Corticolous arthropods under climatic fluctuations: compensation is more important than migration

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Animals can cope with fluctuating climates by physiological tolerance, tracking of climatic fluctuations (migration) and compensatory redistribution among (micro)habitats (compensation). Compensation is less demanding and thus more important than migration at large geographic scales. It is not clear however which strategy is more important at the small scale of a microhabitat landscape. I investigated how six arthropod species (Collembola, Oribatei, Psocoptera, Isopoda) respond to microclimatic fluctuations at the surface of exposed tree trunks. Across a nine-month period I characterized the microclimatic zonation of 299 trunks, and focally sampled the arthropods from different microhabitat types (different cryptogam species and bark crevices) within different microclimatic zones. I found that compensatory microhabitat-use was a general phenomenon. The distribution of all species across microhabitats was influenced significantly by ambient microclimate. Also, the arthropods' microhabitat use changed throughout their ontogeny, and microhabitats were used even if they were rare. Most interestingly, the arthropods responded to microclimatic fluctuations primarily by redistribution among microhabitats and less by fluctuations of overall abundances across all microhabitats. Hence compensation was more important than migration. The animals moved for centimeters to decimeters rather than for decimeters to meters; they perceived and utilized their environment primarily at the finest, but also most complex scale. This has implications for the resilience of arthropod populations, their interactions with cryptogams and the turnover of species between macrohabitats.

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Animals can employ three major strategies to cope with climatic changes (Southwood 1988, Cloudsley-Thompson 1991, Ricklefs and Miller 2000). The first strategy is to tolerate or resist the climatic change physiologically (Worland and Convey 2001). The second is to track the climatic change by large-scale migrations (Holbrook et al. 2002). The third strategy is to compensate the climatic change by a redistribution among (micro)habitats (Allee et al. 1949, Hengeveld 1990, Bos and Carthew 2003). These three strategies correspond to fundamental differences in the life history of species and may thus be a

basic ingredient of the biological diversity on earth (Southwood 1988).

The relevance of the second and third strategy may be scale-dependent. At large, geographic scales tracking of climatic conditions by migration is very costly and often requires fundamental physiological and morphological adaptations (Ricklefs and Miller 2000). Compensatory shifts among habitats are much easier to accomplish. The distances to be covered are smaller for a factor of 10^6 – 10^7 (e.g. a few meters vs thousands of kilometers), and orientation is often comparatively easy as only a

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vertical redistribution between habitat strata is needed. Hence, at the scale of macroclimatic fluctuations animals should not take the risk to migrate when suitable habitats are available. Indeed, most species seem to compensate (Hengeveld 1990), even though some species with apparently similar habitat requirements do migrate (Bezzel 1985). At smaller scales, such as microclimatic fluctuations within a habitat, migration becomes less demanding. For instance, the distance between the sun-exposed and sun-shaded face of a rock may be only 10–100 times larger than that between a rock microhabitat that permits to compensate for shade and one that permits to compensate for sun exposure. (Microhabitats may be defined as structures with distinct food sources and boundary-layer climates, which are small enough that an animal can enter and leave them within only a few minutes.) At the same time compensatory redistribution may become more demanding at small scales as the microhabitats are often arranged in a complex, mosaic-like microlandscape (Lancaster 2000). Simple vertical movement is rarely sufficient to find the appropriate type of microhabitat. Hence, at a small scale, within a habitat, species might respond to (micro)climatic fluctuations by migration (Prinzing 2001, Blouin-Demers and Weatherhead 2001) rather than by compensatory redistribution within the microhabitat landscape (Prinzing 1997, Jacob and Brown 2000 for individual species).

In fact, it is not clear whether, within a habitat, compensatory redistribution among microhabitats plays a significant role. It is not clear whether in a given community the majority of species is capable of responding to microclimatic fluctuations, or to ontogenetic shifts in microclimate tolerances, by compensatory microhabitat use (Silleit and Foster 2000, Martin 2001 for individual species). Nor is it clear whether a given microhabitat can still be used when it is rare and thus difficult to find. Obviously, there are many counter examples of species that fail to compensate abiotic fluctuations by redistribution among microhabitats, including many highly mobile species (Schwerdtfeger 1977, Bezzel 1985, Valimaki and Itamies 2003 for beetles, birds and butterflies). Most crucially, it has to my knowledge never been studied whether species respond to microclimatic fluctuations rather by compensation (redistribution among microhabitats) or by migration (tracking of microclimates). This is an important question because local populations of compensatory species would be much more resilient to microclimatic fluctuations than local populations of migratory species.

Arthropods that colonize the surface of exposed tree trunks, such as Collembola, oribatid mites and Psocoptera, face dramatic microclimatic fluctuations owing to the direct exposure of the trunks to ambient weather conditions. These fluctuations affect also the

availability of food, because most of the food sources – algae and lichens – become hard and unpalatable when they dry out (Seyd and Seaward 1984, Prinzing and Wirtz 1997). The bark-dwelling arthropods do not seem to be specially adapted to tolerating or resisting the unfavorable conditions, given that none of these species is specialized in physiologically extreme habitats, they all also occur, e.g., in the litter of a shaded forest (Den Boer 1961, Nicolai 1985, Büchs 1988, Wunderle 1992, Ponge 1993). Moreover, few species show adaptive traits such as a strong sclerotization, extremely long legs and hairs, flexible dormancy, resistance to waterfilms or the ability to construct shelters (Delamare-Deboutteville 1951, Travé 1963, Shachak 1980, Cloudsley-Thompson 1991, Prinzing and Wirtz 1997). Hence, physiological responses cannot fully explain how the arthropods cope with the microclimatic fluctuations at exposed tree trunks. Responses of birth and death rates are also unlikely to play a role, as most microclimatic fluctuations are much shorter than the animals' time of generation. Long-term seasonal fluctuations of the ambient mesoclimate only have little impact on trunk microclimate (Prinzing 2003a). Hence, behavioral responses, such as migration and compensation, may be important for arthropods to cope with the microclimatic fluctuations at the trunks.

Tree-trunk arthropods can be used as a model system to investigate the importance of compensatory habitat-use at a small scale. The bark of the trunks is characterized by a complex and diverse microlandscape of microhabitats such as different cryptogam species and crevice types (Halaj et al. 2000, Prinzing 2003b). The microhabitats are differentiated at a scale of centimeters to decimeters while the microclimatic fluctuations operate at a scale of decimeters to meters (Nicolai 1986). Hence, I investigated how arthropods at the surface of exposed tree trunks move within this complex microlandscape under fluctuating conditions of temperature, air humidity and water cover. I asked three questions: is the majority of species capable of responding to microclimatic fluctuations, or to ontogenetic changes in microclimate tolerance, by compensatory microhabitat use? Are the microhabitats still used when they are rare? And, most importantly, do the species respond to microclimatic fluctuations rather by compensatory redistribution among microhabitats, or by migratory tracking of microclimates?

Methods

Material

The study was conducted in six areas in northern Germany (Schleswig-Holstein) near the Baltic Sea from August 1993 to April 1994 (details in Prinzing 1997). In each area I investigated large, solitary trees characterized

by a large diversity of microhabitats (≥ 2.5 m circumference at a height of 1.5 m, ca 100–140 yr old), e.g. along roadsides or in meadows. On each tree, I investigated microhabitats at a height of 0.8–1.8 m (see below). The number of trees sampled per month was 60, 47, 41, 38, 29, 21, 19, 36, and 8. I sampled 80 of the trees at night, because the animals are active also during the night (Mayer 1957, Bauer 1979). I investigated trees of different species: 120 oaks *Quercus robur*, 42 lindens *Tilia* spp.; mainly *platyphyllos*, 87 beeches *Fagus sylvatica* and 50 ashes *Fraxinus excelsior*. During most months each tree species was sampled in each area. Investigation of several tree species increased the number of arthropod species for which sample sizes were sufficient for statistical analysis. However, none of the arthropod species was completely absent from any of the tree species, all microhabitat types were present at each tree species, and the general relationship between trunk microclimate and ambient mesoclimate hardly depended on the tree species (Prinzing 2001).

I considered eight microhabitat types (Fig. 1): 1) radial crevices (always perpendicular to bark scales and running inwards from the bark surface; $n=877$); 2) vertical crevices (situated between bark scales; $n=269$); 3) the shrub-like lichen species *Evernia prunastri* ($n=353$); and the following crusts: 4) *Lecanora expallens* (Lichenes;

$n=395$); 5) *Pertusaria albescens* (Lichenes; $n=138$); 6) *Lepraria incana* (Lichenes; $n=627$); 7) algal crusts (*Pleurococcus* sp.; $n=1060$); 8) sparse algae/hyphae covers which are hardly recognizable with the naked eye ($n=144$). Other cryptogam species never covered $>5\%$ of a trunk's surface and were therefore not recorded. These microhabitats did not overlap: cryptogams did hardly grow into the crevices. These different microhabitat types provide different living conditions for the animals (Discussion, Prinzing 1997, Prinzing and Wirtz 1997). Sample sizes differed among microhabitat types because the frequency of the microhabitats differed, e.g. between different microclimatic conditions (Wirth 1980). I took this variation of microhabitat frequency into account when I analyzed the data (see below). Microhabitat types 5–8 turned out to be very sparsely colonized by each of the arthropod species (Prinzing 1996), and were thus pooled as "other crusts" in the analysis.

In the present investigation I focused on the six most abundant arthropod species which were amenable to statistical analysis: *Orchesella cincta*; *Entomobrya nivalis*; *Entomobrya albocincta* (all Collembola); *Cerobasis guestifalica* (Psocoptera); *Carabodes labyrinthicus* (Oribatei) and *Porcellio scaber* (Isopoda). Identification and nomenclature followed Sellnick and Forsslund (1952), Gisin (1960), Günther (1974), and Gruner (1966). All these arthropod species graze on cryptogams (Jentsch 1940, Den Boer 1961, Bauer 1979, Wunderle 1992, Prinzing and Wirtz 1997).

Field methods

I studied the full range of microclimatic conditions at a trunk at a given moment. For this purpose I optically divided each trunk into "microclimatic zones" (Nicolai 1986, Stoutjesdijk and Barkman 1992). I first subdivided the trunk into trunk faces according to their momentary exposure to wind, sun and precipitation and then further subdivided these trunk faces into microrelief zones according to their exposures (see Prinzing [2001] for a detailed description of the procedure). Within each of these microclimatic zones I measured the temperature and humidity and sampled all arthropods from the microhabitat types present. Below I briefly describe the sampling procedure, for more details see Prinzing (2001).

In the centre of each microclimatic zone I measured temperature (thermistor, Gultan Tastotherm D 700, 5 s response time) and air humidity (di-electrical sensors: Valvo-hygrometer, sensor with both cap and ventilator detached; after February 1994: Rotronic hygrometer A1, with same precision and method, identical results in parallel measurements, but faster response). I measured at a height of ca 2 mm from bark and considered only bark that was covered by algae. I took several

Fig. 1. Structure of the microhabitat types considered. Upper and lower parts are at different magnifications (see scale bars). The more dense the lines and dots the more dense and stiff the thalli. In *Evernia prunastri* one branch is drawn in cross section. *Evernia prunastri* thalli can vary strongly in size.

precautions to avoid bias from minute-by-minute fluctuations of temperature (Stoutjesdijk and Barkman 1992; see also Prinzing 2001): 1) I took replicate temperature measurements sequentially at five positions over a total of ca 100 s within each trunk face and calculated the average. 2) At each position, I measured the different microrelief zones within a radius of 5 cm. 3) I recorded temperature after it approached a constant level. 4) I avoided taking measurements when the sun was briefly either covered by clouds during sunny weather or not covered during cloudy weather; and I also avoided taking measurements when precipitation was starting or ceasing.

In each microclimatic zone I focally sampled the animals in the microhabitat types present with a 10 × hand lens (Mayer 1957, Prinzing 1997). I defined plot size according to surface area because the arthropods feed on crusts on this surface or on thin layers below it (Travé 1963, Prinzing and Wirtz 1997). I measured the surface area with a 10 × hand lens. Each field of view equaled 1.8 cm² and each microhabitat sample consisted of 10 fields of view covering 18 cm² of microhabitat surface in total. I selected the fields of view with a grid, with random placement within the grid cells. I examined the inner surfaces of cavities according to the procedure given in Prinzing (1997). In short, the dark cavities of radial crevices and within thalli of *Evernia prunastri* were illuminated and vertical crevices were opened with a knife. By additional sampling with a distance lens I made sure that no animals were lost by chasing them away from bark surface microhabitats into cavity microhabitats (Prinzing 1997).

Approximate individual lengths were estimated to three size categories in the field for most individuals of the Collembola *O. cincta* (ca <1.7/ <3/ >3 mm), *E. albocincta* and *E. nivalis* (ca <0.8/ <1.7/ >1.7 mm), and for the Psocoptera *C. guestifalica* (ca <1.2/ <1.7/ >1.7 mm). These individuals were termed, “juveniles”, “middle-aged” and “adults”, respectively (Joosse et al. 1973, Günther 1974, Prinzing unpubl.). In *C. guestifalica* I additionally differentiated “hatchlings” (<0.6 mm), which were found very frequently at the bark. These classifications were based on knowledge of the complete range of body sizes from laboratory cultures. Age classes were not differentiated in *C. labyrinthicus* and in *P. scaber*. In *C. labyrinthicus* too few juveniles had been sampled, and in *P. scaber* it was often difficult to survey the size of the individuals because they clustered in large and dense groups.

Within each microclimatic zone I also estimated the cover of the cryptogam microhabitats on a rank scale (<20%; 20–<50%; >50%; Prinzing 1997). I did not estimate the cover by crevice microhabitats because this was not feasible without completely peeling off the outer bark.

Data analysis

I first analyzed for each arthropod species how microclimate affects the distribution of arthropods across microhabitat types. The dependent variable of the models was the number of arthropods per microhabitat sample, i.e. their abundance × 18 cm⁻². Theoretically, one might wish to use the relative abundance as the dependent variable, i.e. the abundance of arthropods on a given microhabitat type within a given microclimatic zone divided by the total abundance across all microhabitat types. But this was not practicable because the microclimatic zones often differed in their microhabitat composition (see above).

The independent variables were: A) Microhabitat type, with five categories: *Lepraria incana*, *Evernia prunastri*, radial crevices, vertical crevices; and other crusts (cryptogam crusts other than *Lepraria incana*; see above). B) Four microclimatic variables: 1) temperature [°C]; 2) saturation deficit [kPa; square-root transformed]; 3) water cover of the bark [1 = present; 0 = absent, because it was not raining; -1 = absent even during rainy weather, when other parts of the trunk were covered by water]; and 4) relative temperature [°C], i.e. the temperature difference between the respective microrelief zone and the adjacent microrelief zone of the same trunk face. I included relative temperature because an animal may respond to the local gradient of temperature, rather than its absolute value (Madge 1965). The relative temperature of a microclimatic zone also reflected its relative saturation deficit (r = 0.89). Each of these four variables had been recorded in each microclimatic zone of a trunk. So there was one sample of a given microhabitat type for a given combination of microclimatic conditions on a given tree. C) Tree as a “block factor” (Underwood 1997), because abundances may differ between trees. The interactions between microhabitat and the four microclimatic variables quantified the effect of microclimate on the distribution of arthropods among microhabitat types.

I applied a Generalized Linear Model approach (Crawley 1993, Anon. 1999). This permitted to account for a skewed distribution of data by choosing an appropriate error structure and for a non-constant relationships between independent and dependent variables by choosing an appropriate link function. With species abundances as dependent variable, as in the present investigation, a Poisson error-structure combined with a log link-function is the classical choice (Crawley 1993, Anon. 1999). However, additional “model criticism” is strongly recommended (Crawley 1993), i.e. the exploration whether alternative error structures or alternative link functions, or a transformation of the data, result in a more normal or more homoscedastic distribution of residuals (Crawley 1993). Homoscedasticity was tested by plotting residuals against predictions (Crawley 1993). I found that the

Poisson/log model was indeed always the best choice, but for *C. labyrinthicus* I found that abundances had to be root-transformed to fit the model. Nevertheless, different models mostly yielded similar results.

I also analyzed whether the age of the arthropods (reflecting their microclimate tolerances) affects their distribution across microhabitats. For each arthropod species, I pooled all observations and compared the age-class composition on each microhabitat type to that on the remaining microhabitat types, using a χ^2 test. To account for the multiple comparisons across five microhabitat types I used a sequential Bonferroni correction (Quinn and Keough 2002).

Second, I explored how the utilization of a microhabitat type by an arthropod species changes with the commonness of the microhabitat. In the field I had assessed the commonness of the cryptogam microhabitats into three classes (see above). I selected the three most frequently used cryptogam microhabitats for further analysis. Given that this was only a fraction of the total microhabitat mosaic; the rarity of one cryptogam microhabitat did not imply commonness of the other two cryptogam microhabitats. I quantified the utilization of a cryptogam microhabitat by an arthropod species as its average abundance on that cryptogam divided by the average abundance across all eight microhabitat types. Then, I graphically explored whether the utilization of a cryptogam declined with its commonness. None of the arthropod species showed such a declining utilization in more than one cryptogam species (Results) and hence further statistical tests were superfluous.

Third, I analyzed whether species responded to microclimatic fluctuations rather by compensatory redistribution among microhabitats, or by migratory tracking of microclimates. For each species I calculated three Generalized Linear Models – one that only included tree and microhabitat type as independent variables, a second including additionally the four microclimate variables, and a third including additionally the four microhabitat $\times$ microclimate interactions. I then quantified the effect size r of the three models as the square root of the explained variances, which was then Fisher's z -transformed (Rosenthal 1984). The difference between the effect sizes (calculated as in Rosenthal 1984) of the [tree+microhabitat] model and the [tree+microhabitat+microclimate] model was then a measure of the degree to which species responded to microclimatic fluctuations by migration. The difference between the [tree+microhabitat+microclimate] model and the [tree+microhabitat+microclimate+microclimate $\times$ microhabitat] model was a measure of the degree to which species compensated microclimatic fluctuations by redistribution among microhabitats. Finally, this measure of compensation was compared to the above measure of

migration within each species, using a pairwise t-test and a Wilcoxon rank test (Quinn and Keough 2002).

Results

Microclimate significantly modified the distribution of all species across microhabitats (Table 1). In *E. nivalis*, *E. albocincta*, and *O. cincta* microclimate (marginally) significantly modified the utilization of four microhabitat types. In *C. guestifalica* and *P. scaber* microclimate modified the utilization of three microhabitat types, and in *C. labyrinthicus* only of two (Table 1). Two microclimatic variables, temperature and saturation deficit, affected the distribution of all six species among microhabitats. Water cover was relevant only in *O. cincta*, *E. nivalis*, *E. albocincta*, and *C. guestifalica*. Temperature zonation was only rarely relevant. The extent to which microclimate modified the distribution of species among microhabitats is obvious also from an exemplary graphical analysis (Fig. 2). Microhabitat use also changed throughout the ontogeny of all species analyzed (Fig. 3; Discussion).

Microhabitats were utilized even if they were rare (Fig. 4). Only in one of the fourteen comparisons did I find that the utilization of a microhabitat type by an arthropod species declined consistently with the commonness of the microhabitat type (*E. albocincta* on *Evernia prunastri*; Fig. 4). But even this decline was only weak.

In all six arthropod species a larger part of the variance in abundance could be explained solely on the basis of tree, microhabitat, microclimate and the interaction between microclimate and microhabitat. For three of the species >50% of the variance could be explained (Table 2). The most important factors were tree and, in particular, microhabitat. Hence, variation in structural living conditions was more important than microclimatic fluctuations (see also Fig. 2).

The interaction between microclimate and microhabitat type accounted for a (much) larger part of the variance of arthropod abundances than the direct effect of microclimate. Only in *E. albocincta* was microclimate about as important as the microclimate $\times$ microhabitat interaction (Table 2). Hence, effect sizes of microclimate $\times$ microhabitat were significantly larger than effect sizes of microclimate per se (tests in Table 2). In other words, most species responded to microclimatic fluctuations primarily by a compensatory redistribution among microhabitats, less by migratory tracking of microclimates across all microhabitats.

Discussion

In the present investigation I analyzed how arthropod species respond to microclimatic fluctuations operating

Table 1. Interaction between microclimate and the distribution of arthropods among microhabitats analyzed by Generalized Linear Models. For complete model specification see Methods. Signs and score statistics are given. Significant values ($p \leq 0.05$) are in bold, marginally significant values ($0.05 < p < 0.1$) are underlined. Tests for the fifth microhabitat type (the very rarely colonized "other crusts") had to be omitted to avoid redundancy. N values range from 940 to 1980, reflecting the unequal number of trees colonized by the respective species. See Fig. 2 for a graphical presentation and Table 2 for explained variances.

Species	Microhabitat type	Interaction with microclimatic variables				
		Saturation deficit	Temperature	Warming of microrelief zone	Water cover	
<i>O. cincta</i> (Collembola)	<i>Lepraria incana</i>	—	0.11	—	0.88	
	<i>Evernia prunastri</i>	—	0.41	+	1.36	
	Radial crevices	—	3.41	—	0.05	
	Vertical crevices	+	2.34	+	2.88	
<i>E. nivalis</i> (Collembola)	<i>Lepraria incana</i>	—	16.14	+	0.57	
	<i>Evernia prunastri</i>	+	5.65	+	0.13	
	Radial crevices	+	3.09	—	0.56	
	Vertical crevices	+	0.20	—	2.95	
<i>E. albocincta</i> (Collembola)	<i>Lepraria incana</i>	+	0.04	—	0.03	
	<i>Evernia prunastri</i>	+	0.04	+	0.40	
	Radial crevices	—	7.09	+	0.00	
	Vertical crevices	+	7.35	+	0.13	
<i>C. guestifalica</i> (Psocoptera)	<i>Lepraria incana</i>	—	0.72	—	0.34	
	<i>Evernia prunastri</i>	—	1.72	—	0.03	
	Radial crevices	+	14.34	—	0.06	
	Vertical crevices	+	1.15	+	0.69	
<i>C. labyrinthicus</i> (Oribatei)	<i>Lepraria incana</i>	—	6.89	+	0.68	
	<i>Evernia prunastri</i>	—	1.21	—	1.51	
	Radial crevices	—	0.00	+	0.00	
	Vertical crevices	+	5.16	+	0.33	
<i>P. scaber</i> (Isopoda)	<i>Lepraria incana</i>	—	9.03	+	3.64	
	<i>Evernia prunastri</i>	+	4.48	—	19.14	
	Radial crevices	+	2.10	+	1.54	
	Vertical crevices	+	7.79	+	8.62	
		+			1.50

at short temporal scales, much shorter than the animals' generation time, and small spatial scales (bark micro-relief zones, trunk faces, whole trunks; Prinzing 2003a). I found, first, that all species were capable of responding to microclimatic fluctuations by compensatory redistribution among microhabitats. Moreover, the species also responded to ontogenetic changes of microclimate-tolerances by redistribution among microhabitats. These ontogenetic changes in microhabitat use did not reflect phenological changes in the occurrence of juveniles and adults throughout the year. Species with very similar changes in microhabitat use (*E. albocincta* vs *C. guestifalica*; *E. nivalis* vs *C. guestifalica*) showed very different phonologies (Prinzing 1996, 1997), and vice versa (*E. albocincta* vs *E. nivalis*). Second, I found that the utilization of microhabitats did not decline with the commonness of the microhabitats. Compensatory redistribution among microhabitats was thus even feasible when certain types of microhabitats were rare. Third, and most interestingly, I found that species responded to microclimatic fluctuations primarily by compensatory redistribution within the mosaic-like landscape of microhabitats rather than by migratory tracking of microclimatic fluctuations. The animals thus moved for centimeters to decimeters rather than for decimeters to meters. Thus, the overall abundances of species across all microhabitats were relatively resilient to the drastic microclimatic fluctuations at the surface of the solitary tree trunks.

The results might suffer from a "conspicuousness bias". By retreating into the deeper parts of cavities animals in radial crevices and in *Evernia prunastri* might become inconspicuous and thus overlooked. (This is not possible in the remaining, flat microhabitats.) This bias should be most relevant in animals that can retreat into deeper parts of cavities owing to their small body size, and in animals that must retreat into deeper parts of cavities because of high microclimatic stress (Willmer and Unwin 1981). However, small animals (*C. labyrinthicus* and juveniles of other species) were not generally less abundant in radial crevices and *Evernia prunastri* than large animals (Figs 2 and 3; Prinzing 2003b). Nor were animals that suffer high microclimatic stress due to extreme temperatures or saturation deficits less abundant in radial crevices and *Evernia prunastri* than other animals (Table 1). Overall, the conspicuousness bias did not seem to be relevant.

Fig. 2. Effect of saturation deficit (≤ 100 Pa vs > 100 Pa) on the distribution of species among microhabitats. Microhabitats are li, *Lepraria incana*; oc, other crusts; ep, *Evernia prunastri*; rc, radial crevices; and vc, vertical crevices. Average abundances and standard errors are given. See Table 1 for sample sizes and for the complete, multivariate analyses. These complete analyses show that in each species the utilization of certain microhabitats increases or decreases at least marginally significantly with saturation deficit.

Fig. 3. Percentages of age-classes of arthropod species in different microhabitat types. Black/grey/white/striped indicates "adults"/"middle-aged"/"juveniles"/"hatchlings"; n, number of animals. Microhabitats are li, *Lepraria incana*; oc, other crusts; ep, *Evernia prunastri*; rc, radial crevices; and vc, vertical crevices. The age-class composition for each species on each microhabitat type was compared with those on all other microhabitat types pooled; +, *, ** indicate p values of <0.1; 0.05; and 0.01 (after sequential Bonferroni correction); marked on the age class with the highest χ^2 value. Age-class compositions were also compared across all microhabitats together, yielding $p=0.073$ for *O. cincta*, and $p<0.001$ for the remaining species.

The sampling period was slightly biased towards the cold season, no samples were taken in May, June and July. This raises the question whether the results are also representative for the warmest season (from June to September). In particular, during the warmest season arthropods might be more active and might thus be more inclined to migrate in response to microclimatic fluctuations than to compensate. However, three lines of evidence indicate that such a bias is unlikely. First, arthropod activity might not be higher during the warmer season because the high temperatures are correlated to high saturation deficits which actually reduce arthropod activity (Poinsot-Balaguer 1976). Second, migratory tracking of microclimatic fluctuations might become difficult during the warmer season due to accelerated microclimatic fluctuations reflecting the increased input of solar energy and, given the dry substrate, the low loss of this energy through evaporation or substrate heat flux (Lawrey 1991). Third, throughout the period investigated, I found that species that were most abundant during the warmer season (*C. guestifalica*, *E. nivalis*) did not display a larger tendency to migrate than other species. Overall, it is unlikely that the partial lack of data from the warmer season has biased the results in favor of compensation as compared to migration. The results appear to be representative also for the warmer season.

The present study focused on responses of species to microclimatic fluctuations, changes that arthropods can track, or compensate, by redistribution across the trunk surface. This brings up the question what happens in response to fluctuations of the ambient mesoclimate. I have shown elsewhere that species respond to fluctuations of the mesoclimate (e.g. weather condition, daytime, temperature measured at 2 m distance from the trunks) to a similar extent as to microclimatic fluctuations (Prinzinger 2001). It is thus likely that compensation is more important than migration also in responses to fluctuations of the mesoclimate. In fact, this is to be expected. With an increase of the spatial scale of climatic fluctuations, the distances to be covered by migratory tracking of climates increase overproportionally, and hence migration becomes increasingly difficult (Introduction). Nevertheless, it should be noted that such large-scale migrations do occasionally occur, e.g. between trunks and litter (Bauer 1979).

The observed redistribution between microhabitats did indeed compensate the following stress factors. Desiccation. During dry conditions all species increasingly used either of the cavity microhabitats, in particular the vertical crevices and *Evernia prunastri*, and avoided the crust *Lepraria incana*. Moreover, juveniles, being the stage most sensitive to desiccation (Verhoef and Witteveen 1980), were often overrepresented in vertical crevices (Fig. 3). These redistributions

Fig. 4. Relationship between the commonness of three cryptogam microhabitats and their utilization by arthropods. Commonness is quantified on a rank scale based on the area covered by the microhabitat in the respective microclimatic zone of a trunk. Utilization by arthropods is quantified as the average abundance of the arthropod species on the respective microhabitat type divided by the average abundance across all eight microhabitat types (Methods). For some species I omitted one or two microhabitat types because I could not quantify the utilization for one of the commonness categories (simply, the total abundance across all microhabitats was zero).

clearly reduced the exposure to desiccation (Lewis 1962, Prinzing and Wirtz 1997, Prinzing 1999).

Chill. During low temperatures most species used crevices which were indeed sheltered from hoar frost (Allmen and Zettel 1982, Prinzing unpubl.). *Carabodes labyrinthicus* additionally increasingly used *Lepraria incana*, in which it dug mines which can also provide shelter from frost (Kershaw 1985).

Table 2. Effect of microclimate on the total abundance of species, and on their distribution among microhabitats. The first column gives the proportion of the total variance of species abundances that can be explained solely by tree and microhabitat, without invoking microclimate. Columns two and three give the portion of the remaining variance that can be explained by including the microclimatic variables, and the microclimate $\times$ microhabitat interactions, into the model. The last two columns give the corresponding effect sizes as z-transformed r values (Methods). Pairwise comparison show that effect sizes of microclimate are significantly smaller than of microclimate $\times$ microhabitat ($n = 6$; Wilcoxon rank test: $Z = 2.201$; $p = 0.0277$; paired t -test $t = -3.60$; $p = 0.0155$). Hence, species respond to microclimatic fluctuations by redistribution among microhabitats (compensation) rather than by shifts of total abundance across all microhabitats (migration).

Species	Variance explained by tree and microhabitat	Portion of the remaining variance explained by		Effect sizes	
		Microclimate	Microclimate $\times$ microhabitat	Microclimate	Microclimate $\times$ microhabitat
<i>O. cincta</i>	0.63	0.00	0.13	0.04	2.21
<i>E. nivalis</i>	0.54	0.03	0.11	0.57	2.06
<i>E. albocincta</i>	0.25	0.11	0.10	3.50	3.21
<i>C. guestifalica</i>	0.32	0.01	0.14	0.24	3.17
<i>C. labyrinthicus</i>	0.26	0.00	0.07	0.00	1.36
<i>P. scaber</i>	0.60	0.11	0.21	1.72	3.59

Drowning. When the surrounding trunk was covered with a waterfilm species that are sensitive to waterfilms (*E. nivalis*, *E. albocincta*, *O. cincta* and *C. guestifalica*; Prinzing and Wirtz 1997) used the three microhabitats that provide shelter from inundation: vertical crevices, inner cavities of *Evernia prunastri* or the hydrophobic crusts of *Lepraria incana*. Radial crevices, which become very quickly inundated by a waterfilm (unpubl.), were avoided.

Food. Juveniles with their weak mouthparts overproportionally used *Lepraria incana* the single cryptogam that remains soft when it dries out (Wirth 1980).

These physiological impacts may in fact be the major determinants of microhabitat use in the bark-dwelling arthropods; impacts at the population or the community level may be less relevant. First, several experiments on oribatid mites, Collembolans or Psocopterans demonstrate that even a drastic manipulation of interspecific competition does not induce a consistent shift in microhabitat use (Broadhead and Wapshere 1966, Anderson 1978, Faber and Joosse 1993, but see Broadhead 1958). Moreover, on theoretical grounds Schindler (1988) and Southwood (1988) argue that in most ecological systems, population- or community-level impacts rarely determine the utilization of habitat patches provided that these patches are much smaller than the animals' range and that patch quality fluctuates throughout the animals' life (but see Thomson et al. 2002). Both is clearly the case for the patches of microhabitats on tree bark.

The observed compensatory microhabitat use of the individuals obviously increased the resilience of the total populations on the trunks to microclimatic fluctuations. Moreover, the compensatory microhabitat use may also be responsible for two distinct patterns at the community level:

1) Low species turnover between habitats and landscapes (β - and γ -diversity; Pianka 1988). Compensatory redistribution among microhabitats may enable an

arthropod species to colonize habitats with drastic microclimatic fluctuations. An arthropod species may for instance expand its habitat range from the sheltered litter layer or the shaded bark of forest trees to the exposed bark of solitary tree trunks. Such a wide habitat range of species results in a low turnover of species between habitats and between landscapes (Chust et al. 2003). Forested landscapes, for instance, may share many species with park-like landscapes. In fact, low species turnover is typical for Collembola and oribatid mites (Anderson 1977). This pattern has been explained as an artifact of incorrect habitat definition by researchers (Anderson 1977). However, I suggest that the low species turnover of Collembola and oribatid mites may be real and may be explained by compensatory redistribution of the individual animals at the microhabitat scale.

It should be noted that for several other, more aggregated microarthropod species such as soil-dwelling Collembola, low species turnover between habitats may also be due to aggregative dispersal behavior. Such dispersal can be relatively inert and may not respond to subtle differences between similar habitats. It should also be noted that despite the low species-turnover between habitats there may still be large variation within a given habitat type between different habitat patches. In the present study, for instance, I found that abundances of species significantly differ between trees (i.e. between patches of tree bark). This indicates that also the composition of the overall fauna might differ with a large species turnover from one tree to another. Such a turnover might be caused by the lack of directional movement of microarthropods between trees (Bowden et al. 1976 and Blackith and Disney 1988 for passive, non-directional aerial dispersal).

2) Refuges from grazing for cryptogams. The arthropods preferably used two cryptogam species, *Evernia prunastri* and *Lepraria incana*. Nevertheless, even these species were abandoned by many arthropods during certain microclimatic conditions. *Lepraria incana*, for instance, was abandoned by many *E. nivalis* during dry conditions. *Evernia prunastri* was abandoned during moist conditions. For the cryptogams, these microclimatic conditions represent refuges from grazing. In fact such refuges may be a major protection for the cryptogams of tree bark. Various evidence, from the literature or from personal observations, indicates that other kinds of protection may be inefficient (Gerson and Seaward 1977, Hartley and Jones 1997): there are only few predators or parasitoids of cryptogam grazers on exposed trunks (Prinzing 1996, and unpubl.); the mechanical and chemical defense of the investigated cryptogams against grazers is at most incomplete (Culbertson 1979, Prinzing and Wirtz 1997); C/N ratio and fiber content of the cryptogams are low, at least compared to many phanerogams (Kershaw 1985); and

the apparency of the cryptogams was high, given that the grazers mostly did find the most appropriate microhabitats (present study).

In conclusion, even at the within-habitat scale the major response of arthropods to (micro-)climatic fluctuations was compensatory redistribution among microhabitats across distances of centimeters to decimeters. This is remarkable because at the within-habitat scale compensation is not only relatively difficult to achieve due to the complexity of microhabitat mosaic. It also provides only limited benefits as migratory tracking of microclimates could be accomplished by migrations across only moderately larger distances of decimeters to meters. Nevertheless, such large-scale migrations were relatively unimportant. The animals thus perceived and utilized their environment primarily at the finest, but also most complex scale. Such compensatory use of microhabitats may have implications at a larger scale. It may increase the resilience of the total population to microclimatic fluctuations. It may reduce the species turnover between habitats and landscapes. And it may prevent cryptogams from being overgrazed.

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