

Local and regional species richness in communities of surface-dwelling grassland Collembola: indication of species saturation

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The relationship of local (LSR) versus regional species richness (RSR) provides an insight into patterns of species diversity. We examined communities of surface-dwelling Collembola in ten differently sized, temperate dry grasslands. To register genuine manifestations of saturation or proportional sampling, accurate determination of species pools is essential. Therefore, we applied the first-order jackknife as a species-richness estimator for LSR and introduce here a method for defining a range within which the real RSR probably lies. Our data exhibited similar levels of local Collembolan species richness across all regions, largely independent of regional richness. This curvilinear relationship between LSR and RSR indicates that a limit is present for the number of species that can locally coexist, suggesting local interactions and community saturation. We discuss several conditions that may cause pseudo-proportionality or pseudosaturation, i.e. artificial relationships between LSR and RSR. Furthermore, we test the LSR-RSR relationship for possible effects of autocorrelation.

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Species richness and its determinants seem to be a rich source from which community ecologists can learn about patterns of diversity. Recent investigations have strengthened the hypothesis that a framework of regional and historical as well as local processes form local community structures (Ricklefs 1987, Schluter and Ricklefs 1993, Hugueny et al. 1997, Angermeier and Winston 1998). The occurrence of species, therefore, reflects an inseparable combination of large spatio-temporal processes (e.g. speciation, dispersal, climatic and geographic developments) that govern species availability and small-scale processes (e.g. competition, predation, local disturbances) that act as definite filters (Ricklefs 1987, Angermeier and Winston 1998). Thus, local species richness (LSR) is somehow related to the regional species pool, and regressions of LSR on regional species richness

(RSR) can provide a revealing approach to patterns of species diversity (Cornell and Lawton 1992). In theory, the relationship between LSR and RSR describes the state of local species saturation (for a detailed review, see Cornell and Lawton 1992): if local richness increases proportionately with regional richness, local assemblages are unsaturated with species (“proportional sampling”), whereas asymptotic plots for LSR vs RSR suggest local species saturation caused by strong local interactions.

There are various sources of errors that may spoil tests for saturation where LSR and RSR are compared. Accurate definition, delimitation and investigation of spatial scales and species pools are basic requirements for obtaining unbiased results. In the following, we aim at pointing out some topics that are also relevant when surveying small animals.

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Definition of sites and species pools

Following Angermeier and Winston (1998), ideal regions show homogeneous environmental conditions for all species in the area, without inner barriers to migration and settlement. The outer boundaries are determined ecologically. All species occurring within the region build up the regional species pool. A comparison of LSR vs RSR patterns requires regions with similar environmental and historical conditions, but different species-pool sizes.

Local diversity is defined as the number of species living in a small, ecologically homogeneous area (Ricklefs 1987) where individuals move and interact with each other in the course of their routine feeding and breeding activities (Hanski and Gilpin 1991). Pärtel et al. (1996) term the set of species present in the target community as the "actual pool".

Detection of species

In practice, quantification of actual local and regional species pools is affected by species detectability, sampling effort and environmental conditions. Underestimating species numbers can modify the slope in plots of LSR vs RSR (Caley and Schluter 1997). Therefore, sufficient sampling intensity as well as adequacy and efficiency of sampling method are required (Caley and Schluter 1997). On the other hand, overestimating species richness may cause spurious asymptotes (Angermeier and Winston 1998). For instance, spatial heterogeneity, increasing with the range of the area, can offer niche space for habitat specialists. In this case, total regional richness also includes species unavailable for all local assemblages (Cornell 1985a, b). Moreover, sampling in marginal zones of regions can falsify the results inasmuch as they might provide conditions acceptable to the target and the surrounding community. Especially in small regions, these zones of faunistic overlap could make up a major part of the area. Surveys of the surrounding communities may help to delimit the species pool adapted to the entire region.

Estimation of species richness

Boulinier et al. (1998) emphasise that numerous studies in biodiversity are merely based on observed species numbers. But "count" data often fail to coincide with actual species richness, caused by insufficient sampling and differences in species-detectability. The use of species-richness estimators may help in approaching actual species numbers. These procedures infer total species numbers from patterns of observed species occurrence (Boulinier et al. 1998).

When analysing LSR-RSR patterns, it must be kept in mind that RSR results from regional LSRs. In this case, estimating RSR from estimated LSRs means deduction from previously modified patterns of species occurrence.

The role of endemics

Cresswell et al. (1995) emphasise that plots of LSR on RSR contain an element of autocorrelation. They put forward a method for avoiding this bias and calculating RSR while excluding the target locality, i.e. the endemics, from the regional data set. The regional species richness calculated by this method is marked by an asterisk (RSR*). Caley (1997) argues that this method examines the relationship between LSR and the region surrounding localities, instead of the relationship between LSR and RSR. Moreover, investigations of numerous taxa did not show statistically significant effects of autocorrelation (Caley 1997, Caley and Schluter 1997).

Nevertheless, it might be informative to check data in this regard. However, endemism must be treated cautiously. First, detecting real endemism is problematic due to the difficulty of exhaustive sampling (Caley 1997). Using estimated species numbers even increases the problem: which portion of estimated species is endemic? Second, it is important to decide between possible reasons of endemism. Actually, endemism should be caused by biotic interactions. However, endemics might also be habitat specialists, their occurrence being dependent on spatial heterogeneity (see above).

In this paper, we examine the relationship of LSR vs RSR for surface-dwelling Collembola (Insecta: Apterygota) in ten differently sized, temperate, dry grassland areas. High species abundances and diversity (Hopkin 1997) qualify these communities for investigations of species-richness patterns. We address all of the above-mentioned topics by: 1) choosing regions with similar environmental and historical conditions; 2) choosing regions with sizes ranging over two orders of magnitude, with the smallest regions potentially representing complete faunistic overlap with the surrounding communities; 3) applying a species-richness estimator; and 4) calculating RSR as well as RSR*.

Material and methods

Study area

The study sites are situated 30 km south to 80 km east of Vienna, Austria, i.e. between 16°16'E, 48°4'N and 16°55'E, 48°7'N. This area forms the western border of the Pannonian climatic province, characterised by hot

summers, cold winters, < 700 mm annual precipitation and a mean annual temperature close to 10°C. It harbours a number of dry grasslands that represent relics of former, large pasture land, nowadays appearing as differently sized islands within a sea of intensively managed agricultural fields. It is common knowledge among soil zoologists that grassland supports a richer Collembolan fauna than arable land (Hopkin 1997). Previous investigations in the area have also shown that the species assemblages in the dry grasslands differ considerably from those in agricultural fields (Christian and Kampichler 1984, Kampichler 1991, 1992, Beinhofer 1993, Tiefenbrunner 1993).

We sampled ten dry grasslands with a size of 0.25–57 ha (Table 1). Designation of the sites corresponds to the catalogue of Austrian dry grasslands (Holzner et al. 1986). The codes denote sheet numbers of the official Austrian 1:50000 (ÖK) maps combined with consecutive numbering.

Surface-dwelling Collembola are tiny wingless insects of a few mm body length. Little is known about the spatial range of their routine feeding and reproduction activities. Although, under certain circumstances, some species of surface-dwelling Collembola are able to migrate considerable distances – for example on snow (Hågvar 1995) or during mass occurrence (Lyford 1975), soil zoologists regard them as being confined to a range of up to a few hundred square-metres (Hopkin 1997). Accordingly, we consider the grasslands to represent the regional scale for surface-dwelling Collembola. We assume that even the area of the smallest grassland (0.25 ha) surpasses the distance an average individual Collembolan might migrate in its life-time. Thus, on the Collembolan scale, we define a grassland as a region and all species of a grassland establish the regional species pool.

Sampling design

Local species pools were sampled by arrangements of 36 small pitfall-traps of 10 mm diameter and 40 mm

height, filled with 0.7 ml formaldehyde solution (4%). The pitfall traps were grouped in a quadratic design of 6 × 6 and 300 mm distance, covering an area of 2.25 m². Depending on the size of the grassland region, we used three (grasslands of 0.25–1 ha) to fifteen (grasslands of 32–64 ha) trap arrangements. For each doubling of size, two more local species pools were sampled. Thus, regions up to 1, 2, 4, 8, etc. ha were investigated with 3, 5, 7, 9, etc. trap arrangements. The traps were exposed for 11 d in May 1995, the time of the year when, in east Austrian dry grasslands, the maximum diversity of the Collembolan community may be expected (Kampichler 1992). Altogether, we analysed ca 2600 pitfall traps, representing 74 trap arrangements.

Estimation of LSR and RSR

Previous studies have distinguished the first-order jackknife as one of the most reliable alternatives among a considerable number of species-richness estimators (Heltshe and Forrester 1983, Palmer 1990, Baltanás 1992).

$$\text{“first-order jackknife”}: ES = OS + \frac{N-1}{N} k \quad (1)$$

where ES denotes estimated species number, OS the number of observed species and k the number of “unique species”, i.e. species occurring in only one sampling unit in a sample of N units. We adopted the first-order jackknife for the calculation of LSR (the number of species occurring in a single pitfall-trap arrangement), with N being the number of traps in the arrangement and k being the number of Collembolan species occurring in only one trap within the arrangement (Winklehner et al. 1997).

RSR (the number of species occurring in all trap arrangements within a grassland site) was calculated in the same manner. In this case, “unique” refers to species occurring in only one trap arrangement within a

Table 1. Investigated grassland sites, encoding following the catalogue of Austrian dry grasslands (Holzner et al. 1986). Results are presented for observed (obs) and estimated (est) local (LSR) and regional species richness (RSR). Minimum RSR, estimated RSR and maximum RSR represent three alternatives of estimating RSR (see text for explanation).

Region (ÖK)	Size (ha)	Mean (obs) LSR	Observed RSR	Mean (est) LSR	Minimum RSR	Estimated RSR	Maximum RSR
60/7	0.25	8	9	9.0	10.3	11.1	11.8
60/20	0.50	9	11	10.0	13.0	13.9	14.6
58/24	0.50	12	13	12.0	13.7	13.8	14.2
60/17	2.75	8	14	9.0	15.7	18.3	22.5
60/4	3.00	11	16	12.0	16.9	18.3	24.2
60/6	4.00	9	15	10.0	17.6	19.7	22.1
78/21	7.10	9	14	10.0	16.7	18.6	20.5
58/25	8.00	11	17	12.0	17.9	19.4	25.8
78/22	10.00	10	15	11.0	15.0	15.0	20.3
61/11	57.00	6	11	7.9	11.0	11.0	15.8

grassland. However, since RSR is estimated from estimated LSRs, we must consider how to deal with estimated additional local species (corresponding to the term $[(N - 1)/N] * k$ in equation 1). Do “unique species” hide among them? We calculated three alternatives – using conservative and liberal estimators to examine the robustness of the LSR-RSR patterns: first we defined minimum RSR on the assumption that no estimated additional local species is unique (meaning that only the observed unique species, k , are used for the estimation of RSR). Maximum RSR at the other extreme presumes that all estimated additional local species are unique (meaning that all estimated additional local species are added to k for the estimation of RSR). As a third and rather realistic alternative, we suggest the calculation of estimated RSR, supposing estimated additional local species and OS to contain an equal percentage of unique species (meaning that the estimated additional local species are multiplied by k/OS and added to k for the estimation of RSR).

Estimated RSR* was calculated in the same way, but each time excluding the target locality from the regional data set (Cresswell et al. 1995).

Testing for saturation

Plotting LSR as a cluster of values obtained from several localities in the same region is a pseudoreplicative approach since in that case the number of degrees of freedom used by the regression analysis would be number of localities – 1 instead of number of regions – 1 (Srivastava 1999). Thus, we first determined mean estimated LSR for each dry grassland. The relationship between mean estimated LSR and minimum RSR, estimated RSR and maximum RSR, respectively, was subsequently tested by fitting linear ($y = a + bx$), second-order polynomial ($y = a + bx + cx^2$) and power ($y = ax^b$) models to the data. The linear and the polynomial regressions were examined twice, i.e. once anchoring them at the origin. Forcing regressions through the zero point is logical, but risky. Particularly, if LSR is underestimated in species-rich regions, this approach could result in pseudosaturation, i.e. an artefactual saturation curve (Hawkins and Compton 1992, Caley and Schluter 1997). To enable comparison, we analysed observed local and regional species numbers in the same way.

Relationship between LSR and RSR*

Analogous to the estimation of LSR and RSR, we tested regressions of estimated LSR on estimated RSR*. Plots of estimated LSR vs estimated RSR and estimated LSR vs estimated RSR* were compared and examined for possible effects of autocorrelation.

Table 2. Surface-dwelling Collembolan species trapped in ten dry grasslands in eastern Austria.

Species
<i>Entomobrya atrocincta</i> Schött, 1896
<i>Entomobrya handschini</i> Stach, 1922
<i>Entomobrya marginata</i> (Tullberg, 1871)
<i>Entomobrya multifasciata</i> (Tullberg, 1871)
<i>Folsomia manolachei</i> Bagnall, 1939
<i>Heteromurus major</i> (Moniez, 1889)
<i>Heteromurus nitidus</i> (Templeton, 1835)
<i>Isotoma notabilis</i> Schäffer, 1896
<i>Isotoma viridis</i> Bourlet, 1839
<i>Lepidocyrtus lanuginosus</i> (Gmelin, 1788)
<i>Lepidocyrtus lignorum</i> (Fabricius, 1775)
<i>Lepidocyrtus paradoxus</i> Uzel, 1891
<i>Lepidocyrtus</i> cf. <i>serbicus</i> Denis, 1933
<i>Orchesella albofasciata</i> Stach, 1960
<i>Orchesella cincta</i> Linné, 1758
<i>Orchesella multifasciata</i> Stscherbakow, 1898
<i>Pseudosinella alba</i> (Packard, 1873)
<i>Pseudosinella octopunctata</i> Börner, 1901
<i>Pseudosinella</i> cf. <i>sexoculata</i> Schött, 1902
<i>Seira pallidipes</i> (Reuter, 1895)
<i>Seira</i> cf. <i>squamoornata</i> (Stscherbakow, 1898)
<i>Tomocerus flavescens</i> (Tullberg, 1871)
<i>Tomocerus vulgaris</i> (Tullberg, 1871)

All regression analyses were performed with the multiple regression module of the STATISTICA 5.1 statistical library (Anon. 1994).

Results

According to pigmentation, hair and scale cover, length of extremities and development of eyes, Collembola can be categorized into different ecomorphological life-forms: those typically colonizing deeper soil layers (euedaphic species), superficial soil layers (hemiedaphic species), the soil surface (epigeic species) as well as those inhabiting the vegetation (atmobioc species) (Hopkin 1997). Besides surface-dwelling species, species of life-forms mainly living below-ground (Onychiuridae etc.) or in the foliage (Sminthuridae etc.) also appeared in the pitfall-traps. However, we assume that they were incidentally trapped (euedaphic species episodically move to the soil surface when moisture conditions are suitable; atmobioc species can be blown towards the traps by the wind) and do not regularly interact with the species living on the soil surface. Hence, we did not include them in the analysis. A total of 23 surface-dwelling species was recorded (Table 2), belonging to the families Entomobryidae, Isotomidae and Tomoceridae. Within regions, species occurred quite evenly distributed.

Mean estimated LSR was relatively uniform, amounting to 7.9–12 species (Table 1). The number of observed RSR varied from 9 (ÖK 60/7) to 17 (ÖK 58/25), without a clear indication of size dependence. Few (i.e. 0–1, and once 2) “unique species” were

caught regionally. Estimated RSR ranged from 11 in the largest region (ÖK 61/11) to 19.7 in a smaller, but species-rich grassland (ÖK 60/6).

Regression analyses underpin the observation that estimated LSR tends to be independent from RSR and forms a broad horizontal band (Fig. 1b–d, Table 3). The intercepts of the linear models between mean estimated LSR and the possible values of RSR (minimum RSR, estimated RSR, maximum RSR) were statistically significant, whereas the slopes were not distinguishable from zero with $p < 0.05$. Not surprisingly, adding a quadratic term yielded only non-significant parameters, sometimes even with changed signs. The quadratic term added to the linear models without intercept, however, was statistically significant for the entire range of possible RSR and demonstrate the curvilinearity of the RSR-LSR relationship when forced through the origin. The exponent b of the power model was never different from zero, with $p < 0.05$, and also shows that RSR exerts little influence on LSR.

Restricting the analysis to observed LSR and observed RSR yielded a less clear-cut situation (Fig. 1a, Table 3), which, in contrast to the results above, could be interpreted as a proportional sampling relationship. The number of observed species, however, is known to be a poor estimator of species richness (Palmer 1990, Baltanás 1992, Boulinier et al. 1998). This observation stresses the importance of correcting count data for

possible sampling inefficiencies by using species-richness estimators.

Comparing mean estimated LSR vs estimated RSR and mean estimated LSR vs mean estimated RSR* did not give an indication of appreciable differences (Table 3, Fig. 2). Thus, concerning our data, distorting effects due to autocorrelation may be rejected.

Discussion

The goal of relating local and regional species richness is to gain insight into patterns of species diversity. For this, accurate determination of species pools is a central requirement. Our investigations confirm that manifestation of saturation or proportional sampling depends on such methodological aspects. If we, as is common practice, took count data as a measure of species richness (Boulinier et al. 1998), rather indifferent results were obtained. Neither linearity nor saturation was apparent. However, the number of observed species usually underestimates true species richness (Palmer 1990), particularly regarding the detection of rare species (McArdle 1990). To keep sampling effort feasible, most searches – including ours – are not absolutely exhaustive. Thus, by underestimating RSR, insufficient sampling involves the risk of creating artificial linearity between LSR and RSR, a relationship that could be termed “pseudo-proportionality”. Estimating species numbers should enable the correction of sampling bias. Following Palmer (1990), ideal estimators of species richness adequately reflect ecological patterns. The jackknife appeared to be a reliable LSR-estimator of surface-dwelling Collembola (Winklehner et al. 1997). Concerning RSR, we used conservative and liberal estimators, i.e. determination of minimum estimated RSR, estimated RSR and maximum estimated RSR, which allow the definition of a range wherein real RSR is probable. Normally, minimum estimated RSR and maximum estimated RSR represent rather extreme and unrealistic values. As with observed species richness, minimum estimated RSR is assumed to underestimate real richness, for it excludes the possibility of an estimator ascertaining further, unique species. On the other hand, maximum estimated RSR will overestimate species numbers, since assuming all estimated additional local species to be unique is quite unrealistic. In this case, pseudosaturation (i.e. an artificial flattening of the curve) may be produced (Cornell and Lawton 1992). Estimated RSR is supposed to coincide best with actual species occurrence. In accordance with our data, all three values exhibited comparable results: local species richness of surface-dwelling Collembola tended to remain relatively constant and independent of the regional species pools. This curvilinear relationship between LSR and RSR indicates an upper limit for the number of species that can coexist locally.

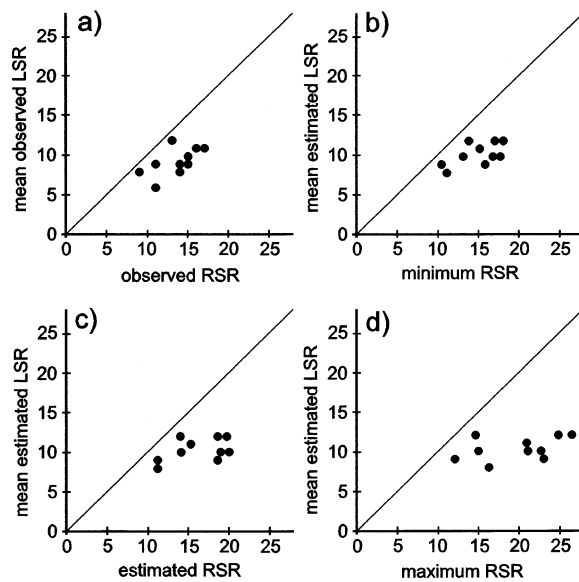


Fig. 1. Mean Collembolan local species richness (LSR) and regional species richness (RSR) in ten dry grasslands in eastern Austria. a) Mean observed LSR vs observed RSR, b) mean estimated LSR vs minimum RSR, c) mean estimated LSR vs estimated RSR, d) mean estimated LSR vs maximum RSR. Minimum RSR, estimated RSR and maximum RSR represent three alternatives of estimating RSR (see text for explanation).

Table 3. Regression statistics of Collembolan LSR and RSR in ten dry grasslands in eastern Austria. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Minimum RSR, estimated RSR and maximum RSR represent three alternatives of estimating RSR (see text for explanation).

Relationship	Regression type	Regression parameters		
		a	b	c
observed RSR – mean observed LSR	$y = a + bx$	3.685	0.416	
	$y = a + bx + cx^2$	7.621	-0.212	0.024
	$y = bx$		0.681 ***	
	$y = bx + cx^2$		0.979 **	-0.021
minimum RSR – mean estimated LSR	$y = ax^b$	1.973	0.593	
	$y = a + bx$	5.784 *	0.304	
	$y = a + bx + cx^2$	-4.226	1.768	-0.052
	$y = bx$		0.684 ***	
estimated RSR-mean estimated LSR	$y = bx + cx^2$		1.158 ***	-0.030 *
	$y = ax^b$	3.127	0.441	
	$y = a + bx$	7.306 **	0.187	
	$y = a + bx + cx^2$	-12.707	2.907	-0.088
maximum RSR – mean estimated LSR	$y = bx$		0.628 ***	
	$y = bx + cx^2$		1.203 ***	-0.034 **
	$y = ax^b$	4.306 *	0.314	
	$y = a + bx$	7.850 **	0.126	
estimated RSR* – mean estimated LSR	$y = a + bx + cx^2$	15.915	-0.787	0.024
	$y = bx$		0.514 ***	
	$y = bx + cx^2$		0.971 ***	-0.022 **
	$y = ax^b$	5.454 *	0.213	
estimated RSR* – mean estimated LSR	$y = a + bx$	7.979 **	0.147	
	$y = a + bx + cx^2$	-2.869	1.735	-0.054
	$y = bx$		0.632 ***	
	$y = bx + cx^2$		1.327 ***	-0.041 ***
	$y = ax^b$	5.435 **	0.232	

Cornell and Lawton (1992) and Cornell and Karlson (1997) reviewed numerous case studies suggesting unsaturated patterns as common and widespread in natural communities. Hints on saturation are less frequent, and primarily refer to parasites (Aho 1990, Aho and Bush 1993). Therefore, speculation that we detected an artificially created curvilinearity is justified. Following Cornell and Lawton (1992), interactions between the species in question are a prerequisite for true saturation. Effects such as density compensation, niche shifting, the absence of identifiable empty niches and/or high ratios of core versus satellite species may be connected (Cornell 1993). Unfortunately, our single surveys of species numbers do not enable us to gain insight into species interactions or species turnover. However, some laboratory experiments give an indication of competition and inference that might influence reproduction and, hence, community structure of Collembola (Christiansen 1967, Culver 1975, Longstaff 1976, Christiansen et al. 1992). Also, the linear relations between log abundance and rank that have been observed in surface-dwelling Collembolan communities are likely to be the result of a niche preemption process (Vegter et al. 1988, Kampichler 1992) and suggest a certain degree of interactivity. Hopkin (1997), however, doubts that interactions between Collembola should be of ecological consequence to species distributions.

Besides true saturation, a variety of other reasons and explanations for asymptotic relationships between

LSR and RSR, i.e. pseudosaturation, exists. For instance, stochastic equilibrium, high local extinction rates, endemism, regional heterogeneity or inadequate sampling come into question (Cornell and Lawton 1992, Cornell 1993, Griffiths 1997, Angermeier and

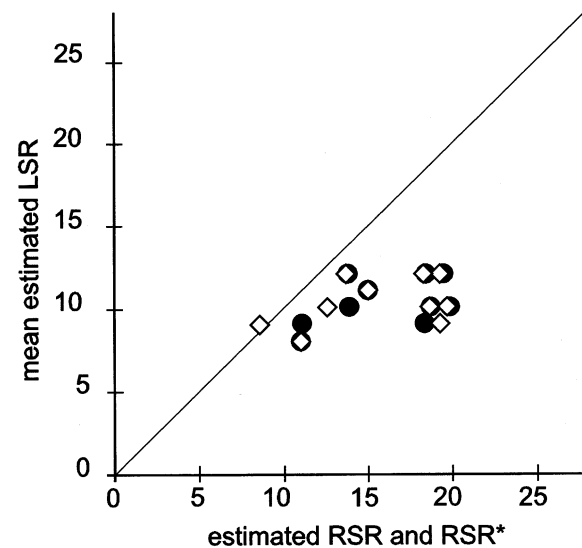


Fig. 2. Comparison of relationship of mean estimated LSR vs estimated RSR (full circles) and mean estimated LSR vs estimated RSR* (white diamonds) for ten temperate dry grasslands in eastern Austria.

Winston 1998). Stochastic equilibrium denotes balanced rates of colonisation and extinction, independent of local interactions. High ratios of tramp species and/or rapid species turnover may derive from this (Cornell and Lawton 1992, Cornell 1993). As mentioned above, interactions and species turnover cannot be measured by our data. Previous investigations in region ÖK 61/11 exhibited a Collembolan fauna largely congruent with our findings (Kampichler 1991, 1992). The possibility of considerable local extinction rates, however, cannot be excluded, since soil desiccation in summer may lead to a seasonal decrease of Collembolan abundance and diversity in east Austrian grasslands (e.g. Loub and Haybach 1967, Kampichler 1992). Regional heterogeneity may cause pseudosaturation if the regional species pool is overestimated (Cornell and Lawton 1992, Cornell 1993, Angermeier and Winston 1998). Primarily large regions are expected to include more landscape features and, correspondingly, more specialists. Hence, RSR includes species not adapted to the given habitat (Cornell 1985a, b). In this case, even pool exhaustion, i.e. all potential species arrived in the habitat in question, results in an asymptotic pattern of LSR and RSR (Cornell 1993). Again, we could not obtain an indication for pool exhaustion such as low turnover, lack of niche shifting, abundance compensation and obvious empty niches (Cornell 1993). However, a relatively uniform distribution of species within regions supports the assumption that our dry grasslands are largely homogeneous. Moreover, the low rate of endemism also suggests this. Srivastava (1999) points out in her methodological review on LSR-RSR plots that differences in region size may result in erroneous asymptotic curves when RSR is positively correlated with region size. Collembolan species richness, however, did not exhibit dependence on the size of the grasslands (Spearman rank correlation between region area and estimated RSR: $r = 0.226$, $p = 0.531$). Above all, the largest region (ÖK 61/11), composed of different grassland-associations, harboured the second smallest species pool. Perhaps this has to do with the high portion of grassland-specific Collembola, amounting to half of all species detected there. Finally, spurious asymptotes can derive from methodical aspects. Caley and Schluter (1997) emphasised the importance of adapting locality size as well as sample size to the range of the regions. If region size increases, constant locality and/or sample sizes will detect a decreasing part of the actual species. We avoided this by choosing a sufficiently high number of pitfall traps (Winklehner et al. 1997), by adapting the number of trap arrangements to the size of the grassland and, above all, by applying a species-richness estimator. Applicability of these methods was tested previously (Winklehner et al. 1997). In addition, the small number of unique species found regionally gives evidence of sampling efficiency.

So far, we have been unable to find convincing evidence of an artificially produced asymptote. Thus, based on our data, plots of LSR vs RSR for surface-dwelling Collembola in temperate dry grasslands might suggest local interactions and community saturation. Investigation of the interactions between Collembola will be of considerable importance in confirming this conclusion.

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