7 Effect of Environmental Conditions on Distribution Patterns of Rove Beetles

Ulrich Irmler and Erhard Lipkow

Abstract

This chapter aims to give a review about the impact of environmental conditions on Staphylinidae. Densities in diverse ecosystems from northern to tropical and from marine to alpine ecosystems are listed. As most Staphylinidae belong to the soil fauna, soil conditions are of main interest. Thus, life forms of soil-dwelling species are described. The effects of the parameter moisture, soil pH, acidity, and salinity on staphylinid occurrence are taken into consideration. Furthermore, the staphylinid faunas of main contrasting ecosystem type are reviewed: forests vs. agricultural fields, coasts vs. montane, and alpine ecosystems. Finally, since many rove beetle species have an affinity to nests, fungi, etc., the importance of microhabitats for Staphylinidae is described. Here, the special ecology of dung-dwelling and fungi-dwelling species is given such as the impact of the ephemeral food resource on the development.

7.1 Introduction

According to Herman (2001), more than 62,290 species with 3418 genera were described in the family Staphylinidae at the end of the second millennium. On that note, Staphylinidae is one of the most species-rich insect families in the world. This high number alone indicates that the Staphylinidae are widely distributed and occur in various habitats, zones, and ecosystems. It is certainly the family of Coleoptera that provides the highest variety of ecological groups. Bohac (1999) differentiated 5 classes of life forms with more than 14 ecological groups. Representatives of the family are found among euedaphic species in deep soil layers, on the soil surface, on the vegetation up to the canopy of forests, and from marine habitats in the eulittoral zone of the sea up to high mountain zones (Thayer 2005). Moreover, the variety of feeding habits is astonishing. Many staphylinids are nonspecialized predators; others prey specific insects or mites; there are many fungus feeders, pollen feeders, and humus feeders but no leaf feeders except few species of genera such as of the genus *Himalusa* (Klimaszewski et al. 2010). Numerous species live associated with social insects such as ants, wasps, or termites, where they feed directly on their hosts, are fed by them, or feed on remnants of their food or waste. Others live in the nests of mammals and birds; often they live either in their holes in the soil, in the large nests of

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O. Betz et al. (eds.), *Biology of Rove Beetles (Staphylinidae)*,
https://doi.org/10.1007/978-3-319-70257-5_7

raptors, or in episitic behavior directly on their skin. Thus, many staphylinid species are adapted to microhabitats such as the under bark habitat, large fungi (*Basidiomycetes*), and carcass. Most species of Staphylinidae have a well-developed flight ability which enables them to move large distances and seek microhabitats with short-term food resources. They are able to find heterogeneously distributed microhabitats such as spatially and temporally restricted dung heaps. Due to the isolated distribution and unpredictable occurrence of dung heaps, dung-inhabiting staphylinids must have a high mobility, e.g., great flight ability, highly sensitive chemical organs, and short larval development.

The following chapter tries to provide a rough overview of the ecological role of rove beetles in different ecosystem layers, zones, and microhabitats.

7.2 Soils and Staphylinids

7.2.1 Densities on Soil Floors

Investigations publishing staphylinid densities are rare. In general, staphylinids are collected by trapping methods, such as pitfall traps, flight intercept traps, etc., or are collected directly by hand. Bohac (1999) published data on staphylinid densities. Table 7.1 combines his data with our own investigations in Germany and in tropical Brazil as well as data from other references. According to these data, ecosystems of temperate zones have higher densities of staphylinids, on average, than tropical ecosystems. Temperate zones and wet ecosystems, e.g., wet alder forests or wet pastures, have higher densities than dry or oligotrophic ecosystems such as peat bogs. High densities are also recorded at sites with high organic detritus, such as wrack at beach sites. However, these sites also show extremely high variances of densities (Ruiz-Delgado et al. 2014). Low densities are recorded at agricultural fields in both temperate and tropical zones and in high alpine zones, but not in northern birch forests. According to these density data, staphylinids are one of the most frequent groups among the macrofauna on the soil floor. Densities are similar to spider densities (Palmgren and Biström 1979; Irmler 1995).

7.2.2 Life Forms and Functional Groups

The affinity to the soil habitat developed in various ways. Bohac (1999) differentiated the life forms Epigeobios and Geobios. In the following classification of life forms, the classic separation in epedaphic, hemiedaphic, and euedaphic species is maintained. Although many groups match the descriptions of Bohac (1999), another arrangement results from the specific focus to the soil.

The epedaphic rove beetles are characterized by large eyes and by moderately long legs. They can be separated into three groups: (1) species running on the soil or litter surface which forage randomly for food (Figs. 7.1 and 7.2), (2) optically oriented species walking slowly on the litter surface or on bare soil surface, and (3) litter-dwelling species living in the litter layer which can be regarded as an intermediate life form between the surface dwellers and the hemiedaphic species.

(1) The species running on the soil or litter surface have moderately well-developed eyes; their femurs are thick due to the well-developed leg muscles used for long and fast running events (Fig. 7.1). The eye-to-head-length ratio ranges between 0.28 and 0.33 for the few investigated species; the meso-femur width-to-length ratios are between 0.40 and 0.50. In general, they are black, dark brown, or colorful. Species that fit into this group look like *Ocypus* and *Philonthus* in temperate zones or *Xenopygus* and *Xanthopygus* in tropical zones. The running behavior is also shown by the high amount of catches in pitfall traps compared to their density (indicator for running activity) (Fig. 7.2). The species exhibit a slightly clumped dispersion pattern (Fig. 7.3).
(2) The optically orienting species have thick and large eyes because they have to fix their eyes on their prey. Legs are long, but femurs are thin; they walk slowly since no long

Table 7.1 Densities (ind. m^{-2}) of Staphylinidae in different ecosystems of temperate and tropical zones

	Mean	SD		
Temperate zone	or range		Country	Reference
Agricultural field	29	(11)	Germany	Own investigation
Dry pasture	84	(33)	Germany	Own investigation
Wet pasture	169	(28)	Germany	Own investigation
Oak forest (sandy soils)	58	(36)	Germany	Irmler (1995)
Oak forest	50–170		Russia	Bohac (1999)
Spruce forest (sandy soils)	66	(33)	Germany	Irmler (1995)
Spruce forest	99–187		Russia	Bohac (1999)
Pine forest	75–118		Russia	Bohac (1999)
Beech forest (sandy soils)	101	(38)	Germany	Irmler (1995)
Beech forest (loamy soils)	100	(51)	Germany	Irmler (1995)
Alder brook	113	(32)	Germany	Irmler (1995)
Alder forest	675–783		Russia	Bohac (1999)
Alder forest	350–470		Czech Rep.	Bohac (1999)
Montane spruce forest	30–110		Slovakia	Bohac (1999)
Heath land	78–110		Russia	Bohac (1999)
Peat bog	85–198		Russia	Bohac (1999)
Peat bog	5–68		Czech Rep.	Bohac (1999)
Peat bog	10–160		Germany	Bohac (1999)
Coastal ecosystems				
Salt marsh (upper)	16.7	(8.3)	Germany	Own invest.
Beach, sandy	825	(403)	Denmark	Larsen (1936)
Beach (wrack)	80–120		Spain	Ruiz-Delgado et al. (2014)
Beach (wrack)	10–420		Brazil	Ruiz-Delgado et al. (2014)
Northern and alpine zone				
Birch forest	120		Finland	Palmgren and Biström (1979)
Alpine zone (Caucasus)	3–10		Russia	Onipchenko (2004)
Alpine zone (3000–3600 m)	19–58		China	Tan et al. (2013)
Tropical zone				
Varzea forest (Amazonas)	74	(19)	Brazil	Irmler (1978)
Varzea forest (Amazonas)	50	(10)	Brazil	Irmler (1978)
Blackwater forest (Amazonas)	73	(54)	Brazil	Irmler (1978)
Agricultural field (Mato Grosso)	13	(19)	Brazil	Own investigation
Cerrado forest (Mato Grosso)	5	(7)	Brazil	Own investigation
Pasture (Mato Grosso)	15	(22)	Brazil	Own investigation

SD Standard deviation

distances have to be passed. The eye-to-head-length ratio ranges between 0.33 and 0.93; meso-femur width-to-length ratios are between 0.16 and 0.35. Typical species of this group are found in the genus *Stenus*, *Rugilus*, or some *Quedius*. In contrast to the former group, the number of catches in pitfall traps is usually lower than their densities because they run less and also spot the traps better (Fig. 7.2). The species are, similar to the preceding life form, dark or colorful. In regard to the dispersion patterns, the optically orienting species show near random values (Fig. 7.3).

(3) The last group of epedaphic species lives in leaf litter. The eyes are less developed and are distinctly reduced in comparison with the preceding two groups, as they live in a darker habitat. Eye-to-head-length ratio ranges between 0.18 and 0.24, which is even smaller than the randomly running species. The meso-femur width-to-length ratios are

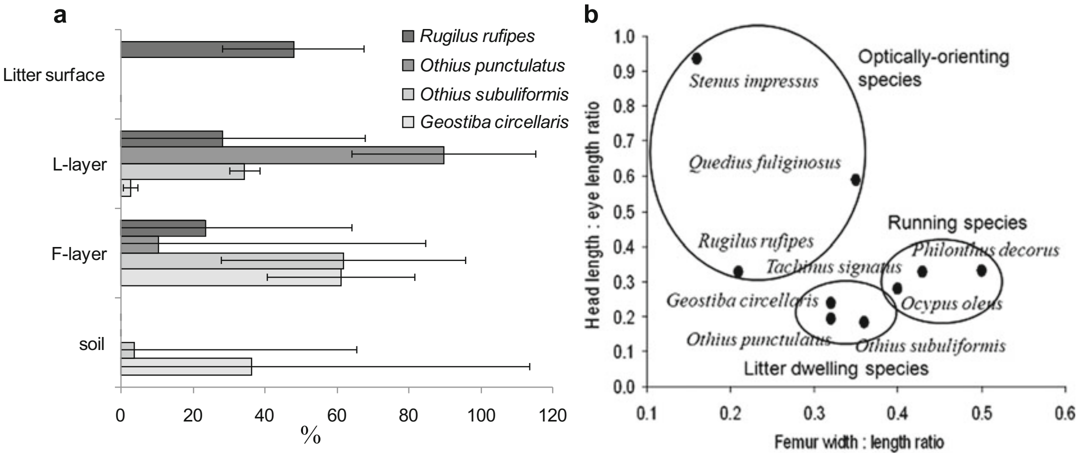

Fig. 7.1 (**a**) Vertical distribution of staphylinids in the litter layer of a northern German beech forest, (**b**) head-to-eye-length ratio vs. meso-femur width-to-length ratio for different life forms of the beach forest floor

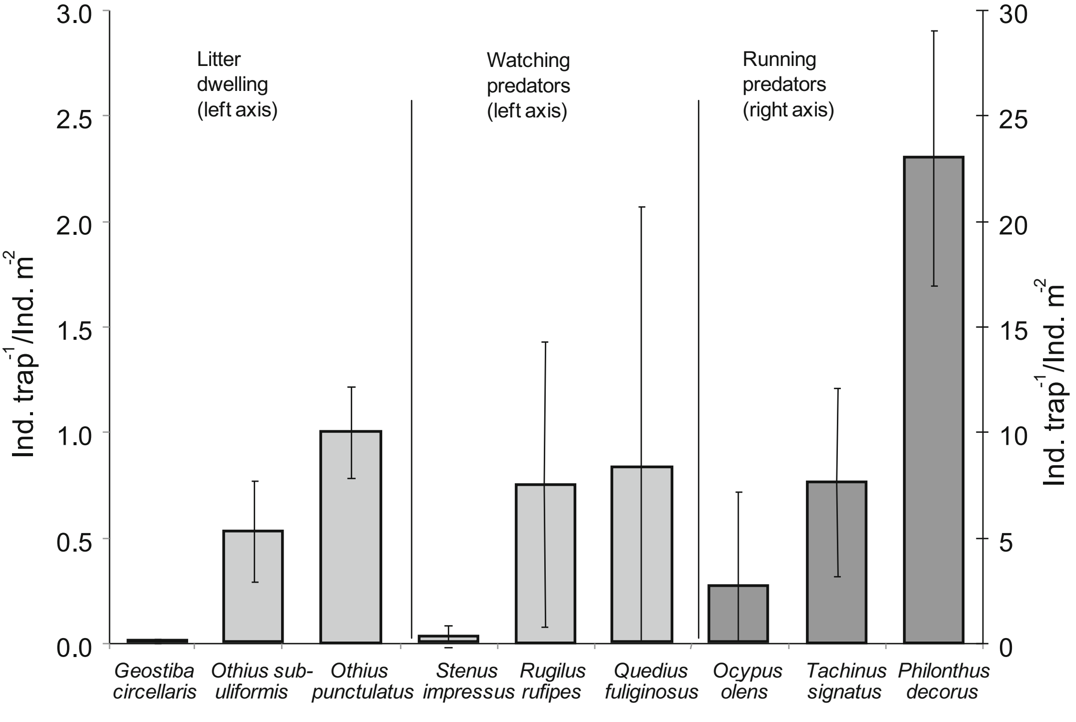

Fig. 7.2 Relation (ind. trap^{-1}/ind. m^{-2}) between activity density (ind. trap^{-1}) and density (ind. m^{-2}) to indicate the running activity of rove beetles

moderately high, ranging between 0.32 and 0.36. They can be named as “sliders” because walking among the narrowly packed foliage is impossible. The sliding movement is also shown by the dorsoventral depressed body and legs which are narrowly attached to the body. They more or less swim among the foliage. Regarding their vertical distribution, they live deeper in the L- or F-layer of the litter than the soil surface dwellers (Fig. 7.1).

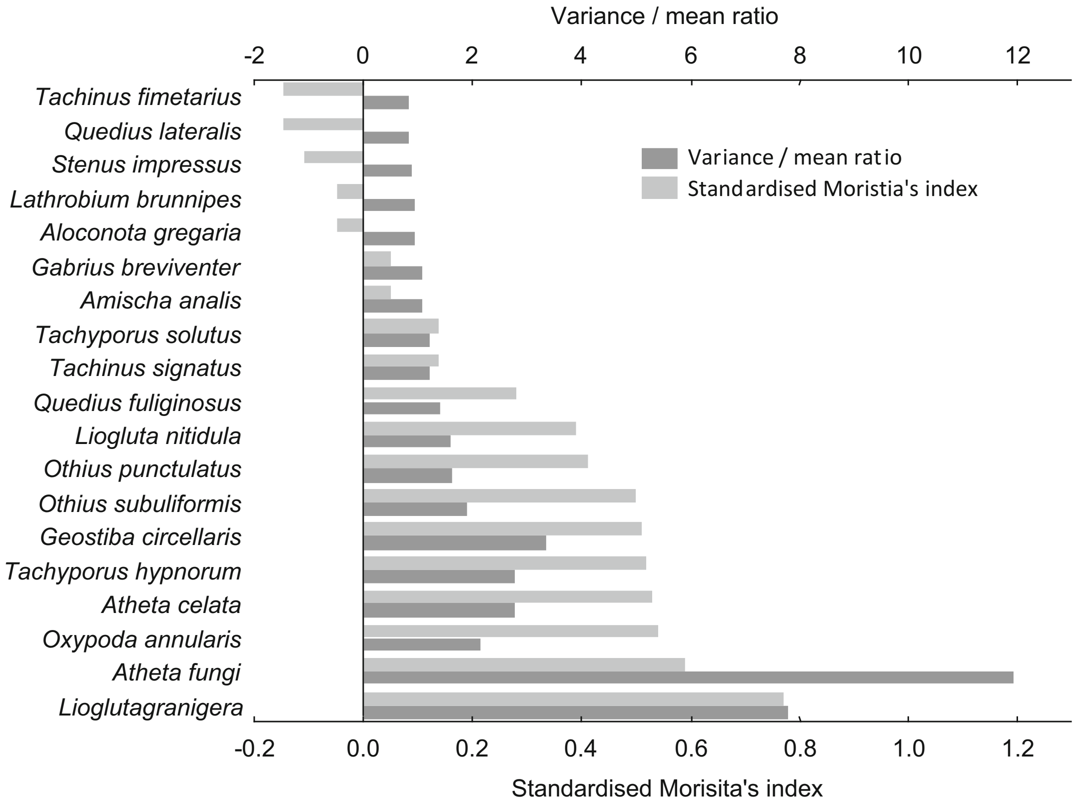

Fig. 7.3 Dispersion indices of different edaphic staphylinid species in a northern German beech forest; Standardized Morisita's index: clumped patterns above zero, uniform patterns below zero; values near zero indicate random dispersions, based on 18 samples in a northern German beech forest

Because resistance by the foliage layers is high, they move slowly (Fig. 7.3). Similar to the optically orienting group, sliders are caught in pitfall traps less often than species with high running activity (Fig. 7.2). In contrast to the two preceding life forms, litter dwellers are usually paler, light brown, or pale reddish because they rarely have direct contact to sunlight. Species of this group are found in the genus *Othius* in temperate zones or *Diochus* in tropical zones.

Dwellers of deep litter layers such as *Geostiba circellaris* also belong to the hemiedaphic life forms. This can be seen by their strongly reduced eyes, small size, short legs, and reduced elytra and hind wings. Within the vertical distribution, they live mainly in the F-layer or even in the mineral soil layer (Fig. 7.1). Running activity is extremely reduced due to the dense packages of litter foliage (Fig. 7.2). Comparing the three investigated species on the vertical gradient, *Othius punctulatus* is ca. 10–15 mm long. *O. subuliformis*, which lives in an intermediate layer, is ca. 4.8–5.5 mm long. *Geostiba circellaris*, which lives in the deepest layer of litter, is ca. 2.2–2.9 mm long. This indicates that the species become smaller the deeper they live in the litter layers. Regarding the dispersion patterns, litter-dwelling species are slightly clumped (Fig. 7.3). However, cumulative dispersion patterns with a tendency to aggregation are also found, e.g., *Atheta fungi*, *Liogluta granigera*, and *Oxypoda annularis*, which might be caused by the fact that some food resources are distributed heterogeneously in the litter, such as

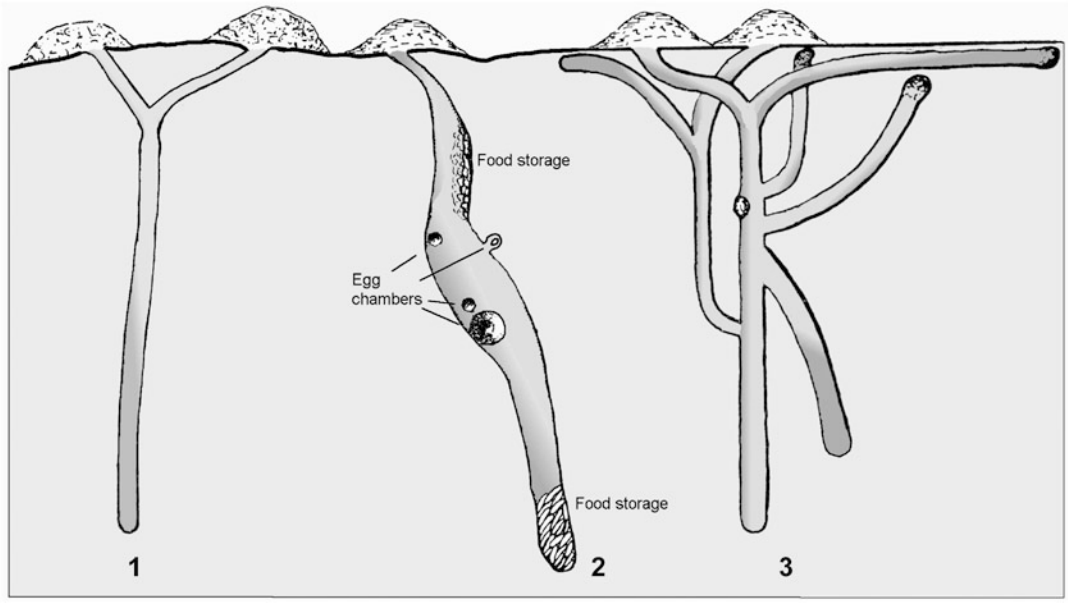

Fig. 7.4 Permanent holes of *Bledius arenarius* (1), *Bledius tricornis* (2), and *Bledius bicornis* (3) (according to Larsen 1936, modified)

specific fungi in the litter layer (Reise and Weidemann 1975).

The hemiedaphic species live in the mineral soil and are able to change the soil structure by burrowing in the substrate. They can be separated into two types: (4) species digging permanent holes in the soil surface and (5) species digging in the soil without producing permanent holes.

(4) Species of this group are represented mainly by the genus *Bledius*. They have broad pro-tibiae and large eyes. First investigations were made by Larsen (1936) on Danish beaches and Wadden sea sites. Larsen (1936) found three different types of permanent holes for the algae-feeding *Bledius* species: (1) simple unbranched holes, (2) more complicated holes with repositories and breeding chambers, and (3) branched hole systems without specific rooms (Fig. 7.4). Larson (1936) emphasized that *Bledius* species burrow their holes by carrying sand particles with their mandibles to deposit them on the adjacent soil surface, such as ants, or press them into the walls to stabilize them. The large tibiae are used for counter bearing against the hole walls and not for digging; the narrowed pronotum is necessary to bend the forebody during this activity.

(5) The species of this group exhibit intermediate morphological characters between the species digging permanent holes and the euedaphic species. Due to their small size, on average smaller than 2 mm, they usually belong to the soil mesofauna. Species of this life form are found in the genera of Aleocharinae and Oxytelinae, e.g., *Diglotta*, *Phytosus*, *Geostiba*, *Taxiera*, *Hydrosmectina*, *Meotica*, *Carpelimus*, and *Thinobius*. They often have long mandibles, such as some *Bledius*, that they use to carry sand particles during burrowing activities. Eyes, antennae, elytra, and hind wings might be reduced, depending on the stability of their habitat. Legs are usually longer than in the euedaphic group. For the species examined, length of mesotiba vs. total length was 0.12 ± 0.02. In unstable habitats, e.g., river margins, wings and antennae are fully developed, because

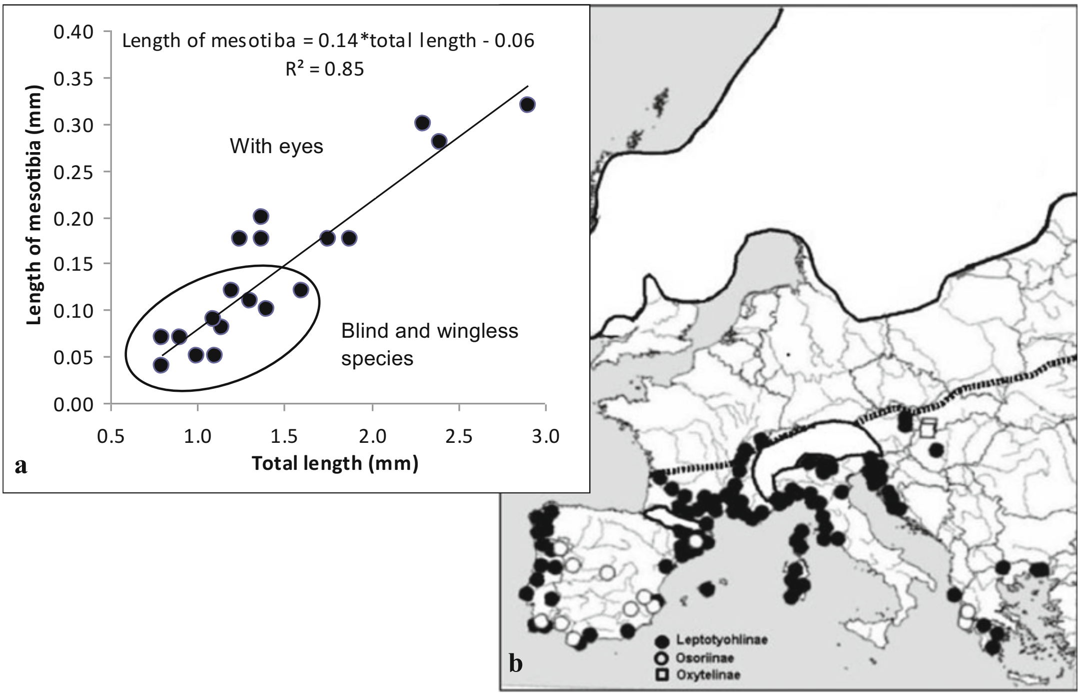

Fig. 7.5 (**a**) Relation between total body length and length of mesotibia for hemiedaphic species (with eyes, with or without wings) and euedaphic species (blind and without wings); data for euedaphic species measured according to graphs given by Coiffait (1972); (**b**) distribution of blind and wingless Staphylinidae in Western Europe (*white*, covered by glaciers in last glacier period; *dotted line*, southern border of permafrost soils)

they have to leave their deep soil habitat during unpredictable flooding events. In stable habitats, such as woods, eyes and wings are usually reduced, e.g., *Geostiba circellaris*.

The last life form of the soil-dwelling species is represented by the euedaphic species that live in deep soil layers and rarely move to the soil surface (6) or in deep holes in the soil made by mammals or other great animals (7).

(6) Typically, euedaphic species are extremely small and belong to the soil mesofauna, because they live in soil gaps, small holes, and similar soil structures. They cannot change the soil structure by burrowing. Although the deep soil is an extreme habitat for staphylinids, species in many subfamilies are found that live euedaphicly in the soil, e.g., Oxytelinae (blind and wingless species of *Thinobius*), Leptotyphlinae (nearly all species), Osoriinae (*Geomitopsis*, *Lusitanopsis*, *Heterocylindropsis*, *Rhabdopsis*, and others), and Aleocharinae (blind and wingless species of *Hydrosmectina*). The eyes are extremely reduced or totally absent. In contrast to the blind cave species, legs are also reduced to adapt to the narrow habitat between the soil particles. The ratio mesotibia length vs. total length is 0.07 ± 0.02, which means that legs are significantly shorter than for the hemiedaphic species (*t*-test: T, 5.7; $p < 0.001$). The morphological adaptations result in a wormlike-shaped body which is necessary to move in the narrow habitat. Species of this group are absent from regions that were covered by glaciers or permafrost soils during the glacial period. In Europe, they are only found south of the Alps (Fig. 7.5).

(7) Species living in the large holes (caverns) of soil-living mammals can hardly count as soil-dwelling. Although they live in soil caverns, their affinity to soils is lower than to the nest

habitat of their host animals. They must be placed to the inquiline life forms even if they also have morphological adaptations to their subterranean habitat in some respect. Some species have reduced eyes and a pale coloration, e.g., *Lathrobium pallidum* Nordmann, 1837; legs and antennae might be elongated, such as in cavernicole species, e.g., *Bisnius scribae* (Fauvel 1867) and *Rheochara spadicea* (Erichson 1837).

7.2.3 Soil Parameters

Although many staphylinids have a close affinity to soils, only few species show a narrow demand on specific soil characteristics. In a study in Northern Germany counting 65 woody and open ecosystems from sandy to organic soils, 265 species were found, but only 14 species were restricted to specific soil conditions (Irmler and Gürlich 2007). Only two species were found in sandy habitats, eight species in systems with high organic matter, and four species in ecosystems with low organic matter. Most species were distributed over a wide gradient of various soils (Table 7.2). This was also evident by the low eigenvalue in an ordination analysis, which was only 0.48 in spite of the high variance in soil parameters. The wide range of various soil conditions used by rove beetles is also emphasized by many other investigations that studied the relation between staphylinids and habitat conditions, including various soils (Vogel and Uhlig 1982; Steinmetzger and Tietze 1982; Rose 2001). Rose (2001) also investigated a wide range of habitat and soil conditions in coastal ecosystems but found a very low differentiation along the parameter gradients, with an eigenvalue of only 0.41. In his study, litter type and canopy cover were the most important factors, while soil pH and moisture and salt content were less important.

In spite of the overall wide range of soils used by staphylinids, few species are restricted to specific soil conditions. In a study on coastal staphylinids along the sand–loam–gravel gradient, *Bledius defensus* and *Oxytelus insecatus* were found in very short ranges of sand–silt–clay mixture (Irmler 2012). *Bledius defensus* was only found in a mixture of approximately 50% sand to 45% silt/clay and *Oxytelus insecatus* in a mixture of 30–60% sand and 35–45% silt/clay. Regarding the sand-shingle gradient, *Cafius xantholoma* preferred a higher percentage of shingle, whereas *Polystomota grisea*, *P. punctatella*, and *Phytosus spinifer* preferred sandy beaches (Fig. 7.6).

According to many investigations, moisture is one of the most important parameters controlling the distribution of staphylinid beetles (Irmler 1993; Ottesen 1996). The moisture of the soil on agrarian fields was a crucial factor for *Philonthus cognatus* when selecting sites for overwintering (Holland et al. 2007). Many species are known to be restricted to moist or wet lake or creek edges. Krogerus (1948) studied the distribution of staphylinid beetles in a wet–dry gradient and found 4 species restricted to wet conditions (80%–90% soil moisture), 5 species to moist conditions (50%–90%) with preference of high moisture, and 13 species that avoid moist conditions. In our own investigations of a wet–dry gradient which included a total of 122 species in forests and 79 species in grassland, 9 species preferred dry conditions (<30% mean yearly soil moisture) and 8 species wet conditions (>50% mean yearly soil moisture) (Table 7.3). Most species demanded intermediate moisture conditions and had a wide tolerance in regard to the high standard deviation of the weighted mean. However, species of both dry and wet habitats had a low standard variation, which indicates that they were restricted to either dry or wet conditions with a short range. For most species, the moisture demands corresponded to forest and grassland habitats. In both grassland and forests, moisture demands are significantly higher for four species and lower for one species.

Larsen (1936) and Krogerus (1948) studied the soil moisture demands under experimental conditions with six coastal and four bank staphylinid beetles. According to their experiments, the results support the field distribution. Living in dry dune habitats, both *Bledius pygmaeus* und

Table 7.2 Results of Spearman correlation analyses (*R*-values) between staphylinid species and soil parameters (Modified according to Irmler and Gürlich 2007)

Species	Sand (%)	pH	Corg (%)	Tree cover (%)	Ecological groups of species on/of
Zyras humeralis	0.35	0.31	−0.37		Alkalic, sandy, humus-poor soils
Atheta eurypтera	0.32	0.38			Alkalic, sandy soils
Ocypus brunnipes		0.45			Alkalic soils
Oxypoda opaca		−0.29			Acidic soils
Ilyobates bennettii			0.43		Humus-rich soils
Lathrobium brunnipes			0.35		
Aleochara bilineata			−0.39		Humus-poor soils
Plataraea brunnea			−0.29		
Anthobium atrocephalum			0.31	0.42	Humus-rich forests
Philonthus decorus			0.34	0.57	
Platydracus fulvipes			0.34	0.32	
Quedius fuliginosus			0.46	0.39	
Tachinus pallipes			0.32	0.33	
Zyras limbatus			−0.35	−0.33	Humus-poor soils of open habitats

Corg: organic carbon

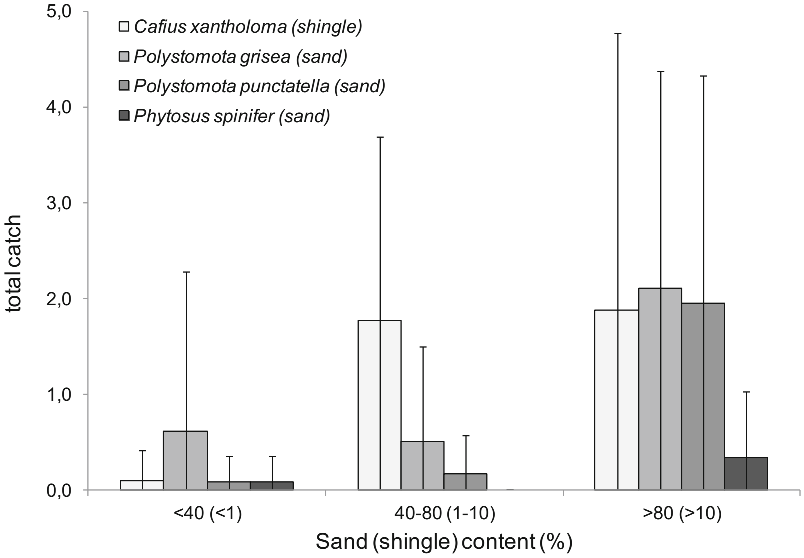

Fig. 7.6 Total catch of four staphylinid species at different beach types of the Baltic Sea (total $n = 40$, based on data of Irmler 2012)

B. opacus selected dry conditions of 2.5–7% and 3–10% moisture in the experiment and the field, respectively. In contrast, *Bledius diota* demand soil moisture at a minimum of 21%. This also corresponds to the field investigation where *Bledius diota* was not found at sites with moisture of 17 % and lower. The bank species investigated by Krogerus (1948) reflected both corresponding results between field and experiment (e.g., *Paederus riparius*, *Oxytelus rugosus*) and contrasting results between experiment and field (e.g., *Stenus cicindeloides*, *Philonthus quisquilarius*). There may be various reasons for the discrepancy between soil moisture demands in the field and the physiological demands. It might be referred either to moisture demands of eggs or larvae or a combination of effects between temperature and moisture.

Table 7.3 Weighted mean with standard deviation of soil moisture (%) for species in northern German deciduous forests and grassland indicating soil moisture demands and tolerance

Species	Deciduous forest		Grassland	
	W. mean	SD	W. mean	SD
Tachyporus nitidulus	–	–	10.9	0.2
Xantholinus linearis	–	–	10.9	0.2
Oligota pusillima	–	–	10.3	0.6
Oxypoda sericea	–	–	10.8	4.1
Tachinus corticinus	–	–	15.7	13.2
Tachyporus dispar	–	–	22.6	18.6
Oxypoda exoleta	–	–	23.7	19.0
Geostiba circellaris	29.7	11.1	–	–
Philonthus cognatus	31.0	4.2	37.3	18.7
Philonthus laminatus	31.6	1.8	–	–
Oxypoda annularis	32.4	4.1	–	–
Lathrobium brunnipes	32.6	11.3	50.5	0.0
Tachinus rufipes	33.0	5.2	–	–
Stenus impressus	33.9	6.7	–	–
Othius subuliformis	34.3	10.3	–	–
Othius punctulatus	34.5	12.0	–	–
Philonthus decorus	34.8	10.4	–	–
Quedius fuliginosus	35.2	10.5	50.5	0.0
Rugilus rufipes	36.7	11.2	49.6	6.0
Stenus clavicornis	32.8	2.0	37.3	18.7
Stenus juno	38.0	6.7	43.9	14.8
Gabrius subnigritulus	–	–	38.9	18.2
Anotylus rugosus	44.2	13.3	46.6	12.1
Stenus bimaculatus	45.8	2.0	50.5	3.4
Carpelimus elongatulus	46.7	5.7	50.5	0.0
Anthobium atrocephalum	47.3	14.0	–	–
Anthobium unicolor	47.6	13.3	–	–
Atheta aquatica	58.6	6.6	–	–
Olophrum piceum	59.5	7.3	–	–
Atheta volans	–	–	50.5	0.0
Stenus cicindeloides	–	–	50.5	0.0
Stenus similis	–	–	50.5	0.0
Myllaena intermedia	55.2	9.1	–	–
Atheta elongatula	56.1	9.1	47.7	10.1
Ocalea picata	57.9	8.7	50.5	0.0

W. mean Weighted mean, *SD* standard deviation

According to Bong et al. (2013), *Paederus fuscipes* develops better under higher temperatures than under cold conditions. However, they need high moisture conditions for their development at higher temperatures. Eggs need high water uptake for their development, which may differ from the water demands of adults, e.g., for *Ocypus olens* (Lincoln 1961).

Soil moisture shows a high variation throughout seasons, with high values during winter or spring or during rainy seasons. Moreover, the groundwater table varies in the same way. Irmler (2009) investigated the time lag between the moisture changes over a period of 7 years and the reaction of staphylinid beetles. He found time lags of 0–2 months between strong rainfall

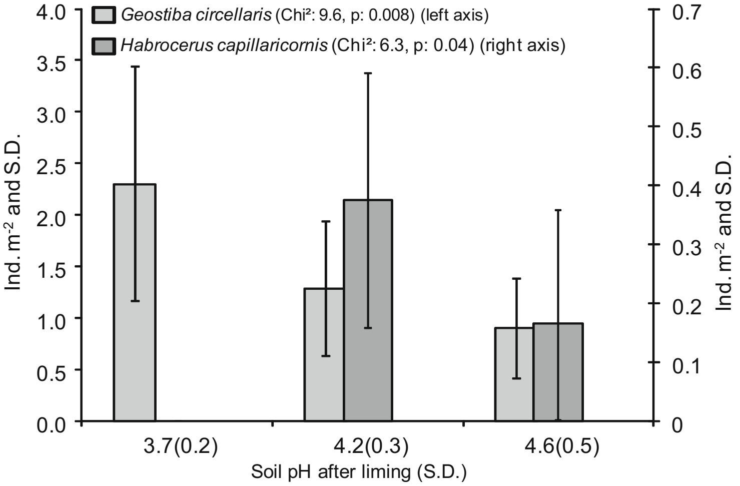

Fig. 7.7 Effect of liming on the density of *Geostiba circellaris* and *Habrocerus capillaricornis* in a northern German beech forest ($n = 9$ in each plot), with results of Kruskal–Wallis ANOVA between the three liming groups including Chi^2 and p values

events and the reaction of *Anthobium atrocephalum* populations. The species reaction to high rainfall events was positive. In an alder wood, time lag was both 3 and 4 months between groundwater table changes and the reactions of *Ocalea picata* and *Myllaena intermedia* populations, respectively. The negative correlation coefficients indicate that under high groundwater tables with backwater conditions, the species retreat from the wettest sites to avoid submersion.

The acidity of substrate also plays a role in the distribution of staphylinid species. Typical species of acid bogs, e.g., *Acylophorus wagenschieberi* and *Stenus kiesenwetteri*, may be restricted to that habitat, not only by the wet conditions but mainly by the acid substrate. The two European *Acylophorus* species prefer moist conditions with contrasting soil acidity: *A. wagenschieberi* on acid bogs (Staniec 2005) and *A. glaberrimus* alkaline mire conditions at pond edges. According to Gryuntal (2009), *Geostiba circellaris* prefers acid forests on moder litter, whereas *Tachinus marginellus* avoids acidic conditions. Preference experiments using Staphylinidae in an acid–alkaline gradient are not available. However, liming experiments in forests may show the reaction of staphylinid beetles under changing soil pH (Fig. 7.7). With an increase of soil pH in a northern German liming experiment in a beech forest, the densities of both *Geostiba circellaris* and *Habrocerus capillaricornis* decreased and increased, respectively. However, among the 64 species recorded, there were only these 2 species that reacted to the pH increase, which means that rove beetles rarely react to slightly changing soil acidity.

According to Frank and Ahn (2011), 392 staphylinid species were confined to coastal habitats worldwide. Moore and Legner (1976) mentioned ecological details but gave no information on the dependence on or the tolerance to salinity. Larsen (1936) tested the preferences of various rove beetles in her thesis about the burrowing beetles of the coast. According to her preference experiments, the species that do not live directly at the sea margin, such as *Carpelimus despectus* and *Bledius opacus*, avoided salinity greater than 5‰. Others, e.g., *Bledius longulus*, *B. arenarius*, and *Bledius tricornis*, showed a wide range, from 0 to 20‰. Only the species directly living under submersion conditions, e.g., *B. spectabilis* and *B. diota*, preferred salinities between 30‰ and 60‰. Larsen (1936) assumed that the species preferred the sites with high salinity in order to avoid the parasitoid ichneumonids. Topp and Ring (1988) also made experimental studies with intertidal rove beetles, including studies on the influence of the salinity. They studied the two species

Liparocephalus cordicollis Le Conte and *Diaulota densissima* Casey from British Colombia. Both species survive a submergence of more than 2 weeks under marine water. *L. cordicollis* has an osmotic regulation and can stabilize their body weight at a range between 2‰ and 45‰. Respiration was constant within the salinity range of 2–30‰, but at higher levels of 45‰, oxygen consumption increased.

7.3 Ecosystem Preferences, Diversity, and Occurrence

7.3.1 Temperate and Mediterranean Forests

Forests are one of the most diverse ecosystems, which is due to the habitat diversity offered by trees. Living trees with their diverse structure offer different climate conditions in the vertical layers and the bark; dead trees, in addition, offer still more habitats due to the succession of decaying wood. The group of Staphylinidae is regarded to be an essential group for the evaluation of forest biodiversity (Parmain et al. 2015). Besides the alpha diversity at a site, forests differ in their tree composition and soil conditions, e.g., moist vs. dry forests or sandy vs. loamy forests. The sand–moisture gradient was primarily accountable for the ordination of forest ecosystems in Northern Germany using the staphylinid composition (Irmler 1993).

The ascertained species richness mainly depends on the sampling effort, the different collecting methods, and the duration of the investigation. In Europe, total species richness of forests was 42 species, with 12.3 ± 4.5 species in each of 10 forests in Norway (Andersen et al. 1990), and 205 species, with 48 ± 30.6 in each of 12 forests in Northern Germany (Irmler 1993). In the 12 German forests, a lowest number of species was found in the extremely wet alder forests (17 species); the highest numbers were found in the moderately moist alder forest (121 species). Dry forests on sandy or loamy soils exhibited intermediate species richness (24–83 species). A total of 132 species, with 40.2 ± 24.3 species in each of 9 forest sites, were found on sandy soils with pine forests in Central Germany (Steinmetzger and Tietze 1982). Bohac (1999) published values ranging between 12 and 52 species for diverse Russian forests and 23–81 species for Czech forests. In beech forests of Central Germany, the species richness varied between 91 (Karlsruhe) (Friebe 1982), 87 (Berlin) (Weigmann et al. 1989), and 117 (Göttingen) (Hartmann 1976). Few investigations pertain to the biodiversity of Mediterranean forests. Zanetti (2011) recorded 80 species out of 1200 specimens from a Sardinian *Quercus ilex* forest area, which is less than in the Central European region.

A survey on rove beetles living on dead wood in three different deciduous and spruce forests of Northern Germany recorded 170 species (Irmler et al. 1997). Age of dead wood was the major factor controlling the species richness of rove beetles (Fig. 7.8). The species richness increased with increasing age and was highest on the soil surface. Density of rove beetles living on dead wood ranged between 5 and 137 ind. m^{-2} of wood surface; on the soil surface, it ranged between 27 and 120 ind. m^{-2} (125 and 190 ind. m^{-2} including larvae) (Irmler 2009). The species composition was more similar between the different ages of decay than between the forests standing on different soil conditions and having different tree compositions. Some species were exclusively found on dead branches of beech wood; other species were additionally found on alder wood or on beech, alder, and spruce wood (Table 7.4). Whereas young branches had species exclusively found there, stumps had no exclusive species and shared many species with the surrounding soil surface.

Seasonality in temperate forests is controlled by the temperature. Most species have their highest activity in spring and early summer (Kasule 1968; Hartmann 1979; Friebe 1982). Little knowledge is available about the long-term fluctuations. Irmler (2009) published a 7-year study and found a negative cross-correlation between the population density and temperature for the six species *Oxypoda*

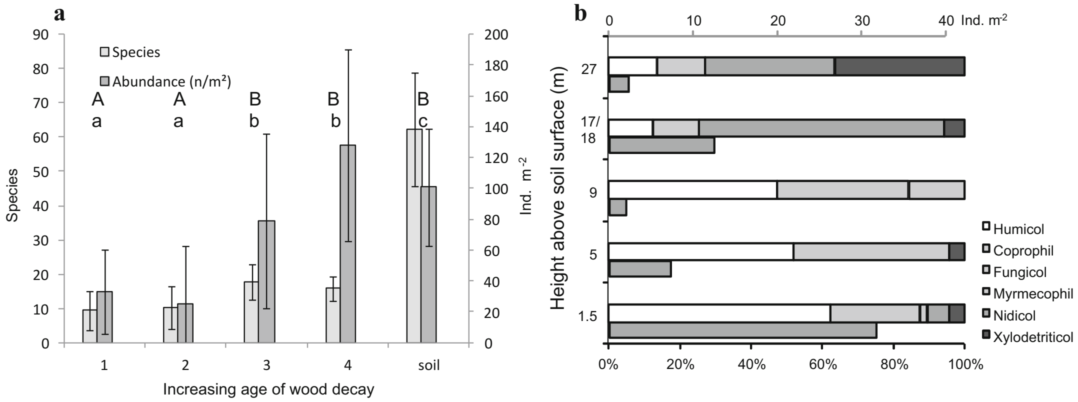

Fig. 7.8 (**a**) Number of species and abundance of rove beetles on dead wood of different age of decay compared to the soil; (1) bark closely fixed to the log, partly with fungi; (2) bark loosely fixed to the log, already with moss; (3) the original structure of the wood is still visible, but the wood is already rotten; (4) the structure of the wood is amorphous, but single wood pieces are still existent; different capitals indicate significant differences (small for species, large for abundance); (**b**) vertical distribution of total number of specimens and percentages of ecological groups in northern German beech and alder forests; humicol species include phytodetriticol species (Modified Irmler et al. 1997; Irmler 1998)

annularis, *Geostiba circellaris*, *Atheta fungi*, *Othius subuliformis*, *Anthobium atrocephalum*, and *Anthobium unicolor*, which means that the populations of these species decreased in years with a low mean temperature. Reaction time ranged from a few months to 1 year, depending on the number of generations. Large species, e.g., *Othius subuliformis*, reacted slower than smaller species, e.g., *Atheta fungi*. However, several species responded positively to high amounts of litter fall, such as *Oxypoda annularis*, *Geostiba circellaris*, *Atheta fungi*, and *Othius punctulatus*. As Collembola densities also corresponded with litter fall (Irmler 2006), the reaction of rove beetles on litter fall fluctuations may be referred to either their collembolan food, e.g., *Othius punctulatus*, or to a higher amount of fungi or beech nuts.

Another specific character of forests is the distinct vertical structuring in different layers, i.e., several layers of soil, soil vegetation, bushes, and different tree layers. Little knowledge is available about the staphylinid fauna of the canopy layer. In Northern Germany, the vertical distribution of staphylinids was investigated in beech and alder forests using flight intercept traps at different heights from 1.5 to 27 m above the soil surface (Irmler 1998). The total number decreased with an increase in height (Fig. 7.8). Lowest numbers were found at lower and upper borders of the canopy at 9 m and 27 m. Mainly species living in the litter layer or in rotting plant matter were found close to the soil surface at a height of 1.5 m. Among these groups, only a few species occurred that primarily lived in the forest leaf litter; most species live in rotting plant litter and switch between agricultural and forest ecosystems in the course of the year, e.g., *Tachinus rufipes*, *Tachyporus* spp., and others (Lipkow 1966). They generally use the forest resources after harvest and for overwintering. Mainly species living in the nests of birds or on dead wood were found in the canopy layer. Many species near the soil surface layer must be regarded as species unspecific for forests, because they use resources of different ecosystems. In contrast, the species of the canopy are specific for the forest ecosystem because they use resources that are only found there. They were caught by the flight intercept traps because their resources are heterogeneously distributed within the forests. Coprophilous species were recorded over the whole vertical gradient in high percentages. They are extremely active flyers because their resources are also distributed quite heterogeneously. None of the

Table 7.4 Density of rove beetle species (ind. m^{-2}) exclusively found on dead wood in three northern German forests ($n = 50$ emergence traps filled with dead wood); density refers to surface area of wood; significant values due to Bonferroni corrected Kruskal–Wallis ANOVA with $p < 0.05$ italic (Modified according to Irmler et al. 1997)

	Beech				Alder				Spruce			
	Young log/stump		Old log/stump		Young log/stump		Old log/stump		Young log/stump		Old log/stump	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Anomognathus cuspidatus	2.9	7.2	1.1	3.2	0.3	0.4	0.1	0.2	.	.	.	.
Atheta celata	0.1	0.1	*1.0*	*1.6*	0.3	0.5	.	.	.	.	.	.
Atheta coriaria	3.6	11.4	*23.1*	*45.5*	.	.	.	.	.	.	.	.
Baptolinus affinis	0.6	2.0	1.0	2.9	.	.	.	.	.	.	.	.
Bolitochara obliqua	*0.3*	*0.4*	.	.	.	.	.	.	.	.	.	.
Dinaraea aequata	0.4	0.6	*1.0*	*2.9*	0.5	0.5	0.2	0.5	.	.	.	.
Leptusa pulchella	0.5	1.3	*2.1*	*3.1*	.	.	0.5	1.5	.	.	.	.
Lordithion exoletus	0.1	0.2	*0.8*	*1.6*	.	.	.	.	.	.	.	.
Lordithion trinotatus	0.1	0.1	*7.7*	*7.2*	.	.	.	.	.	.	1.7	2.4
Phloeocharis subtilissima	0.1	0.1	0.9	1.8	0.8	1.3	1.3	2.2	5.9	8.4	3.4	4.8
Phloeonomus punctipennis	2.1	5.2	*3.8*	*10.6*	0.4	0.8	0.5	1.5	0.4	0.6	.	.
Phloeopora angustiformis	0.1	0.2	0.4	1.1	.	.	.	.	.	.	.	.
Phoeopora teres	.	.	0.3	1.0	.	.	.	.	.	.	.	.
Quedius invreae	1.5	4.1	*6.0*	*9.9*	.	.	2.1	3.9	2.0	1.7	3.0	0.7
Quedius maurus	0.5	1.2	3.8	7.6	.	.	1.9	5.9	.	.	2.5	3.5
Quedius xanthopus	0.1	0.3	*6.9*	*5.4*	0.5	0.9	0.7	2.3	.	.	*6.4*	*5.5*

M Arithmetic mean, *SD* standard deviation

species can be regarded as being specific for the forest ecosystem. They are found in a variety of ecosystems in which feces are available.

Many of the coprophilous and humicolous/phytodetriticolous species that occurred in the investigated vertical gradient were also recorded by aeroplanes at extreme heights (Weidel 2010): *Anotylus rugosus* and *A. tetracarinatus* were recorded at 300 m and *Philonthus cognatus* and *Xantholinus longiventris* at 1500 m.

7.3.2 Agricultural Fields

In contrast to the stable forest ecosystems, arable land is extremely unstable due to yearly agricultural management such as tilling, the change of agricultural crops, etc. Staphylinidae are mainly predators and are thus considered to be beneficial insects on agricultural land. In particular, *Tachyporus* species, e.g., *Tachyporus hypnorum*, are effective predators on cereal aphids (Vickerman and Sunderland 1975; Coombes and Sotherton 1986). In spite of their beneficial effects, densities of staphylinids under intensive farming conditions are distinctly lower than in forests or other agricultural systems (Table 7.1). Although the staphylinid fauna of agricultural land is strongly influenced by the surrounding habitats from where species invade the fields yearly (Topp 1977; Sotherton 1985), an autochthonous staphylinid fauna must exist, as can be seen by the dynamics of larvae and adults (Fig. 7.9).

Several staphylinid species are able to overwinter in arable fields and reproduce there in early spring (Gilgenberg 1986; Basedow 1990). They produce larvae that live in late spring. According to Basedow (1990), the rate of reproduction varies between crops and intensities but may be even higher under intensive agriculture, such as for *Lathrobium fulvipenne*, if moisture conditions favor the living conditions. Other species, e.g., *Tachyporus hypnorum* or *Tachinus rufipes* (Lipkow 1966), mainly overwinter at field margins or in adjacent forests and must

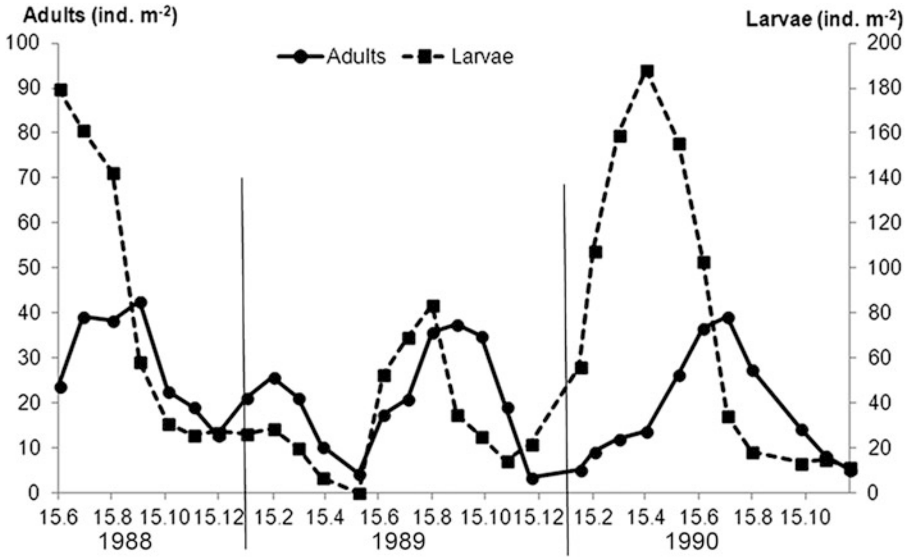

Fig. 7.9 Dynamics of adults and larvae on an agricultural field in Northern Germany based on fluctuating mean of 3 months (monthly samples of four replicates over 3 years gained by heat extraction)

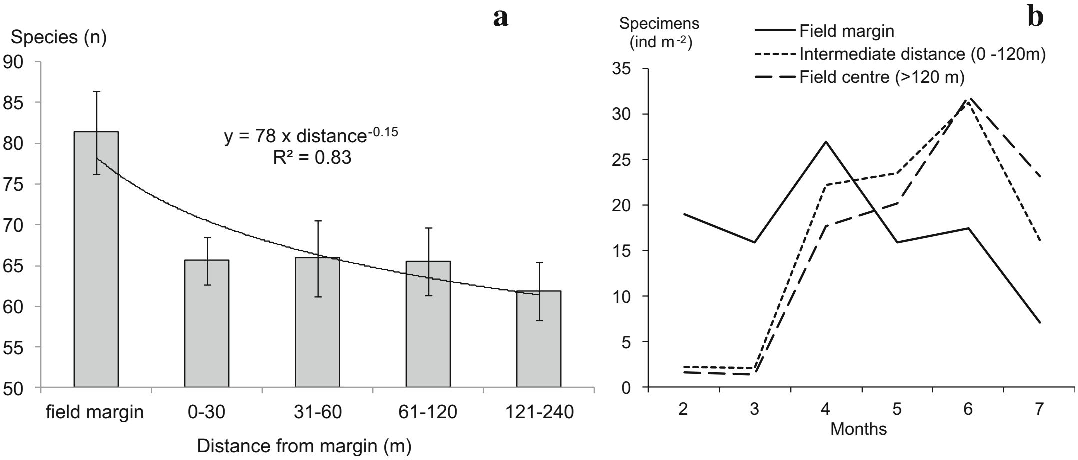

Fig. 7.10 (**a**) Species richness calculated as sample rarefaction for ten pitfall traps in a northern German agricultural field; (**b**) seasonal occurrence of *Tachyporus hypnorum* in different areas of an arable field ($n = 122$ pitfall traps, year 2001) in Northern Germany

actively fly into the field center (Fig. 7.10). They are active in the summer time when activity has already decreased in the field margins.

Although field margins usually have higher numbers of staphylinid species (Fig. 7.10), after the change from intensive to organic farming in long-term investigations, no significant increase of species or specimens was found during the succession (Andersen and Eltun 2000; Schröter 2010). According to Schröter (2010), 11 species profited from the organic practices on arable fields, e.g., *Tachyporus obtusus* and *Tachinus fimetarius*, and the same number of species profited from conventional farming, e.g., *Philonthus rotundicollis* and *Lathrobium fulvipenne*. Several of the specific species of

Table 7.5 List of dominant Staphylinidae restricted to coastal habitats in Northern Europe

Eulittoral		Supralittoral		
Rocky	Sandy	Silt mudflat	Sandy beach	Shingle beach
Micralymma marinum	*Diglotta mersa*	*Bledius tricornis*	*Bledius spectabilis*	*Polystomota grisea*
	Diglotta sinuaticollis	*Bledius frisius*	*Phytosus balticus*	*Cafius xantholoma*
	Bledius subniger	*Brundinia marina*	*Phytosus spinifer*	*Omalium riparium*
			Polystomota punctatella	
			Atheta vestita	
			Omalium riparium	

arable fields show a wide distribution. Due to the similar conditions under agriculture, they are dominant on most European agricultural fields such as *Xantholinus linearis*, *X. longiventris*, *Tachyporus hypnorum*, *Philonthus cognatus*, and *Anotylus rugosus* (Bohac et al. 1999; Andersen and Eltun 2000; Gilgenberg 1986; Lupi et al. 2006; Schröter 2010). Moreover, European species are invaders in North America, e.g., *Gyrohypnus angustatus*, *Tachinus corticinus*, *Sepedophilus marshami*, etc. (Levesque and Levesque 1995, see also Chap. 5 in this book).

7.3.3 Coasts

The 392 species specialized on coastal habitats (Frank and Ahn 2011) have to be divided into several ecological groups (Table 7.5). Few species occur under intertidal conditions and live under submersion conditions two times per day. Among these species, some live on rocky cliff coasts such as *Micralymma marinum* (Thayer 1985) and others in sandy mudflats (Topp 1975) or in tropical mangroves (Frank and Ahn 2011) such as *Bryothinusa sakishimana* or *Linoglossa murphyi* (Sawada 1991). According to Topp (1975), the two species *Diglotta mersa* and *D. sinuaticollis* use the same resources of a small area of aerated sand a few centimeters below the sand surface at a distance of 60 m from the mean high tide level. They overwinter in the dune zone above the mean high tide level and inhabit their eulittoral habitat again by hydrochory in each summer.

Most of the coastal species, however, live in the supralittoral zone under fewer, but unpredicted, submersion conditions. These species are either restricted to salt grassland in northern or in southern regions (e.g., Heydemann 1962; Irmler and Heller 2002) or to beaches that have to be divided into sandy beaches and shingle beaches (Irmler 2012) (Table 7.5).

On salt marshes covered by grassland, the species richness increased with increasing elevation and concurrently with decreasing tidal floods (Fig. 7.11). The number of specialized species, e.g., *Brundinia marina*, decreases with an increase in elevation. Other species such as *Bledius tricornis* have their maximum at intermediate elevations (60 cm above mean high tide level; MHT). The rise in species richness with increasing elevation is mainly referred to the high number of species invading from fresh grassland sites to high elevated salt marshes, e.g., *Amischa analis* and *Oxypoda brachyptera*.

The wave and wind energy at beaches are decisive factors for the occurrence of coastal staphylinid species (Irmler 2012). At sandy beaches with moderate wave and wind impact, the species composition differs significantly from wind- and wave-exposed shingle beaches (Table 7.5). Wrack is another important habitat on beaches (Ruiz-Delgado et al. 2014). According to Ruiz-Delgado et al. (2015), the common staphylinid species in SW Spain, e.g., *Carpelimus rivularis*, *Cafius xantholoma*, and *Remus sericeus*, were not correlated with temperature, moisture, or carbohydrate concentration. The wide distribution of coastal staphylinid species as documented by

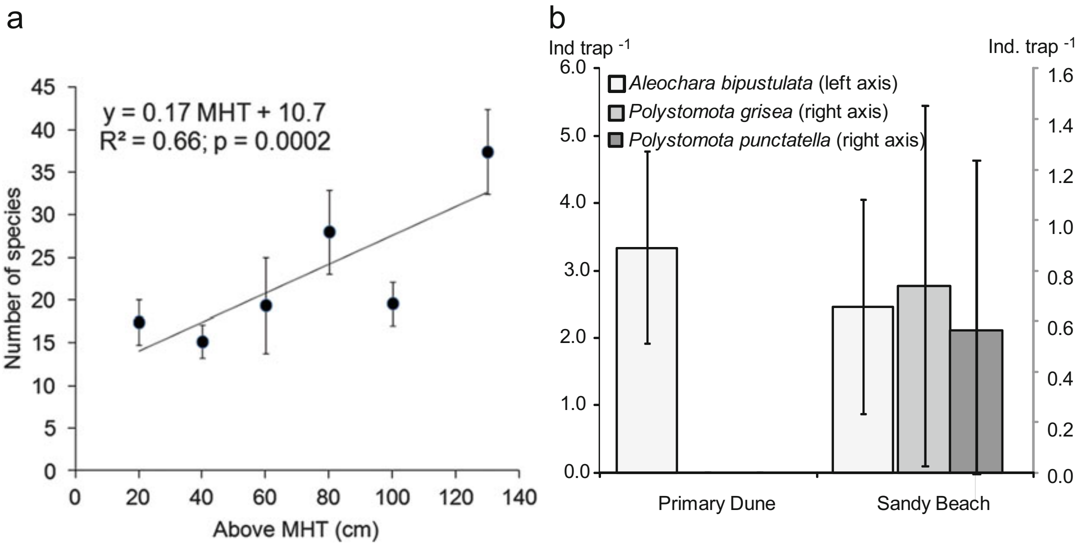

Fig. 7.11 (**a**) Vertical increase of species number (species trap^{-1} year^{-1}) of Staphylinidae in northern German saline grassland at the North Sea; (**b**) distribution of three rove beetles in the beech dune gradient; MHT, Mean high tide level (according to Irmler and Heller 2002 and Irmler 2012)

Frank and Ahn (2011) indicates that coastal species have a wide range of ecological demands on the nearshore conditions.

Many of the species found on sandy beaches are restricted to that habitat and do not even occur at adjacent sites such as primary dunes (Fig. 7.11). However, species of the dune habitat can invade the sandy beaches, e.g., *Aleochara bilineata*. Thus, the habitat of the specialized beach species is very narrow, mostly no wider than 10–20 m in the vertical direction. For the intertidal species *Diglotta brasiliensis*, which lives under similar conditions as the European *Diglotta submarina* and *D. mersa*, the coastal habitat zone is only 4–5 m wide (Da Rosa et al. 2008).

7.3.4 Montane and Alpine Habitats

In his fundamental work on the distribution of alpine and subarctic Coleoptera, Holdhaus (1954) mentioned several staphylinid species of the high alpine zone of the European high mountains, e.g., *Stenus hoelzeli*, *Leptusa winkleri*, and *Chilopora holdhausi* for the Southern Alps. Several species have a boreo–alpine distribution because they occur in Scandinavia and the Alps, e.g., *Atheta depressicollis*, *Oxypoda tirolensis*, and *O. nigricornis*. Many of the alpine staphylinid species are endemic in extremely small areas; some live only on the top of one mountain such as many *Leptusa*, *Geostiba*, and *Alpinia* species. Zerche (2006) reported that the species of the genus *Ophthalmoniphetodes* (Omaliinae: Coryphiini) live under snow patches in early spring. They are flightless and occur in numerous endemic species in alpine and subalpine zones of the Balkan Peninsula. As one of the best investigated countries regarding Staphylinidae, 44 endemic and subendemic species have been recorded in Austria (Paill and Kahlen 2009). Along the altitude zones, the highest number of species is found in a range from 1500 to 2500 m above NN in different alpine habitats, e.g., alpine grassland and alpine dwarf shrub heath (Fig. 7.12). The high number of endemic species in the mountains of Southeastern Europe is derived from the isolation during the glacial period.

In the Dolomite Alps, Schatz (2008) differentiated four assemblages of Staphylinidae on alpine grassland: calcareous boulder grassland, shady rock face, alpine calcareous grassland, and

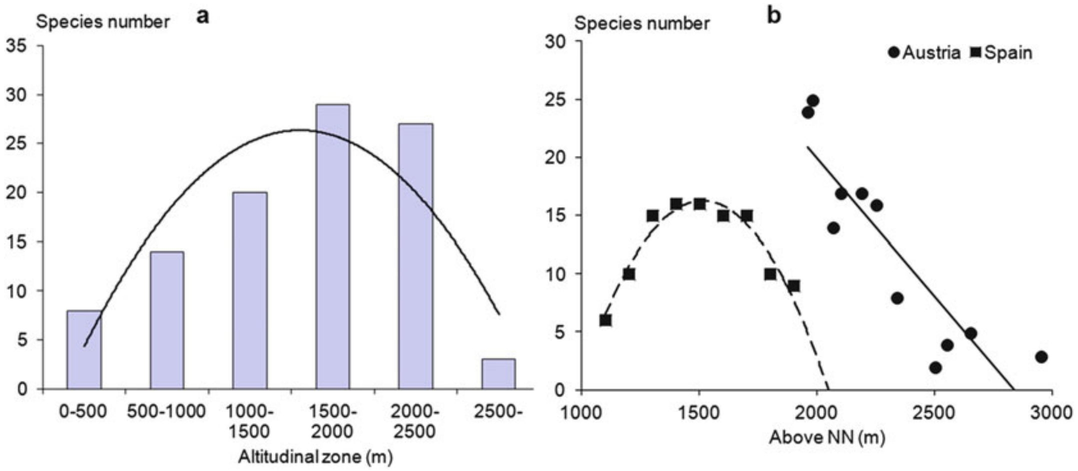

Fig. 7.12 (**a**) Vertical distribution of endemic and subendemic Staphylinidae in Austria according to Paill and Kahlen (2009); elevation range of species is considered; (**b**) vertical distribution of species richness of Staphylinidae gradients of the Central Alps (Austria) and in Sierra de Guadarrama (Central Spain; only the subfamily Staphylininae was considered)

volcanic boulder grassland. Typical species are, for example, *Ocypus alpestris*, *Philonthus frigidus*, and *Philonthus montivagus*. In the central Alps, De Zordo (1979) reported four assemblages at an altitude of 1900–3100 m: valley grassland, dwarf shrub heath, lichen heath, and alpine grassland with typical species, e.g., *Tachyporus macropterus*, *Omalium ferrugineum*, *Atheta leonardi*, and *Coryphium gredleri*. According to this investigation, the species richness decreased corresponding to the altitude gradient (Fig. 7.12). Fernandez et al. (2010) investigated the staphylinid fauna of the Central Spain Sierra de Guadarrama and found the highest species richness in an intermediate altitude of 1500 m. Several species, e.g., *Quedius latinus* and *Ocypus olens*, were restricted to this intermediate altitude. In Norway, alpine Staphylinidae assemblages were composed of species with affinities to dry and humid meadows as well as mires (Ottesen 1996). They showed niche segregation along the humidity, altitude, and season gradients. For example, characteristic spring species were *Stenus carbonarius* in wet habitats at low altitudes (~1300 m) and *Bryoporus rugipennis* in dry habitats at high altitudes (~1500 m); characteristic summer species were *Olophrum boreale* in humid habitats at high altitudes and *Stenus ludyi* in dry habitats at low altitudes. Only a few groups exhibited slightly separated niche dimensions, e.g., *Boreophilus henningianus*, *Arpedium quadrum*, and *Psephidonus longipes* (all in autumn at intermediate soil moistures and high latitudes). In contrast to their overall well-developed flight ability, alpine species displayed a low dispersion potential. Half of the 21 species found in the foreland of a Norwegian alpine glacier were found in sites that were more than 63 years old (Bråten et al. 2012). Sites with *Tachinus elongatus* and *Mycetoporus erichsonanus* had to have a minimum age of 200 years.

Little is known about Staphylinidae for the tropical mountain region. Some species at high altitudes of the Andean mountains are known that belong mainly to the Aleocharinae subfamily, e.g., *Atheta chimborazicola* at 4400 m or *Atheta atacazomontis* at 3890 m in the high montane paramos of Ecuador (Pace 2008). In regard to the leaf litter of montane forests of the Colombian Andes, two altitude zones were differentiated by staphylinid assemblages: one below approximately 1500 m and the other above 1500 m elevation (Gutièrrez Chacòn and Ulloa Chacòn 2006). High tropical mountains also seem to have a high rate of endemic staphylinid species, e.g., 39% are reported for the African Kilimanjaro (Hemp and Winter 1999).

7.4 Microhabitats

7.4.1 Dung-Inhabiting Staphylinidae

Coprobiontic Staphylinidae, e.g., *Platysthetus arenarius*, feed and reproduce in dung. Coprophilous Staphylinidae are not dependent on dung as a food source or reproduction habitat, e.g., *Philonthus* species are found in diverse decaying organic matter such as rotting plants, carrion, and fungi which contain *Diptera* larvae. In dung, *Philonthus*, *Tachinus*, *Megarthrus*, *Anotylus*, *Platystethus*, *Autalia*, *Aleochara*, *Atheta*, and *Oxypoda* are common and frequent European staphylinid genera (Koskela 1972). Staphylinidae are considered to be the most important predators in dung. Due to the diversity of species and high population densities, *Philonthus* species are the most important predators on eggs, larvae, and adults of Staphylinidae and other Coleoptera in dung, e.g., Scarabaeidae and Hydrophilidae.

Some of the dung-inhabiting Staphylinidae are considered invasive species in America, e.g., the European species *Philonthus rectangulus* and *P. longicornis* in Argentina and Chile. Larvae of the Staphylinidae have been also found in the dung of cows, horses, and/or sheep (Table 7.6).

7.4.1.1 Development and Overwintering

Three types of egg-laying behavior are differentiated for dung-inhabiting Staphylinidae (Fig. 7.13): (A) *Philonthus* species lay individual eggs under the cow pats between dung and soil, 1–4 cm from the cow pat margin; (B) *Platystethus arenarius* females build egg chambers inside the dung to deposit 10–20 eggs; (C) *Tachinus lignorum*, *T. rufipes*, and *T. laticollis* females move the tip of their abdomen with the fixed egg over the substratum (soil) to stick soil particles to the shell for camouflage to protect eggs against predators.

Table 7.6 Number of common larvae of Staphylinidae (ind. l^{-100}) living in dung of different farm animals in Northern Germany (according to Lipkow 2011)

	Dung of		
Species	Cattle	Horse	Sheep
Philonthus splendens F.	13.3	6.8	–
Philonthus cruentus Gmelin	–	–	8.7
Philonthus marginatus Stroem	7.0	9.8	7.8
Philonthus varians Payk.	4.7	2.0	1.7
Gyrohypnus angustatus Steph.	–	2.0	–
Oxytelus laqueatus Marsh.	5.5	2.9	1.7
Platystethus arenarius Fourc.	7.8	2.4	1.7

The time of larvae development from L1 to adulthood depends on the temperature and differs among species. Dung-inhabiting staphylinid species have a shorter development time than species that do not live in dung (Fig. 7.14). The development time of the investigated dung-inhabiting species (*Philonthus marginatus*, *P. varians*, *P. carbonarius*, *P. splendens*, and *P. cruentatus*) ranged from 18 to 25 days. The non-dung-inhabiting species (*Tachinus rufipes*, *P. rubripennis*, *P. cognatus*, *P. decorus*, *Tachyporus hypnorum*, *T. dispar*, *Atheta lividipennis*, *Anotylus rugosus*, *Stenus comma*, *Acylophorus wagenschieberi*, and *Drusilla canaliculatus*) have a longer development time, ranging from 21 to 49 days. The two regressions are significantly different according to the *t*-test ($t = 12.04, p < 0.01$).

Larvae of dung-inhabing Staphylinidae leave the dung for pupation. Pupation occurs under the dung heap after a chamber is built near the dung.

Dung-inhabiting Staphylinidae usually leave the dung for overwintering in forests, in hedges, and at meadow margins, e.g., *Philonthus splendens*, *P. marginatus*, *Tachinus laticollis*, *T. marginellus*, *Oxytelus laqueatus*, and *Autalia rivularis* (Renken 1956).

7.4.1.2 Settlement and Food Uptake

Diptera are the first insects that arrive at fresh dung for food uptake and reproduction. Shortly afterward, Hydrophilidae reach the dung and

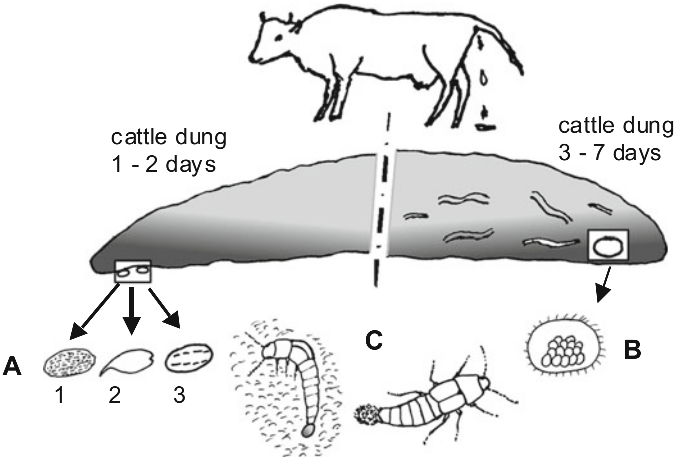

Fig. 7.13 Types of egg deposits in dung-inhabiting Staphylinidae: (**a**), eggs laid separately beneath the dung by *Philonthus splendens* (1), *P. marginatus* (2), and *P. varians* (3); (**b**), eggs laid in clusters into egg chambers in the dung by *Platystethus arenarius*; (**c**), eggs camouflaged with soil particles by *Tachinus* species (According to Lipkow 2011)

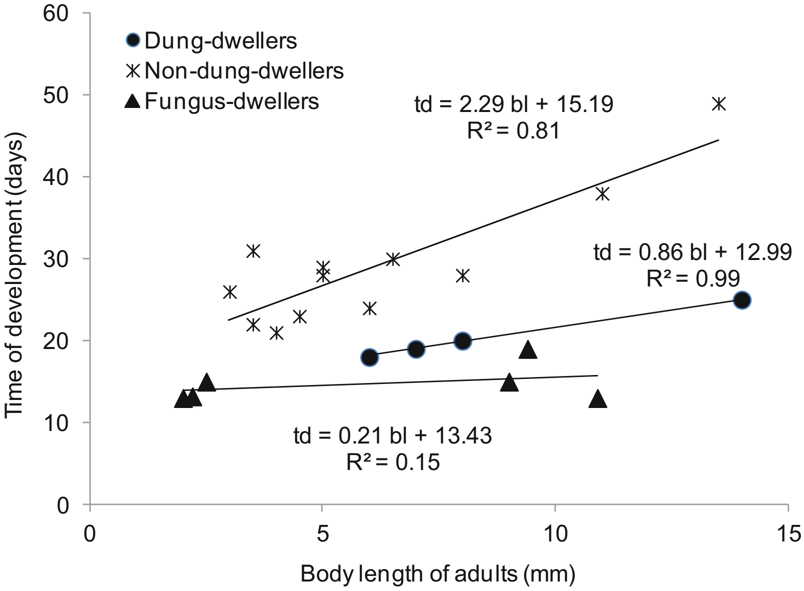

Fig. 7.14 Correlations between body length (bl) of adults and time of development (td) from egg to adult of dung-inhabiting, fungus-inhabiting, and soil surface-dwelling species under ~20 °C temperature conditions; data based on own research and from Staniec and Pietrykowska-Tudruj (2007), Eghtedar (1970), Wildschut et al. (1981), Lipkow (1966), Topp (1971), Weinreich (1968), Schminke (1978), Ashe (1981), Andresen (1984), Henley and Goodrich (1994), and Leschen and Allen (1988)

swim inside. In general, dung-inhabiting Staphylinidae arrive a few hours to a few days later. The time of arrival differs for species and depends on the dung conditions. According to observations in the field, most of the coprophilous Staphylinidae preferred 3–6-day-old dung: *Philonthus marginatus* preferred fresh dung; *P. splendens*, *Oxytelus laqueatus*, and *Platystethus arenarius* were found in fresh and 3–6-day-old dung; *P. fimetarius*, *P. albipes*, and *Anotyles tetracarinatus* preferred dung older than 7 days (Lipkow 2011). Most of the predatory Staphylinidae use tunnels of other dung beetles, e.g., *Sphaeridium*, *Cercyon* (Hydrophilidae), *Aphodius* (Aphodiidae), and larvae of *Diptera*, to enter and move in the dung.

Although *Oxytelus laqueatus* and *Platystethus arenarius* are considered to be coprophagous (Schlüter 1988), they are also found in other decaying matter. At present, a coprophagous feeding behavior is not verified. In contrast to the carnivorous *Philonthus* and *Tachinus* species, Oxytelinae do not feed on sliced larvae of *Tenebrio molitor* in the laboratory. The predator *Ontholestes murinus* waits near the dung heap to catch flies by running and grasping with the mandibles after landing. Petrenko (2013) observed that dung beetles are caught by *O. murinus* after they raise their hard elytra and open their vulnerable soft abdominal tergites. After catching the prey, the predatory rove beetles immediately disappear with the prey into the dung tunnels. *Philonthus* usually lands next to the dung. After landing, *Philonthus splendens* either disappears under the dung pat, e.g., for egg-laying, or roam on the pat surface. *P. splendens* can only walk on dried surfaces of cow pats. While walking on the pat, *P. splendens* searches tunnels made by the dung beetle *Sphaeridium*. After finding an entrance, *P. splendens* puts its head into the tunnel and either enters it or pulls the head back and continues searching for other tunnel entrances. After successful preying, *P. splendens* leaves the pat. Most of its prey, e.g., adults and larvae of dung beetles, small Staphylinidae, or larvae of flies, is found inside the dung. When the larvae of flies have disappeared from the dung for pupating in the soil, *Philonthus* species also disappear.

In Panama, the large Xantholini *Eulissus chalybaeus* (14–17 mm) and *E. rutilus* were observed to prey on the 5–7-mm-long Scarabaeinae *Canthon angustatus*, *C. lamprinus*, and the large *Dichotomius satanas*. Predation was probably inside the tunnels of *D. satanas* (Young 2011). The staphylinid *Leistotrophus versicolor* was observed roaming the neighborhood of a human dung pile and attacked the dung beetle *Canthidium cupreum* by grasping it with the mandibles (Noriega and Navarrete-Heredia 2013). *Philonthus*, *Tachinus lignorum*, and *T. rufipes* larvae have preoral digestion. They catch their prey with their mandibles, infuse digestion fluid into the food, and absorb the pulp (Lipkow 2011).

Philonthus and *Ontholestes* species have a specific mandible brush that may function as a filter to separate liquid and solid components of the food.

7.4.1.3 Dung-Inhabiting Staphylinidae and Biological Control of Pests

Predatory Staphylinidae, e.g., *Philonthus* species, are antagonists of the dung-inhabiting larvae of the horn fly *Haematobia irritans*, a pest of cattle (Cabrera Walsh and Chani-Posse 2003), and have already been used for biological control in Texas (Hunter et al. 1991). *Philonthus* species in Argentina have been documented as predators of dung-breeding flies that are assumed to be an invasive European species (Chani-Posse 2004).

Aleochara species are also antagonists of dung-breeding flies. Adults hunt on eggs and larvae of flies, whereas larvae are ectoparasitoids of fly pupae. The first larval instars actively search for host pupae, chew an opening, enter, and begin to feed. Subsequently, the entrance hole is clogged with fecal material. Pupation occurs either inside the host pupae or outside in cocoons. South African *Aleochara* species were introduced to Australia to control the buffalo fly *Haematobia irritans exiqua* (Wright and Müller 1989). Coprophilous Sarcophagidae (*Diptera*) are the most frequent hosts of *Aleochara verberans* in Argentina (Walsh and Chiani-Posse 2003).

7.4.1.4 Dung Preferences

Recent investigations show that Staphylinidae have no preference for dung of specific mammals (Lipkow and Irmler 2016).

In contrast to the many investigations of the relation of Staphylinidae to dung of domesticated mammals, e.g., cows and horses, few investigations have been made with the dung of wild mammals, e.g., *Anotyles* sp. preferred dung of Sika deer in coniferous forests in Southwest Japan (Yamamotu et al. 2014).

Many of the dung-inhabiting Staphylinidae inhabit pastures and woods (e.g., *Oxytelus*

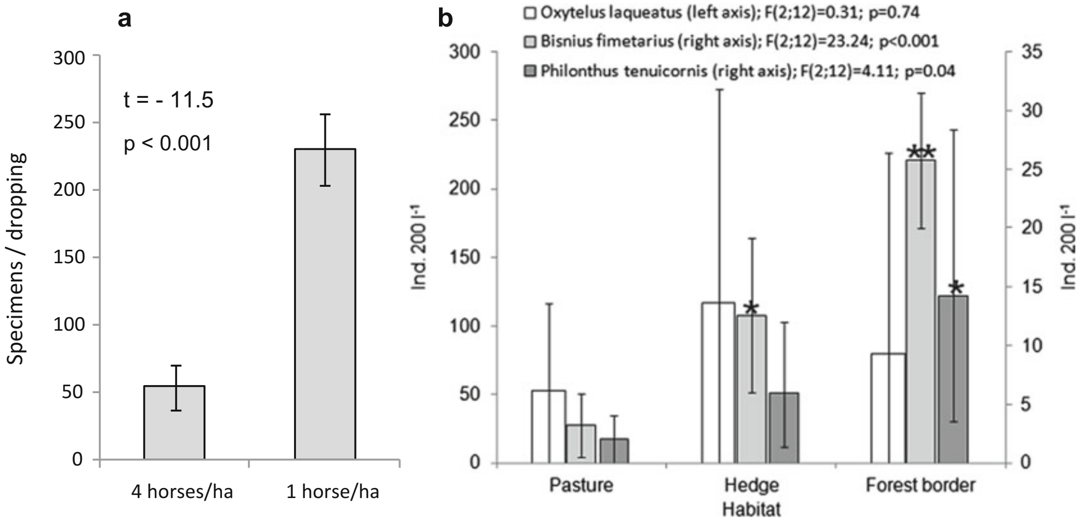

Fig 7.15 (**a**) Number of specimens on horse drops on pastures with different number of horses with results of *t*-test between means; (**b**) number (ind. l^{-200}) of three staphylinid species in horse dung; asterisks indicate significant differences with * $p < 0.05$ and ** $p < 0.01$

laqueatus) in equal abundance, but few species prefer woods, the border of woods, or hedges, e.g., *Tachinus pallipes*, *T. humeralis*, *T. proximus*, *Rugilus rufipes*, *Quedius scintillatus*, *Q. cinctus*, *Bisnius fimetarius*, or *Philonthus tenuicornis* (Fig. 7.15).

Abundance of Staphylinidae correlates with the density of dung droppings (Fig. 7.15). If only a few dung droppings were available on a pasture, more specimens of dung-inhabiting staphylinids were found on the individual droppings (Lipkow 2011).

7.4.2 Associations Between Staphylinidae and Fungi

7.4.2.1 General Traits

A general overview of life history and morphology of the mouthparts of fungus-dwelling Staphylinidae is published by Lipkow and Betz (2005). Associations with fungi, including mycophagy (fungus-feeding), are found in many subfamilies of Staphylinidae (Newton 1984). A clear distinction between saprophagy and mycophagy is difficult because both feeding items are mixed in wood and leaf decay. Fungi are probably a secondary feeding item because Staphylinidae, in general, are primarily predators (Thayer 2005). Shifts in feeding preferences are found between tribes and genera as well as in the same genus (e.g., *Sepidophilus*). Normally *Tachinus rufipes* (L) is a predator but can switch to feed exclusively on yeast (Protoascomycetidae) in laboratory conditions.

Interactions with fungi occur in each of the four subfamily groups in the form of mycophagy or of predation on other fungus-dwelling organisms (Scheerpeltz and Höfler 1948; Benick 1952; Thayer 2005). Fungivorous species are found in numerous subfamilies, e.g., Micropeplinae, Neophoninae, Habrocerinae, and Aleocharinae. In Aleocharinae larvae and adults of *Gyrophaena* Mannerheim, *Phanerota* Casey, and *Eumicrota* Casey obligatorily feed on spores of the hymenium of *Agaricales* and *Polyporales* (Andreesen 1984). Larvae and adults of *Placusa* Erichson and some species of *Homalota* Mannerheim feed on subcortical spores and hyphae (Ashe 1993). *Meronera* Sharp feed on surface hyphae. *Stictalia* Casey, *Pseudatheta* Cameron (Ashe 1993), *Pagla* Blackwelder, and *Polylobus* Solier are considered spore feeders (Betz et al. 2003), and *Oxypoda* Mannerheim feed on spores of agaricoid *Basidiomycetes* (Henneberg 2004). In the Tachyporinae subfamily *Sepedophilus* Gistel, *Tachinus* Gravenhorst, and *Coproporus* Kraatz are fungus feeders. In the Scaphidiinae and Oxyporinae subfamilies, e.g., *Scaphium* Kirby, *Scaphisoma* Leach, *Cyparium* Erichson, *Oxyporus* Fabricus, *Baeocera* Erichson, and *Scaphobaeocera* Csiki, respectively, feed on fungi (Betz et al. 2003).

A more general description of fungus-feeding and host associations is published by Schigel (2012). DNA gut content analysis of abundant Staphylinidae shows that the mycobiota in posterior gut extracts was dominated by Saccharomycetales and Sordariomycetes (Stefani et al. 2016).

Fleshy, short-lived mushrooms (*Agaricales*) are ephemeral microhabitats, similar to dung heaps, and can be used only for a few days. The beetles respond to these short-time food resources by colonizing the mushroom immediately after the opening of the pileus and by rapid larval development (Fig. 7.14). The development time of the fungus-dwelling species (*Phanerota fasciata*, *Gyrophaena joyioides*, *G. gentilis*, *Oxyporus stygicus*, *O. vittatus*, and *O. major*) from egg to adult ranges from 13 to 19 days and is almost independent from the size of the species. The difference from the soil-dwelling species is significant using the t-test (significance between the two regressions: $t = 39.3$, $p < 0.001$). Because pupation of both ecological groups occurs in the soil, the development of the pupae lasts nearly an equal amount of time (fungus dwellers, 9.7 ± 0.8 days; soil dwellers, 10.4 ± 1.8 days).

Hymenomycetales (macrofungi) with hymenial fruiting bodies, belonging to the *Basidiomycetes*, have been the focus of most investigations. Hence, special adaptations of fungus-breeding beetles are expected to be seen in specific life-history traits, such as short developmental time. Life-history traits in fungus-dwelling staphylinids have not been studied in detail. In long-living tree fungi (*Aphyllophorales*), the density of Staphylinidae is lower than in fleshy fungi (Krasutski 2010).

Little is known about the association between Staphylinidae and fungi in deeper soil layers and in decaying plant material, dung, or carrion (i.e., Myxomycetes, *Ascomycetes*, Fungi imperfecti).

Fungivorous Staphylinidae (e.g., *Oxyporus*, *Gyrophaena*, *Sepedophilus*) and some predatory or parasitoid Staphylinidae, e.g., *Bolitobius* and *Aleochara*, prefer young fresh mushrooms containing spores. In contrast, decaying mushrooms mainly attract predaceous Staphylinidae, e.g., *Tachinus*, *Philonthus*, *Ontholestes*, and *Atheta*. Predaceous Staphylinidae (e.g., *Aleochara*) found in mushrooms feed on the fungivorous larvae of flies (e.g., Anthomyiidae).

7.4.2.2 Life History

Gyrophaena

Most species of the Gyrophaenina prefer several species of mushrooms and are not restricted to feeding on single fungus species. When the preferred mushrooms are not available, less preferred mushrooms are used (Ashe 1984; Andreesen 1984). The Central European species *Gyrophaena joyioides*, *G. gentilis*, *G. affinis*, *G. fasciata*, and *G. nana* feed on a wide spectrum of fungi, whereas the feeding spectrum of *G. minima* and *G. bihamata* is narrower. In the laboratory, *G. joyioides* fed on fungal "tissue," if spores of the preferred fungus were not available (Andreesen 1984). According to Henneberg (2004), several species of *Gyrophaena* might coexist on the same host mushroom. He concludes that interspecific competition between different *Gyrophaena* species is probably more important for the larvae than for the adults. In dry summers with a low density of mushrooms, thousands of adults of *Gyrophaena* might live on a single "fruiting body." Despite the high density, their individual distances might be more or less uniform (Fig. 7.16). At high population densities, e.g., 25 ind. cm^{-2}, gyrophaenine beetles show aggressive behavior; they defend their small territory. Most gyrophaenine beetles leave a mushroom before the decaying process starts. It seems that the sex ratio of the species in the mushrooms is balanced. In Central Europe, *Gyrophaena* species have 2–3 generations per year.

Mating of *G. joyioides* Wüsthoff was observed at the base of the mushroom cup and lasted about 20 min. *Gyrophaena* species prefer

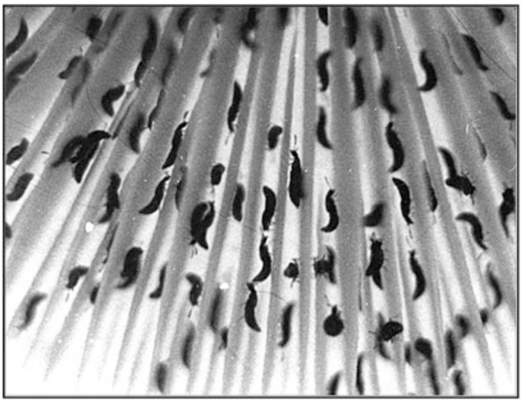

Fig. 7.16 Adults of *Gyrophaena joyoides* in the interlamellar space of a fruiting body of *Megacollybia platyphylla* (*Agaricales*) (Modified according to Andreessen 1984)

young fruiting bodies of *Agaricales* for oviposition and deposit their eggs in the hymenium when sporulation begins. The placement of egg deposition differs between *Gyrophaena* species and range between the distal part (*G. affinis*) to the proximal basis of the gill (*G. joyioides*). *G. minima*, *G. affinis*, and *G. joyioides* deposit individual eggs, whereas *G. joyioides* also produce clusters of three eggs. The eggs are covered with material from the periphery of the gills. *G. gentilis* is ovoviviparous. The first instar completely develops in the egg in the female body. Viviparity in *G. gentilis* seems to be an adaptation to the rapid decay of fungi as hosts (Andreesen 1984).

The development of the ovarioles and the maturation of the eggs seem to be induced after the female comes in contact with the mushroom (Henneberg 2004). The larvae feed almost continuously during the day and night. The development of the larvae of *G. joyioides* can be finished in just 1–2 days at 20 °C.

Eumicrota beetles, which prefer persistent polyporous fungi, have a longer larval development than *Gyrophaena* beetles, which prefer fleshy gilled mushrooms. The females of *Eumicrota* construct egg chambers at the ventral side of the hymenium of mushrooms. Mating takes place adjacent to the egg chamber. After oviposition, the female takes up the egg with the mandibles and places it in the egg chamber cleaned beforehand. The number of eggs per chamber varies between 5 and 24. Females of *Eumicrota* remain 5–6 days in the egg chamber. They groom the eggs and repel intruders such as older larvae, males, and other females (Ashe 1987).

Oxyporus

Some species of the New World Oxporinae prefer specific mushrooms out of a wide range of “acceptable” hosts. The larvae seem to be specialized to one or two species of mushrooms (Hanley and Goodrich 1994). Because of the large head with its long and crossing mandibles, entomologists assumed that *Oxyporus* species are predaceous; however, larvae and adults feed exclusively on the fungal tissue of *Agaricales* (Lipkow 1997). Fungal material chewed by the mouthparts is saturated with digestive fluid. Both larvae and adults digest their food preorally. Larvae begin feeding just minutes after leaving the egg. In *O. occipetales* Fauvel, both the first and the second instars last about 1 day, whereas the third instars need about 6 days (Goodrich and Hanley 1995). The third instars dig burrows into the soil to build pupal chambers. The pupal stage lasts 6 days.

Females of *O. japonicus* construct egg chambers in the stipe or cap of mushrooms (*Agaricales*). They pile up material of chewed fungus at the opening of the chambers after oviposition and cover the eggs with bits of chewed fungus. The young larvae presumably feed on this material. Females remain in the egg chamber and repel conspecific females and predaceous insects. Most fruit bodies contain only one egg chamber (Setsuda 1994). *O. germanus* have been found on various fleshy fungi (Hwang et al. 2002).

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