), Shannon-Wiener diversity and species evenness (Pielou's J index) (Ludwig and Reynolds, 1988). To calculate the differences and similarities between the habitats, α -diversity for each of them was measured using Shannon-Wiener's index. A posteriori Statistic T-test was carried out in order to analyze the null hypothesis of no difference between the Shannon-Wiener's values (Magurran, 2004).

To investigate the changes in species composition between habitat partitions (β -diversity) they were grouped by their abundance using the chord distance coefficient, from relative euclidian distance indices, as a metric and the unweighted pair group method average (UPGMA) as the clustering method (Ludwig and Reynolds, 1988). A simple discriminant analysis (SDA) was carried out to test the significant differences in air temperature and humidity between communities delimited by cluster classification (Ludwig and Reynolds, 1988).

Considering the Parque Municipal das Araucárias as the measure unit, γ -diversity was calculated using Shannon-Wiener's index. This diversity index can be used to compare biotopes with the same dimensions.

Jaccard's index was also used to measure the similarity among the habitats in relation to presenceabsence of species (Ludwig and Reynolds, 1988).

3. RESULTS

3.1. Species abundance and dominance

The abundance of each species in a trapnesting bee community was illustrated by plot-



Figure 1. Whittaker plot for species nest abundance of trap-nesting bees. 1: *Centris tarsata*, 2: *Megachile brasiliensis*, 3: *Colletes* sp, 4: *Epanthidium nectarinioides*, 5: *Megachile* (D.) sp₁, 6: *Anthodioctes claudii*, 7: *Megachile* sp₁, 8: *Megachile* sp₂, 9: *Megachile* (A.) *fiebrigi*, 10: *Xylocopa augusti*, 11: *Megachile* (Moureapis) sp₁.

ting the number of specimens collected for each species in order of its rank, from greatest to least abundance (Whittaker plot, Fig. 1). One hundred and twenty solitary bee nests, belonging to eleven species of Megachilidae (72.7%), Apidae (18.2%) and Colletidae (9.1%) families, were collected.

The most abundant species were Centris (Hemisiella) tarsata with 44 nests (37%), Megachile (Melanosaurus) brasiliensis with 30 nests (25.2%) and *Colletes* sp with 13 nests (10.9%)(Fig. 1). Intermediate species were C. tarsata (D = 36.67%; FO = 26.92%), M. brasiliensis (D = 25.00%; FO = 23.08%), Colletes sp (D = 10.83%; FO = 15.39%), Epanthidium nectarinioides (D = 7.50%; FO = 11.54%), Megachile (Dactylomegachile) sp_1 (D = 6.67%; FO = 11.54%). Anthodioctes claudii (D = 4.17%; FO = 9.62%), Megachile sp₁ (D = 3.33%; FO = 5.77%) and Megachile sp₂ (D = 2.5%; FO = 5.77%). Megachile (Austramegamegachile) fiebrigi (D=1.67%; FO=3.85%), Xylocopa (Neoxylocopa) augusti (D = 0.83%; FO = 1.92%) and Megachile (Moureapis) sp_1 (D = 0.83%; FO = 1.92%) were the rare species.

Anthodioctes claudii and M. (Moureapis) sp_1 were found only in araucaria forest, Megachile sp_2 only in swamp and X. augusti only in grassland. On the other hand, C. tarsata, M. brasiliensis, Colletes sp, E. nectarinioides and M. (Dactylomegachile) sp_1 were found in both swamp and grassland areas. Only Megachile sp_1 was found in araucaria forest and

Table I. Number of trap-nesting bee species and their nests abundance in three habitats in the Parque Municipal das Araucárias.

Table II. Abundance (A), richness (D _{Mg}), diversity									
(H') and	d evenne	ss (J	') inc	lex of tra	p-nesting be	es in			
three l Araucá	habitats rias.	in	the	Parque	Municipal	das			

	HABITAT					
SPECIES	swamp	grassland	araucaria forest			
Apidae						
Centris tarsata Smith	13	31	0			
<i>Xylocopa augusti</i> Lepeletier	0	1	0			
Megachilidae						
<i>Megachile brasiliensis</i> Dalla Torre	29	1	0			
<i>Megachile</i> sp ₁	0	1	3			
Megachile sp ₂	3	0	0			
<i>Megachile (A.) fiebrigi</i> Schrottky	1	0	1			
Megachile (M.) sp ₁ Raw	0	0	1			
<i>Megachile</i> (<i>D</i> .) sp ₁ Mitchell	6	2	0			
<i>Anthodioctes claudii</i> Urban	0	0	5			
Epanthidium nectarinioides Schrottky	8	1	0			
Colletidae						
Colletes sp	3	10	0			
Nests number	63	47	10			
Species number	7	7	4			

grassland and *M*. (*A*.) *fiebrigi* in araucaria forest and swamp (Tab. I).

3.2. Species association

The hypothesis of no association between the species was accepted (W = 5.51; variance ratio was 2.28, essentially equal to the expected value of 1.0 under the null hypothesis of no associations (0.5 < P < 0.1).

3.3. Species diversity

The number of species found in swamp (S = 7) and in grassland (S = 7) was similar and they were higher than in araucaria forest (S = 4). In relation to nest abundance (total number of trap

fraucarias.				
HABITAT	А	H'	D _{Mg}	J'
araucaria forest	10	0.507	3.00	0.843
swamp	63	0.662	3.34	0.784
grassland	47	0.463	3 50	0 548

nests occupied), they were higher in swamp (n = 63) than in grassland (n = 47) and araucaria forest (n = 10) (Tab. I). α -diversity in swamp was significantly greater than in araucarias forest (t = 4.497; *P* < 0.001) and grassland (t = 2.636; *P* < 0.01). Although Shannon-Wiener's index showed a greater α -diversity in araucaria forest than in grassland (Tab. II), it was not significantly different (0.753; 0.5 > *P* > 0.2). In relation to species evenness, araucaria forest showed a greater value (J' = 0.843) than swamp (J' = 0.784) and grassland (J' = 0.548). On the other hand, grassland showed greater species richness (D_{Mg} = 3.59) than swamp (D_{Mg} = 3.34) and araucaria forest (D_{Mg} = 3.00).

The estimated species richness for the Parque Municipal das Araucárias as fitted by lognormal distribution was of 12 species. γ - diversity value for the Parque Municipal das Araucárias was H' = 0.789.

3.4. Habitat similarity

In relation to presence-absence of species in the three habitats, the similarity between swamp and grassland areas was the highest (J = 0.625). The similarities between swamp and araucaria forest (J = 0.100) and between araucaria forest and grassland (J = 0.100) were similar.

β-diversity can be represented by a dendrogram (Fig. 2). It is possible to see that the greatest similarity, in relation to species abundance, occurred between swamp and grassland areas. On the other hand, araucaria forest was the habitat with the greatest dissimilarity. Despite the air temperature in araucaria forest being significantly lower than in swamp and grassland (F = 5.3676; P = 0.0002; n = 47) and its air humidity significantly higher (F = 4.8689; P = 0.0005; n = 47) (Figs. 3, 4), by discriminant analysis the Mahalanobis distance was not significant



Figure 2. Dissimilarity dendrogram between the habitats related to their bees abundance. S_1 : swamp 1, S_2 : swamp 2; G_1 : grassland 1; G_2 : grassland 2; AF_1 : araucaria forest 1; AF_2 : araucaria forest 2.



Figure 3. Air humidity conditions (%) in different habitats from February 2002 to December 2003.

(F = 8.329 at df = 2,3; P > 0.05). Thus, these two environmental variables were not found to be significantly different between the two groups and could not be used to distinguish between them.

4. DISCUSSION

Overall, my results indicate that there was a significant difference in the diversity of cavitynesting bees between the swamp and the other



Figure 4. Air temperature (°C) in different habitats from February 2002 to December 2003.

two habitats. However, by Cluster analysis the swamp and grassland were more similar in relation to species abundance and species presence-absence as measured by Jaccard's index. This might be due to similarities between the two habitats, such as insulation ratio, since air temperature and humidity were not found to be significantly different between the two groups and could not be used to distinguish between them. Perez-Maluf (1993), Camillo et al. (1995) and Aguiar and Martins (2002) also found a high bee nesting activity in disturbed and open areas here in Brazil.

Another similarity between swamp and grassland areas is probably the greater availability of flower resources. Fye (1972) noticed that in disturbed and open areas the activity of trap-nesting bees was more pronounced than in continuous forest. According to the author these areas were colonized by pioneer plant species that represented an important food resource for these insects and, consequently, their populations increased. Diverse vegetation obviously supplies a greater amount of nutritious pollen, thereby supporting more bee species (Gathmann et al., 1994). Bees need much less time to provision their nests in the diverse vegetation of naturally developed fields than in the uniform environment of sown fields (Tscharntke et al., 1998).

An important factor that can probably affect the sampling of cavity-nesting bees, and consequently their diversity index, is the natural

nest sites in the habitat. Since the use of artificial nests is random, perhaps the greater availability of natural substratum for nesting can decrease the rate of trap-nest occupation (Viana et al., 2001). Coville and Coville (1980) observed this tendency in Costa Rican habitats where the number of natural nests was greater. As such, we need to cover this point in order to interpret diversity index results. In this study the low species richness and abundance in Araucaria forest might have been influenced by this factor as well as by the lack of vertical variation in the sample, since bees were trapnested only at 1.5 m above the ground. Morato and Campos (2000) observed that species diversity was significantly greater in continuous forest and natural gaps than in deforested areas in Central Amazonia. Morato (2001) investigated the effects of forest fragmentation on the patterns of vertical abundance and richness of solitary bee communities and found that in both continuous primary forest and isolated forest fragments, bee species richness at 15 m was almost twice that at 1.5 m above the ground. According to Roubik (1982) this pattern is probably due the great availability of canopy flowers resource. Wolda and Roubik (1986) noticed some bee species flying at different heights in tropical forests. Thus, the fact that all of my traps were located at a height of 1.5 m may have limited the number of species I collected.

The number of species (S = 11) sampled in this study and the one estimated by lognormal distribution (S = 12) were very similar to that found by Morato and Campos (2000) in Brazilian Central Amazonia (S = 14) and higher than those found by Viana et al. (2001) (S = 7) and Aguiar and Martins (2002) (S = 8) in the states of Bahia and Paraíba northern Brazil, respectively. In relation to nest abundance, a total of 405 bee nests were collected by Morato and Campos (2000). This number was three times higher than that collected at the Parque Municipal das Araucárias, but the total monitored area in his study (122 ha of forest fragments, natural gaps and deforested areas) was also more extensive than that in mine (43 ha of araucarias forest, 6.8 ha of grassland and 11.1 ha of swamp). Aguiar and Martins (2002) also collected in a larger area (3994.2 ha) and the nest abundance was 138, very similar to that registered in the present study. On the other

hand, the total number of nests sampled by Viana et al. (2001) was almost half that of the present study (n = 62), although the authors did not report the total sampled area, in their study.

According to Heithaus (1979) differences in sample sizes as well as the sizes of the sampled areas may account for some of the differences between species richness of temperate and tropical areas. Comparing species richness among assemblages using different sample sizes may produce erroneous conclusions due to the strong positive relationship between richness and sample size (Melo et al., 2003). The species richness data discussed here are, presumably, dependent upon the area sampled as well as sample intensity, but it is possible to suggest that both species richness and diversity were greater in the Parque Municipal das Araucarias than in all those regions, since the sampling effort of my study was the smallest and the species richness and their abundance was very similar to those registered by these authors. Moreover, we can notice a bee richness pattern that has been documented in the literature, that these insects are most abundant in semi-deserts and temperate areas (Silveira et al., 2002). In South America the bee species richness increases from the Savannas to Grassland in the south of Brazil and, in Argentina's semi-desert regions (Michener, 1979). All these investigated Brazilian regions are tropical with the exception of Guarapuava which is subtropical. It is located at 1 120 m above sea level and has been considered one of the coldest cities in the state of Parana.

Several hypotheses have been proposed to explain the low bee diversity in tropical regions (Silveira et al., 2002). One of them, proposed by Roubik cited by Michener (1979), suggests that these regions are inhabited by a larger number of eusocial species than subtropical and temperate regions. Each one of these eusocial species forms populous colonies which are composed mostly of works that lead their nestmates to rich food resources, which are in time exhausted. Thus, they could be the main factor responsible for species richness reduction in the tropics.

The distribution of bee families also seem to be related to latitudinal gradients. In the Neotropical region, Anthophoridae (sensu stricto) and Apidae have a great proportion of species in tropical areas, and the abundance of Halictidae species increases with higher latitudes in southern Brazil and in disturbed areas (Laroca et al., 1982). On the other hand, the proportion of Megachilidae can fluctuate in different sites since it was high in both southern Brazil (Wittmann and Hoffman, 1990) and near to Ecuador (Roubik, 1989). In the present study bees belonging to the family Megachilidae were the predominant group. Frankie et al. (1998) monitored bee species in wooden trap nests in six sites in northern Central California, during 3 years, and found that all bees belonged to this family. Different results, related to Megachilidae species abundance, have been found in some Brazilian tropical region (Perez-Maluf, 1993; Aguiar and Martins, 2002; Morato and Campos, 2000; Viana et al., 2001).

Centris tarsata was the most abundant species trapped during this study as well as in those carried out by Perez-Maluf (1993), Viana et al. (2001) and Aguiar and Martins (2002). Nevertheless, *M. brasiliensis*, the second most abundant species, and all the other species, were not recorded in the monitoring carried out by these authors and by Morato and Campos (2000) and Morato (2001). Garófalo et al. (2004) reported that members of the families Apidae and Megachilidae have been frequent in wood traps, but *M. brasiliensis* was not present in their list of species caught in trap nests in some studies performed in Brazil.

All the results presented in my study reflected that trap nests can be a useful tool, not only for studies on the biology and development of solitary species of bees, but also for investigating species assemblages and community structure. By this technique it was possible to find the common pattern of communities, with some intermediate and rare species, and a bee richness pattern consistent with that previously documented for South America.

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Apoidea / abeille solitaire / diversité écologique / biocénose / piège à nidification

Zusammenfassung-Artenvielfalt und Vergesellschaftungsstruktur in Fallen nistenden Bienen im südlichen Brasilien. Ziel dieser Untersuchung war in drei verschiedenen Habitaten des Parque Municipal das Araucárias die in vorgefundenen Höhlungen lebende Fauna solitärer Bienen zu erfassen. Die in dieser Untersuchung hauptsächlich angesprochenen Fragen waren: Gibt es signifikante Unterschiede in der Zusammensetzung der Bienenarten an den verschiedenen Habitaten? Können Umgebungsvariable wie Lufttemperatur und Feuchtigkeit zu diesen Unterschieden in Beziehung gesetzt werden? Sind ausgewählte Arten in den Habitaten konstant? Gibt es Assoziationen zwischen den Arten? Nester dieser Insekten wurden durch die Verwendung von Fallennestern mit 7,0, 10,0, and 13 mm Durchmesser und 80 mm Tiefe gewonnen. Jedes Nest wurde 1,5 m über Bodenhöhe angebracht und alle 2 Wochen untersucht. Die Nestsammlungen wurden von Dezember 2001 bis Dezember 2003 durchgeführt und wurden in einem sehr heterogenen Gelände durchgeführt, das Araukarienwälder, Moore und Grasland einschloss. Zur Beschreibung der Artenvielfalt und der Unterschiede oder Ähnlichkeit der Habitate wurden Indizes der Reichhaltigkeit und Eveness berechnet. Die Diversität wurde für jeden Standort anhand des Shannon-Wiener Index berechnet. Um Änderungen der Artenzusammensetzung zwischen Unterteilungen der Habitate zu erfassen, wurde die Diversität berechnet. Auf Grundlage dieser Ergebnisse wurden Klusteranalysen und Dendrogramme erstellt. Eine einfache Diskriminanzanalyse (SDA) wurde als Test auf signifikante Unterschiede in der Lufttemperatur und Feuchtigkeit zwischen den durch Klusterklassifikation abgegrenzten Gesellschaften durchgeführt. Da der Mahalanobisabstand in dieser Analyse nicht signifikant war, konnten diese Variablen zur Unterscheidung der Habitate nicht herangezogen werden. Die Diversität wurde unter Nutzung des Shannon-Wiener Index berechnet. Einhundertundzwanzig Nester von solitären Bienen wurden gesammelt, diese gehörten 11 Arten der Megachilidae (72,7 %), Apidae (18,2 %) und Colletidae (9,1%) an. Die häufigsten Arten waren Centris (Hemisiella) tarsata, Megachile (Melanosaurus) brasiliensis, Colletes sp, und Megachile (Dactylomegachile) sp1. Arten mittlerer Häufigkeit waren C. tarsata, M. brasiliensis, Colletes sp, EpaAnthidium nectarinioides, Megachile (Dactylomegachile) sp1, Anthodioctes claudii, Megachile sp1, die seltenen Arten waren Megachile sp2. Megachile (Austramegamegachile) fiebrigi, Xylocopa (Neoxylocopa) augusti und Megachile (Moureapis) sp1. Gemeinsame Spezies wurden in der Studie nicht gefunden und es gab keine Assoziationen zwischen den Spezies. Die Moore zeigten die größte Vorkommenshäufigkeit und Diversität. Die Ähnlichkeit zwischen diesem Habitat und dem Grassland war in Beziehung auf die Artenvielfalt als auch bezüglich des Vorkommens oder Nichtvorkommens der Arten am höchsten.

Solitäre Bienen / Gesellschaften / Diversität / Fallennester / Apoidea

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