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Characteristic processes in the succession of snail assemblages in the plant associations of continental sand dunes of the Danube-Tisza Midregion and of the Kiskunság National Park (Hungary).

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Zusammenfassung

Die Schneckengesellschaften anthropogener Pflanzengesellschaften des Donau-Theißgebietes und des Kiskunság Nationalparkes in Ungarn wurden untersucht. Die Sukzession war durch vergleichbare Veränderungen von drei Artengruppen gekennzeichnet. Drei Methoden wurden angewandt: eine phytozönologische Beschreibung und zusätzlich zwei Beschreibungen mit Hilfe der Pflanzensubassoziationen basierend auf dem Programm "Principal Components Analysis" und mit Hilfe der Pathways zwischen den Subassoziationen mit "Pascal Algorithm". Aus diesen drei Methoden lassen sich die gleichen Tendenzen ablesen. Die Artenzusammensetzungen der sekundären Steppen und der Aufforstungen sind verschieden. Auf Grund der Pathways kann man im Laufe der Sukzession einen Vernetzungsvorgang zwischen Trocken- und Naßbiotopen erkennen.

Abstract

The snail assemblages of the extrazonal successional plant communities of the Danube-Tisza Midregion and of the Kiskunság National Park were surveyed. The succession was indicated by complementary changes of 3 species groups. 3 approaches were used: a phytocoenological approach and two approaches according to the subassociations of the vegetation created by "Principal Components Analysis" and according to the pathways between subassociations obtained by "Pascal algorithm". The same tendencies can be seen in all three approaches. The species structure of the secondary grasslands and forest plantations are diverse. According to the pathways the succession is a network-process with drying-moistening pathways.

Key words: succession, sand dunes, species groups, pathways.

Summary

Habitat moistening or drying and forest canopy closure associated with the succession of sand vegetation are all indicated by reciprocal changes in the abundance of certain snail species groups and in the species composition of snail assemblages. As succession proceeds, some groups attain higher abundance (A/m2). Steppe dwellers (St) and species of open areas (OA) are characteristic in open grasslands. Secondary grassland habitats are somewhat dryer and support less diverse snail assemblages (*Helicella* dominates in the *Potentillo-Festucetum* phytocoenosis, *Truncatellina* in *Brometum* stands, while *Granaria*, *Chondrula* and *Pupilla* are the most abundant snails in *Festucetum vaginatae* grasslands). Forest plantations are similarly species poor (Table I). During the course of successional forest formation, forest dwellers (HF), bush forest dwellers (B), sciophilous (S) and photophilous (Ph) groups change reciprocally with steppe elements [steppe dwellers (St) and snails of open areas (OA)]. Concerning nutritional types, herbivorous (H) and saprophagous species (SP) dominate in early successional phytocoenoses, while omnivorous snails are the most abundant in more advanced stages. Cutting of grasslands leads to the dominance of saprophagous species. Steppe elements and omnivorous snails reach extreme abundance values in dry stationary plant subassociations. Secondary grasslands and forest plantations segregate according to the species composition and structural characteristics of their snail assemblages.

Introduction

Forest steppe with sand grassland mosaics is one of the most characteristic vegetation formations on the Great Hungarian Plain and in the Kiskunság National Park (SOÓ 1980). In this region the semiarid continental climate and soil properties are the principal determinants of ecological conditions. Snail assemblages have been studied since 1967 along with the phytosociological status of plant communities in the extrazonal successional series of sand vegetation.

Material and Methods

The quadrat method with plots of 10x25x25 cm size was used on five collection sites in altogether 18 subassociations of the following plant communities (Figure 1): three seminatural phytocoenoses (*Festucetum vaginatae danubiale* SOÓ 1929, *Junipero-Populetum albae* Zólyomi 1950, Szodfridt 1969, and *Convallario-Quercetum roboris danubiale* SOÓ 1934, 1957), two secondary plant associations (*Brometum tectorum* SOÓ 1925, 1939, and *Potentillo arenariae-Festucetum pseudovinae danubiale* Bodrogközy 1959) and two forest plantations (pine and poplar). Study sites were set up either in the area of the Kiskunság National Park (East Bugac, Kunpeszér, Kunbaracs, Kunadacs and Kunfehértó) or elsewhere in the Danube-Tisza Midregion (Ásotthalom, Csévharaszt, Isaszeg and Pusztavacs).

Field data were evaluated by using a standardized PCA technique (PODANI 1988) and by the structural analysis of snail assemblages with the help of species groups listed in Table I. Species groups were formed on base of the following characteristics: ecology (FEOLI & ORLÓCZI 1979 - block clustering method), habitat type (amalgamating Lozek's 1964 types) and nutritional type (after the laboratory tests of FRÖMMING 1954). The structural analyses were conducted in three arrangements: groupings according to plant associations, to groups created by PCA (Figure 1) and to the most probable pathways between subassociations obtained by a Pascal algorithm (Figure 6, BÁBA 1986).

The ratio of constant, subconstant and accessorial species, the species number (NP), individual density (ID), mean species number per quadrat, diversity and the proportion of juvenile individuals were also considered during the evaluation.

Abbreviations used in Tables and Figures:

Ecological species groups (E): OA = species of open areas, S = Sciophilous, Ph = photophilous, R = riparian, P = swamp dweller.
Nutritional types (N): O = omnivorous, H = herbivorous, SP = saprophagous.
Habitat type (H): HF = forest dweller, B = bush forest dweller, RU = riparian ubiquist, St = steppe dweller, P = swamp dweller.

Numbers referring to plant associations (in brackets) and their subassociations:
1. *Potentillo-Festucetum* (03); *Brometum tectorum* (01): 2. *cynodontetosum*, 3. *juniperetosum;* *Festucetum vaginatae* (02): 4. normale, 5. *stipetosum sabulosae*, 6. *Salicetum rosmarinifoliae;* *Junipero-Populetum* (22): 7. *caricetosum liparicarpos*, 8. *ligustretosum*, 9. *crataegetosum*, 10. *populetosum*, 11. *calamagrostetosum*, 12. *polygonetosum latifolii;* *Convallario-Quercetum* (25): 13. *betuletosum*, 14. *convallarietosum*, 15. *populetosum*, 16. *brachypodetosum*. Forest plantations (both replacing phytocoenosis 22): 17. black pine, 18. poplar.

Results and Discussion

Species encountered

Field studies yielded a collection of 4060 snail individuals belonging to 36 species. Species frequencies vary considerably with habitats. Species 1-11 and 28 are frequent in grasslands, while in thickets species 1-11, *Acanthinula* (12) and *Punctum* (20) occur. Forested areas are inhabited by forest dwellers and riparian snail species.

The swamp dweller *Monacha* and the riparian *Zonitoides* turn up in forest plantations established over wet grasslands. In the *Convallario-Quercetum* woods at Isaszeg-Mártonberek (biogeographically belonging to the Great Hungarian Plain) snails, common in hilly regions (*Trichia*, *Ena*), appear as well. *P. incarnata* and *Nesovitrea* occur sporadically in the former flood area of the Danube. Slugs (30, 31 & 35, Table I) can be found in forested areas.

The stages of vegetation succession can be distinguished according to their snail assemblages, including forest plantations and secondary grasslands as well.

Structural characteristics

From grasslands to closed forests the changes in the structural characteristics of snail assemblages follow the same tendencies according to all three groupings used. Thus species number (NP), individual density (ID), abundance (A/m^2) and diversity (H') increase in this direction (Figure 7). Exceptions are the *Brometum tectorum* (01) and *Potentillo-Festucetum* (03) plant associations and forest plantations (27; Figure 2), where habitat wetness (W), species number and diversity decrease. Parameters H', NP and W change similarly for snail assemblages arranged according to PCA groupings (Figure 3) or to the most probable paths. Individual density and abundance values decline in the successional climax phytocoenosis (*Convallario-Quercetum*) and in forest plantations for all groupings (Figures 2, 3 & 7) ,

Considering characteristic species the proportion of subconstant and accessorial elements increases during succession (Figure 2).

Evaluation according to plant associations

The diversity of species groups increases during succession. For ecological groups, several reciprocal changes occur: the group OA (species of open areas) behaves in a complementary way with the hygrophilous S (sciophilous) and Ph (photophilous) groups. In poplar plantations established on wet meadows species belonging to the Ph (*Monacha carthusiana*) and R (*Zonitoides*, *Perforatella rubiginosa*) groups also appear.

Concerning nutritional types the proportion of omnivorous snails increases during the course of vegetation succession (i.e. forest formation), although in secondary grasslands herbivorous and saprophagous species may become abundant. The proportion of herbivorous and saprophagous snails becomes similarly higher in forest plantations (27).

Evaluation according to PCA groupings

Seminatural communities are clearly different from secondary phytocoenoses and forest plantations on the PCA dendrogram plot (Figure 1). The *Brometum* and *Potentillo-Festucetum* associations are distinguishable within the plot area occupied by the *Festucetum vaginatae* phytocoenosis. A degraded *Convallario-Quercetum* stand (40-41) and the poplar and pine plantations are situated close to grasslands.

The stationary *Carex liparicarpos* stand (14) - representing the valley type juniper-poplar wood - segregates from all other plant (sub)associations on the dendrogram. Several discontinuities occur in the characteristics H', ID, W and A/m2 (Figure 3). Mean habitat wetness index (W) is very low in phytocoenoses 01 and 03, while among subassociations it can reach extreme values in seminatural wet (02/6 *salicetosum*) and extremely arid (22/7 *Caricetosum liparicarpos*, 22/8-10 *populetosum*, *ligustretosum*, *crataegetosum*) stands of stagnant nature. Individual density values are also high in these subassociations. Species of open areas (OA), steppe dwellers (St) and omnivorous snails reach high abundances in stationary phytocoenoses. In the somewhat wetter *Salicetum*, saprophagous species predominate (Figure 5). Due to forest management most characteristics decrease in subassociations representing the terminal successional stage.

Evaluation based on most probable paths

The most probable paths obtained by a Pascal algorithm (BÁBA 1986) contain seminatural and secondary subassociations (Figure 6). The behaviour of species groups corresponds with that found during the previous two evaluation methods. Periods of habitat moistening and drying (8 *crataegetosum*) alternate during the course of vegetation succession. In contrast with the findings of the previous two methods the successional series is short here - being completed within 5-7 consecutive subassociations. Due to an increasing canopy closure (in subassociations 22-25) the structural changes of species groups are more pronounced.

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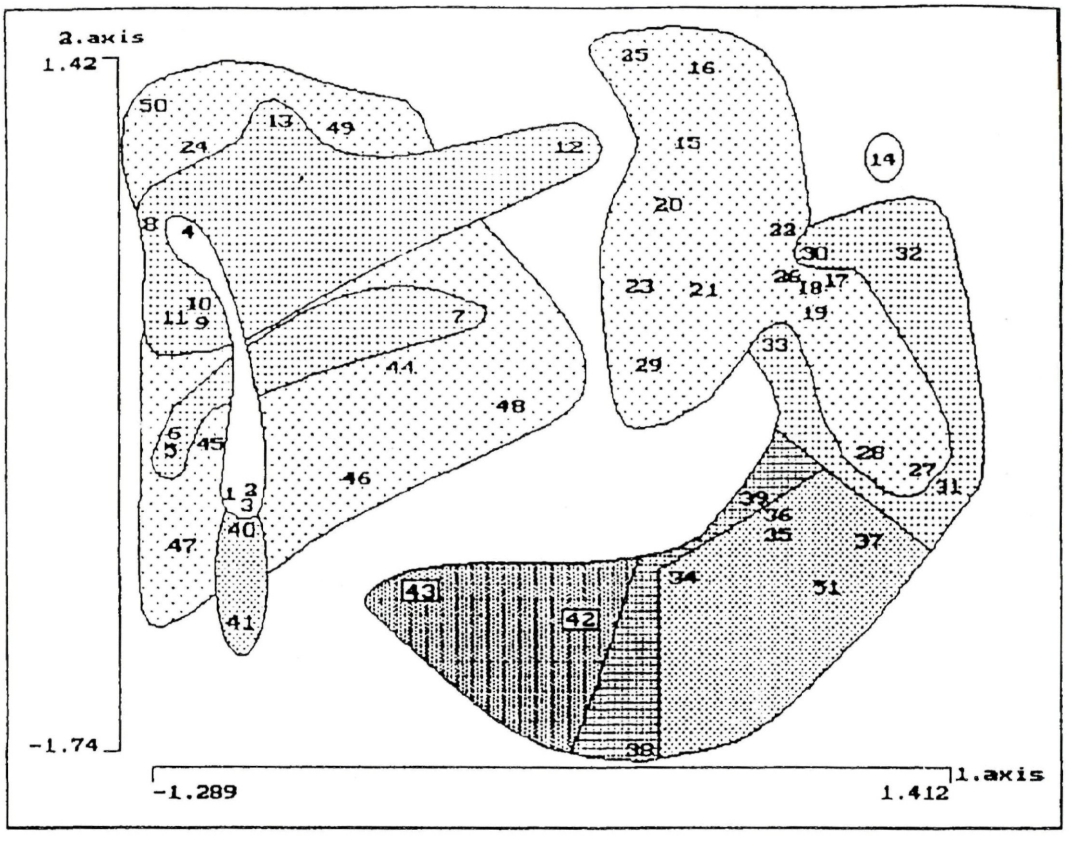
Subassociation numbers as in Table 1. Collection sites are denoted by numbers 1-51.



02 **Festucetum vaginatae danubiale** Soó 1929

4 (8, 10) normale
5 (9, 11, 13) stipetosum sabulosae
6 (12) salicetosum rosmarinifoliae

22 **Junipero-Populetum albae** (Zólyomi 1950) Szodfriedt 1969

7 (14) carex liparicarpos
8 (15-16) ligustretosum
11 (17-21) calamagrosetosum
10 (22-23) populetosum
9 (24-25) crataegetosum
12 (26-29) polygonetosum latifolii

25 **Convallario-Quercetum roboris danubiale** Soó 1957

13 (30-33) betuletosum
(34-37, 51) populetosum
16 (42-43) brachypodietosum
14 (38-41) convallarietosum

27 **Plantation**

17 (44) black pine plantation at site 22
18 (45-50) poplar-black locust plantation at site 22

01 **Brometum tectorum** Soó 1939

2 (5-6) cynodonetosum
3 (7) juniperetosum communis

03 **Potentillo arenariae-Festucetum pseudovinae danubiale** Bodrogközy 1959

1 (1-4) euphorbietosum

Fig. 1: Plant subassociations (1-18) in the continental sand dune successional series distinguished by standardized PCA (PODANI 1988).

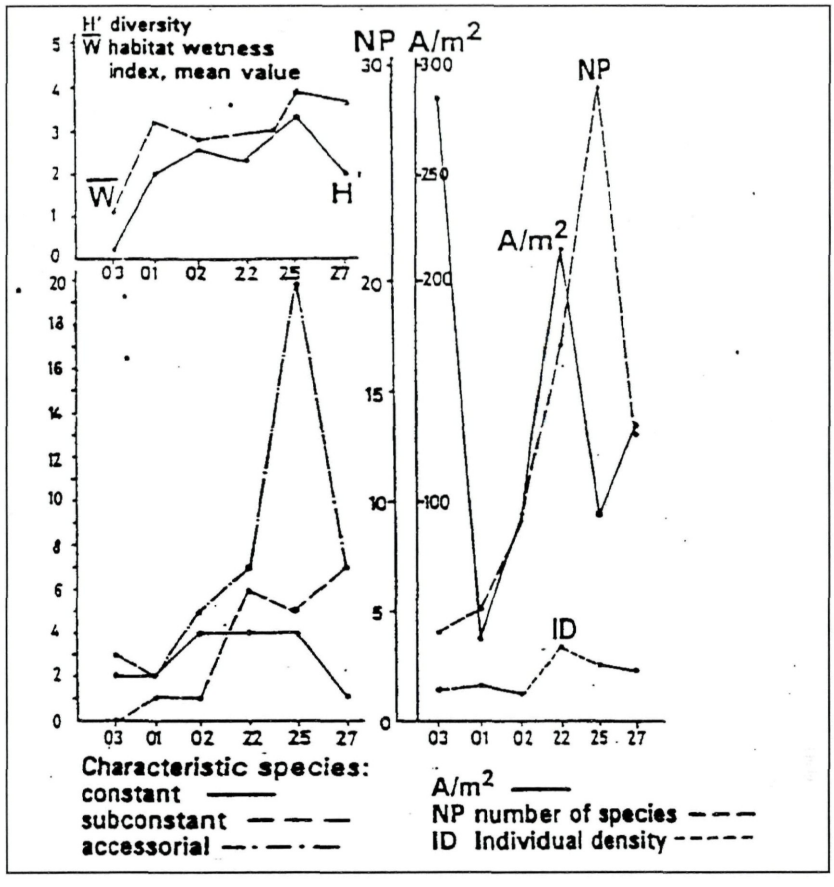


Fig. 2: Structural characteristics of snail assemblages in the continental sand dunes according to the plant associations.

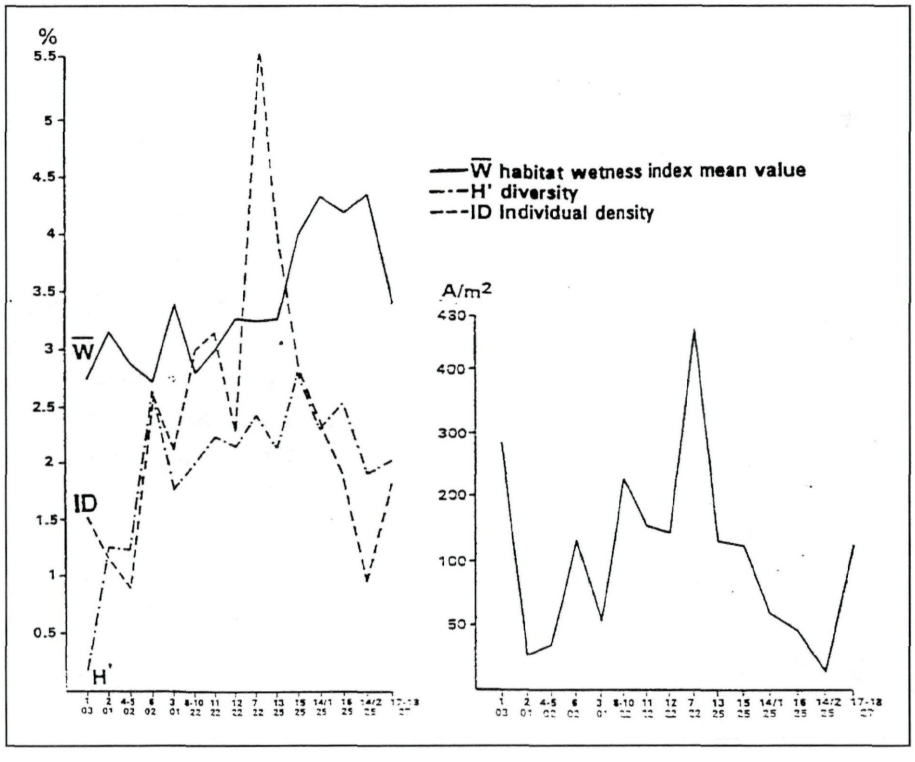


Fig. 3: Structural characteristics of snail assemblages in the continental sand dunes according to groups obtained by standardized PCA.

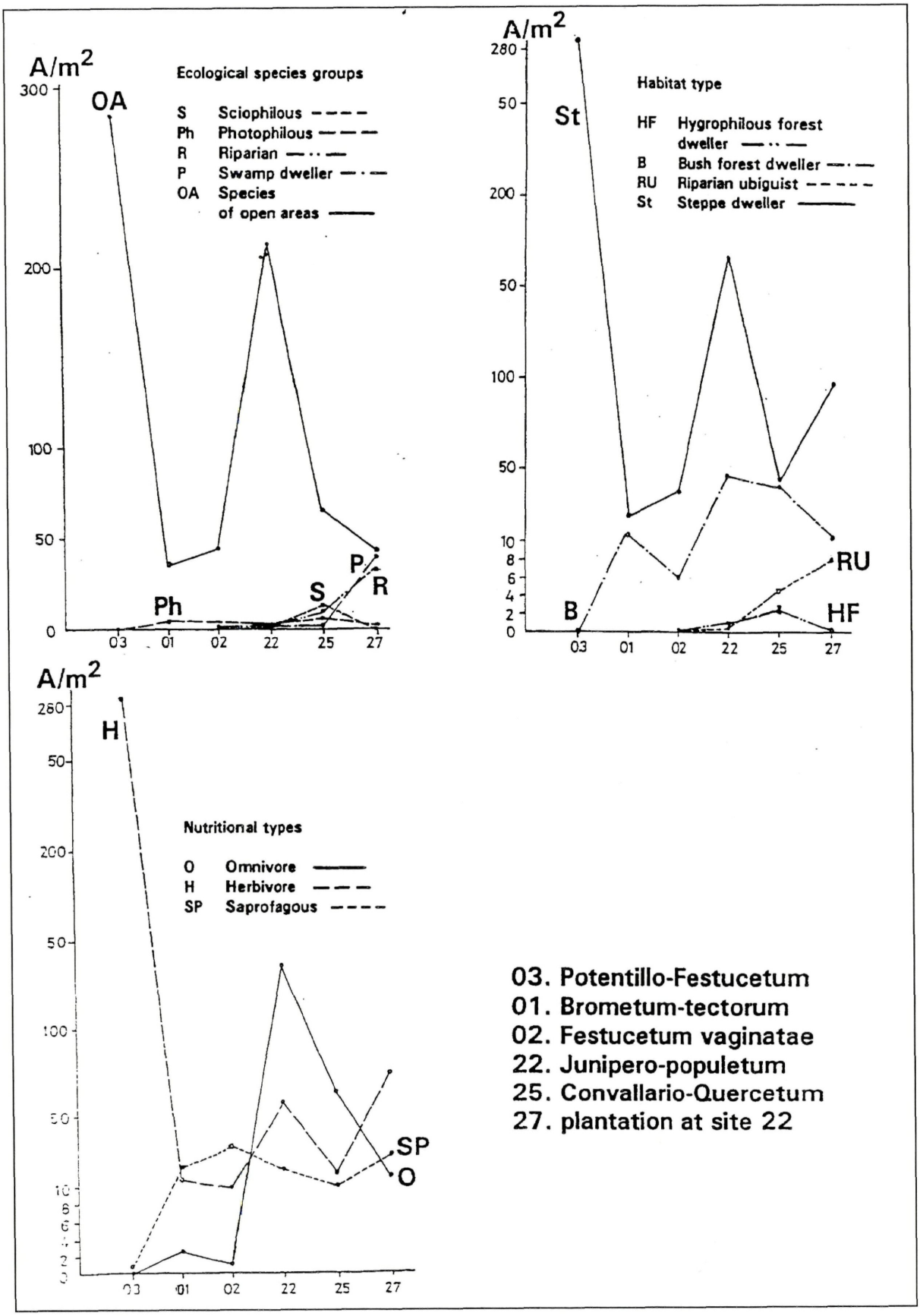


Fig: 4: Abundance (A/m2) of species groups according to the plant associations.

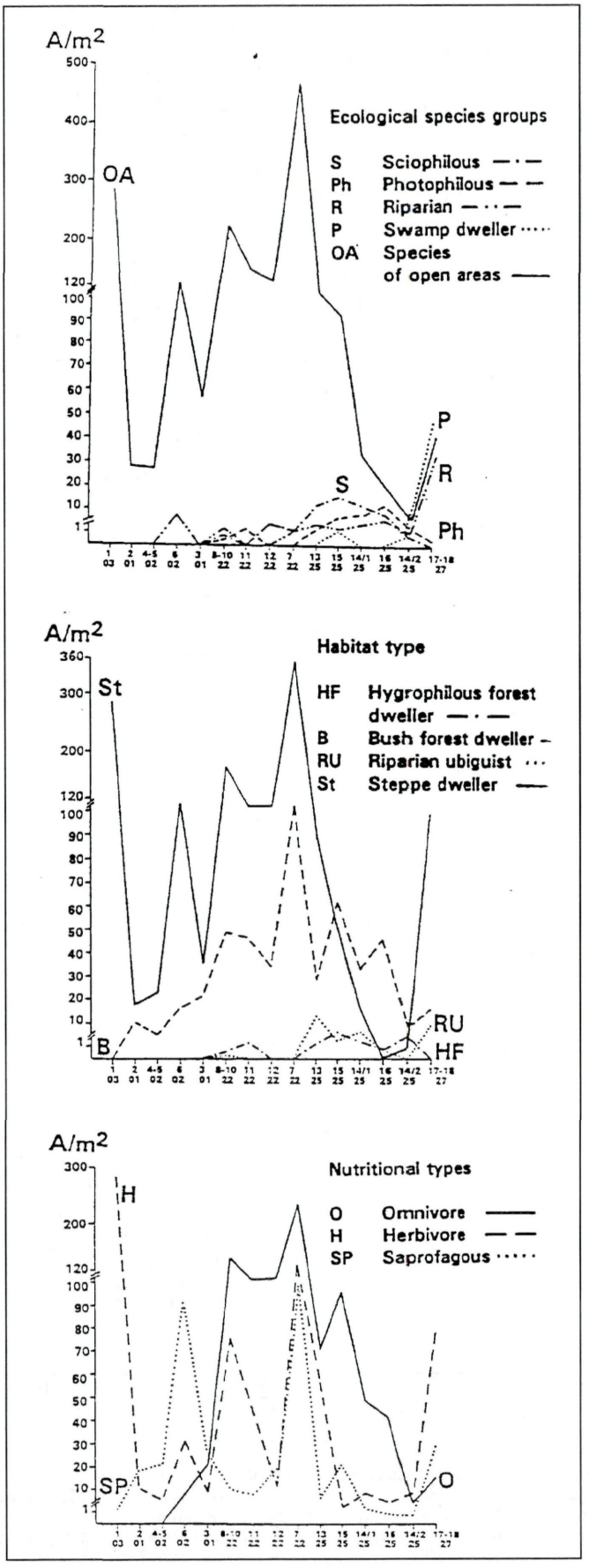
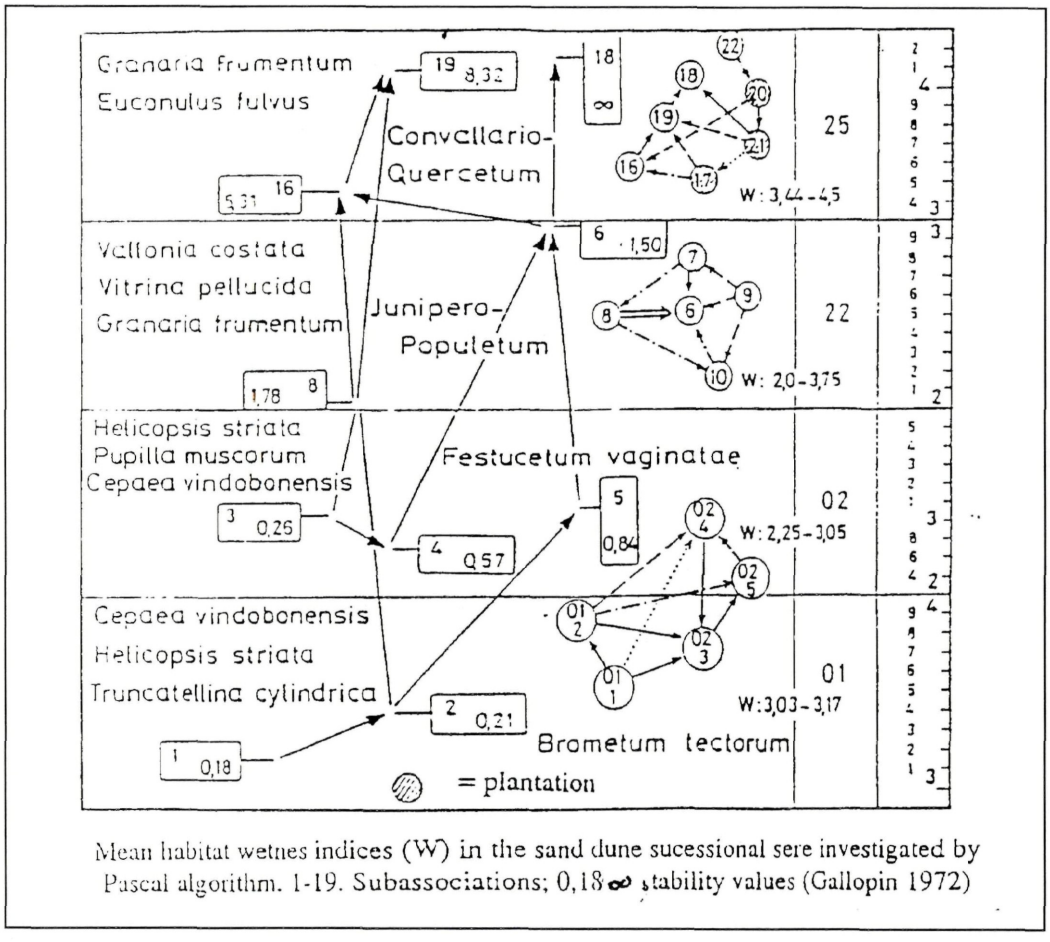


Fig. 5: Abundance (A/m2) of species groups according to PCA groupings.



Mean habitat wetnes indices (W) in the sand dune sucessional sere investigated by Pascal algorithm. 1-19. Subassociations; 0,18 ∞ stability values (Gallopin 1972)

Fig. 6: The most probable path ways.

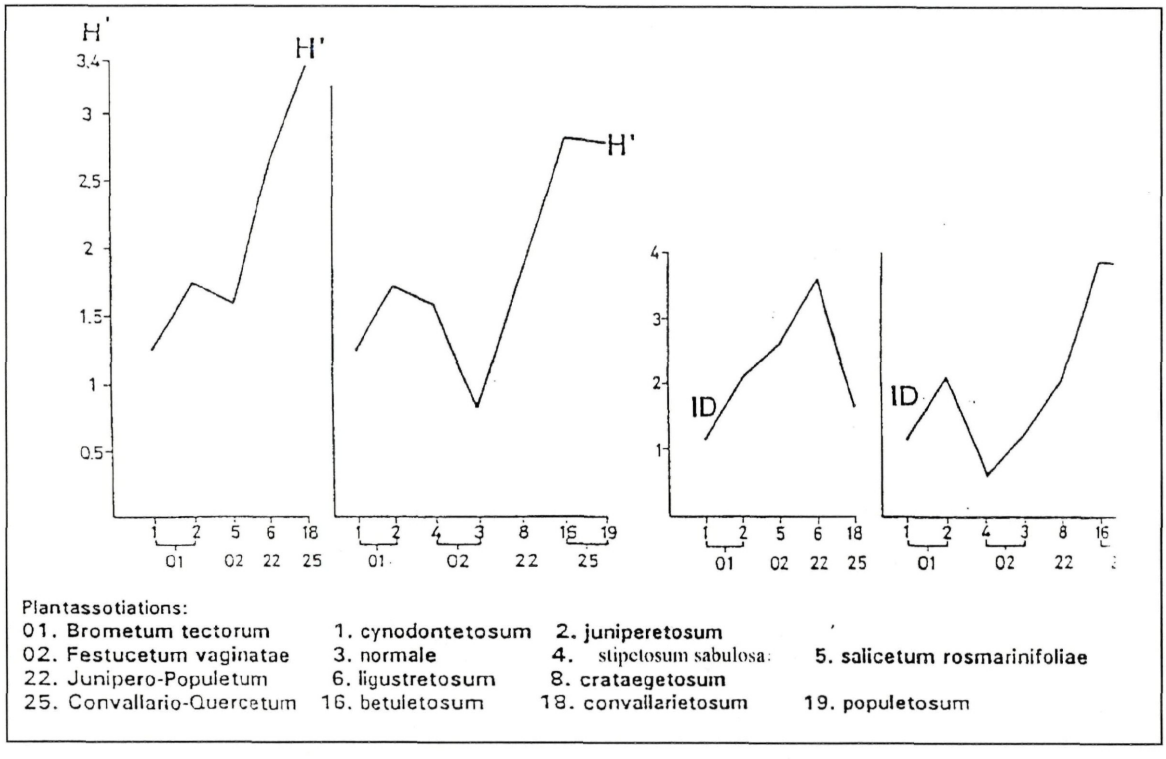


Fig. 7: Structural characteristics of snail assemblages on continental sand dunes according to the paths (H' = diversity, ID = Individual Density).

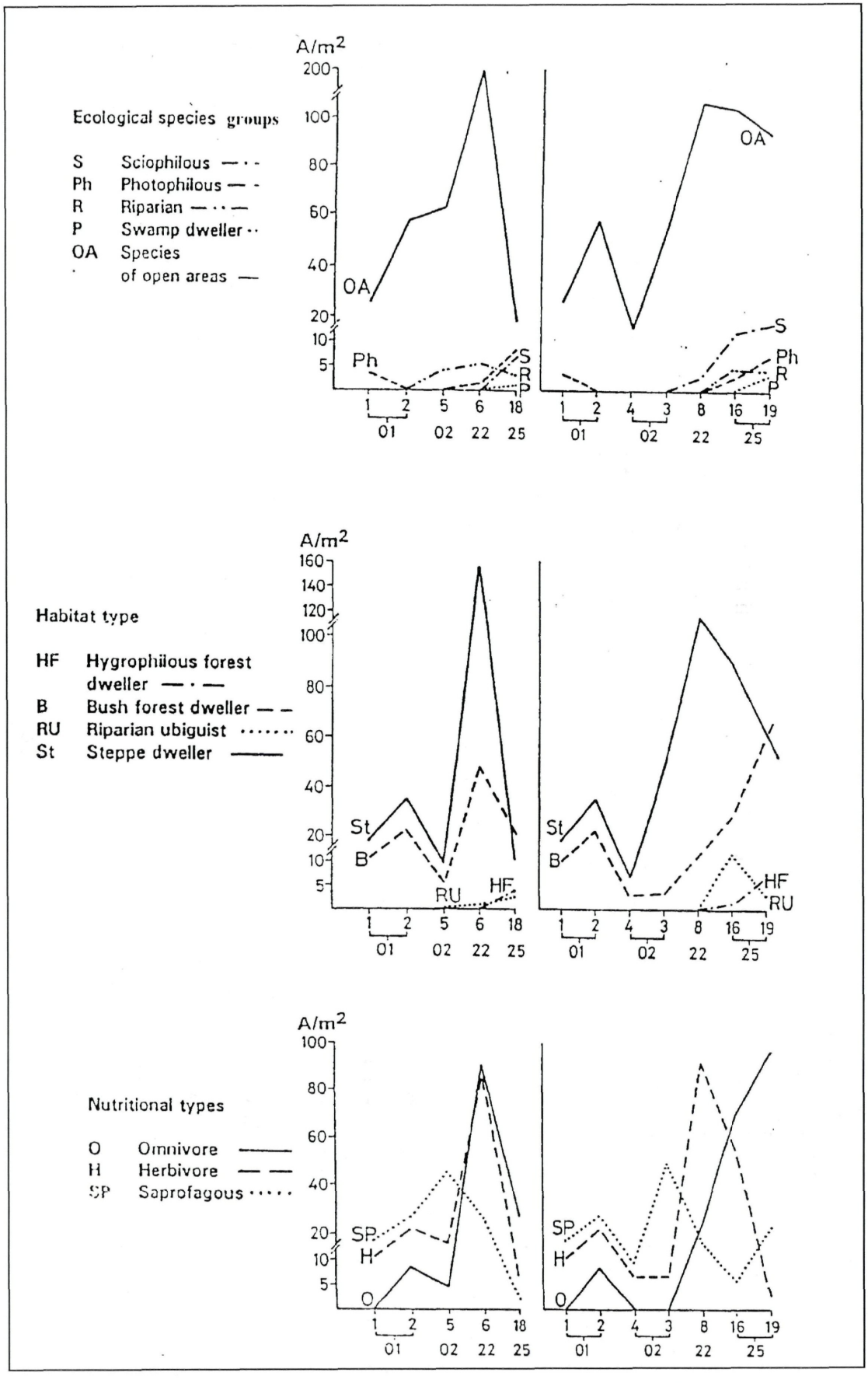


Fig. 8: Abundance of species groups according to the paths.

Tab. 1: Snail species of the sand dune successional series arranged according to the subassociations and ecological species groups.

					13	14	15	16	17	18	19	20	21	22
						Convallario-Quercetum		25		27	Σ 01 Σ25	Σ 02	Σ 22	
No.	E	N	H	Sample number (N)	4	4	5	2	1	6	3	6	16	15
1	OA	O	St	Cochlicopa lubricella (Porro 1838)	19	2	6	-	3	-	-	-	42	27
2		Sp	St	Truncatellina cylindrica (A. Ferussac 1807)	5	1	10	-	-	6	14	20	143	16
3		H	St	Granaria frumentum (Draparnaud 1801)	99	-	-	-	23	10	-	-	498	99
4		H	ST	Pupilla muscorum (Linne 1758)	-	-	-	-	-	31	-	15	20	-
5		O	St	Vallonia costata (O. F. Müller 1774)	93	20	137	-	-	-	5	3	938	250
6		Sp	St	Chondrula tridens (O. F. Müller 1774)	3	-	-	-	-	4	-	30	17	3
7		O	B	Vitrina pellucida (O. F. Müller 1774)	36	2o	110	22	-	32	-	3	375	188
8		O	B	Euconulus fulvus (O. F. Müller 1774)	16	1	26	2	-	-	-	-	25	45
9		H	St	Helicella obvia (Menke 1828)	-	-	-	-	-	48	-	1	3	-
10		Sp	St	Helicopsis striata (O. F. Müller 1774)	-	-	-	-	-	1	26	73	13	-
11		H	B	Cepaea vindobonensis (A. Ferussac 1821)	9	1	4	1	12	22	23	22	71	15
12	Ph	Sp	HF	Acanthinula aculeata (O. F. Müller 1774)	-	-	1	-	-	-	-	-	8	1
13		O	HF	Arion subfuscus (Draparnaud 1805)	-	4	1	-	-	-	-	-	-	5
14		O	B	Aegopinella minor (Stabile 1864)	1	-	18	17	-	-	-	-	-	36
15		O	HF	Bradybaena fruticum (O. F. Müller 1774)	4	4	-	-	-	-	-	-	-	8
16		H	B	Helix pomatia Linne 1758	-	14	2	-	-	2	4	-	-	16
17	S	H	Ru	Columella edentula (Draparnaud 1801)	29	2	1	-	-	-	-	-	-	32
18		Sp	HF	Vertigo pusilla (O. F. Müller 1774)	-	-	16	-	-	-	-	-	-	16
19		H	HF	Ena obscura (O. f. Müller 1774)	-	-	1	-	-	-	-	-	-	1
20		Sp	B	Punctum pygmaeum (Draparnaud 1801)	4	3	28	1	-	-	-	-	16	36
21		Sp	HF	Vitrea crystallina (O. F. Müller 1774)	-	-	1	-	-	-	-	-	-	1
22		O	B	Nesovitrea hammonis (Ström 1765)	-	11	4	5	-	-	-	-	-	20
23		H	HF	Perforatella incarnata (O. F. Müller 1774)	-	-	1	-	-	-	-	-	-	1
24		H	B	Trichia hispida (Linne 1758)	-	-	-	1	-	-	-	-	-	1
25		H	B	Euomphalia strigella (Draparnaud 1801)	-	2	1	3	-	-	-	-	-	6
26	R	O	Ru	Succinea oblonga (Draparnaud 1801)	-	-	-	-	1	12	-	-	-	-
27		O	B	Cochlicopa lubrica (O. F. Müller 1774)	4	1	1	6	-	-	-	-	1	12
28		Sp	St	Vallonia pulchella (O. F. Müller 1774)	4	1	7	-	-	116	-	5	6	12
29		O	Ru	Zonitoides nitidus (O. F. Müller 1774)	-	-	-	-	-	-	-	-	1	-
30		O	Ru	Deroceras reticulatum (O. F. Müller 1774)	-	-	-	1	-	-	-	-	-	1
31		O	Ru	Deroceras agreste (Linne 1774)	4	4	2	-	-	23	-	-	-	10
32		H	Ru	Perforatella rubiginosa (A. Schmidt 1853)	-	1	-	-	-	-	-	-	-	1
33	P	Sp	St	Vertigo pygmaea (Draparnaud 1801)	-	1	-	-	-	-	-	-	-	1
34		Sp	Ru	Vertigo angustior Jeffreys 1830	-	-	8	-	-	-	-	-	-	8
35		O	HF	Arion circumscriptus Johnston 1828	-	1	-	-	-	-	-	-	-	1
36		H	St	Monacha cartusiana (O. F. Müller 1774)	-	-	-	-	-	194	-	-	1	-

	13	14	15	16	17	18	19	20	21	22
	Convallario-Quercetum			25	27		Σ 01	Σ 02	Σ 22	Σ 25
Σ Number of individuals	330	94	385	60	39	501	72	172	2178	869
Number of juvenile individuals	111	45	199	34	14	315	26	88	1029	389
Percentage of juvenile individuals	33,63	47,87	51,68	56,66	36,8	62,87	38,11	51,16	47,68	44,81
Abundance (A/m²)	132,0	57,6	124,2	48,0	62,4	133,6	38,4	91,73	215,8	92,53
Individual density (ID)	3,9	1,65	2,84	1,9	1,5	2,13	1,62	1,46	3,334	2,57
Habitat wetness index, mean value (W)	3,62	4,11	4,01	4,2	2,87	3,93	3,28	2,83	2,01	3,98
H' diversity	2,848	3,374	2,805	2,549	1,393	2,67	2,015	2,407	2,344	3,42
Σ Number of species	15	19	21	11	4	13	5	9	17	30

Tab. 1: Snail species of the sand dune successional series arranged according to the subassociations and ecological species groups.

					1	2	3	4	5	6	7	8	9	10	11	12
					Pot. vaginatae 03	Brometum Fest.		Festucetum tectorum 01		02	Junipero- 22		Populetum			
No.	E	N	H	Sample number (N)	4	2	1	2	3	1	1	2	2	2	5	4
1	OA	O	St	Cochlicopa lubricella (Porro 1838)	-	-	-	-	-	-	4	6	-	1	21	10
2		Sp	St	Truncatellina cylindrica (A. Ferussac 1807)	-	-	14	-	1	19	59	13	5	9	21	36
3		H	St	Granaria frumentum (Draparnaud 1801)	16	-	-	-	-	-	70	86	109	30	82	22
4		H	ST	Pupilla muscorum (Linne 1758)	-	-	-	1	2	12	8	2	3	3	1	3
5		O	St	Vallonia costata (O. F. Müller 1774)	-	-	5	-	-	3	80	61	19	275	208	195
6		Sp	St	Chondrula tridens (O. F. Müller 1774)	2	-	-	3	-	27	-	7	9	1	-	-
7		O	B	Vitrina pellucida (O. F. Müller 1774)	-	-	-	-	-	3	59	43	11	108	100	54
8		O	B	Euconulus fulvus (O. F. Müller 1774)	-	-	-	-	-	-	5	5	-	1	-	13
9		H	St	Helicella obvia (Menke 1828)	690	-	-	-	-	1	-	12	-	1	-	-
10		Sp	St	Helicopsis striata (O. F. Müller 1774)	1	23	3	58	9	6	2	6	3	2	-	-
11		H	B	Cepaea vindobonensis (A. Ferussac 1821)	-	9	14	8	7	7	2	11	2	-	49	7
12	Ph	Sp	HF	Acanthinula aculeata (O. F. Müller 1774)	-	-	-	-	-	-	-	2	-	-	6	-
13		O	HF	Arion subfuscus (Draparnaud 1805)	-	-	-	-	-	-	-	-	-	-	-	-
14		O	B	Aegopinella minor (Stabile 1864)	-	-	-	-	-	-	-	-	-	-	-	-
15		O	HF	Bradybaena fruticum (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	-
16		H	B	Helix pomatia Linne 1758	-	4	-	-	-	-	-	-	-	-	-	-
17	S	H	Ru	Columella edentula (Draparnaud 1801)	-	-	-	-	-	-	-	-	-	-	-	-
18		Sp	HF	Vertigo pusilla (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	-
19		H	HF	Ena obscura (O. f. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	-
20		Sp	B	Punctum pygmaeum (Draparnaud 1801)	-	-	-	-	-	-	1	-	3	-	-	12
21		Sp	HF	Vitrea crystallina (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	-
22		O	B	Nesovitrea hammonis (Ström 1765)	-	-	-	-	-	-	-	-	-	-	-	-
23		H	HF	Perforatella incarnata (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	-
24		H	B	Trichia hispida (Linne 1758)	-	-	-	-	-	-	-	-	-	-	-	-
25		H	B	Euomphalia strigella (Draparnaud 1801)	-	-	-	-	-	-	-	-	-	-	-	-
26	R	O	Ru	Succinea oblonga (Draparnaud 1801)	-	-	-	-	-	-	-	-	-	-	-	-
27		O	B	Cochlicopa lubrica (O. F. Müller 1774)	-	-	-	-	-	-	-	1	-	-	-	-
28		Sp	St	Vallonia pulchella (O. F. Müller 1774)	-	-	-	-	-	5	1	5	-	-	-	-
29		O	Ru	Zonitoides nitidus (O. F. Müller 1774)	-	-	-	-	-	-	-	1	-	-	-	-
30		O	Ru	Deroceras reticulatum (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	-
31		O	Ru	Deroceras agreste (Linne 1774)	-	-	-	-	-	-	-	-	-	-	-	-
32		H	Ru	Perforatella rubiginosa (A. Schmidt 1853)	-	-	-	-	-	-	-	-	-	-	-	-
33	P	Sp	St	Vertigo pygmaea (Draparnaud 1801)	-	-	-	-	-	-	-	-	-	-	-	-
34		Sp	Ru	Vertigo angustior Jeffreys 1830	-	-	-	-	-	-	-	-	-	-	-	-
35		O	HF	Arion circumscriptus Johnston 1828	-	-	-	-	-	-	-	-	-	-	-	-
36		H	St	Monacha cartusiana (O. F. Müller 1774)	-	-	-	-	-	-	-	-	-	-	-	1

	1	2	3	4	5	6	7	8	9	10	11	12
	Pot. Fest. 03	Brometum tectorum 01		Festucetum vaginatae 02			Junipero- Populetum 22					
Σ Number of individuals	769	36	36	70	19	83	292	261	164	431	488	353
Number of juvenile individuals	126	22	4	33	8	47	135	126	73	211	267	217
Percentage of juvenile individuals	16,38	61,1	8,0	47,4	42,1	56,6	46,39	49,02	44,51	48,85	54,71	61,47
Abundance (A/m²)	283,6	28,8	57,6	56,0	15,2	132,8	465,7	205,6	131,2	344,8	156,1	141,2
Individual density (ID)	1,52	1,15	2,1	1,2	0.6	2,6	5,6	3,65	2,05	3,3	3,14	2,3
Habitat wetness index, mean value (W)	2,74	3,17	3,4	2,58	3,2	2,71	3,26	2,7	2,65	3,07	3,02	2,3
H' diversity	0,199	1,265	1,754	0,865	1,607	2,659	2,435	2,827	1,791	1,465	2,245	2,154
Σ Number of species	4	3	4	4	4	9	11	15	9	10	8	10