



Distribution, diversity gradients and Rapoport's elevational rule in the black scavenger flies of the Swiss Alps (Diptera: Sepsidae)

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Abstract. 1. Elevational gradients influence the distribution and abundance of species drastically and can lead to variation in community composition. Although coprophagous flies are of ecological and economic importance, their biodiversity and distribution are largely neglected. We studied the impact of steep elevational gradients and geography on the distribution of sepsid flies in the Swiss Alps.

2. Sepsidae are a family of acalyptate flies strongly associated with decaying organic matter and vertebrate dung, and characterised by a high extent of sympatry in their breeding substrates. Historical, haphazardly sampled specimens from 116 locations covering an elevational range from 200 to 2000 m were available in ethanol collections of various Swiss museums.

3. Nineteen species encompassing all native genera (*Meroplius*, *Nemopoda*, *Saltella*, *Sepsis* and *Themira*) were recorded. Local species richness increased linearly with elevation, while area-corrected regional species richness of elevational belts increased asymptotically. Species occurring at higher altitudes had lower wing loadings and greater elevational ranges than lowland species, supporting Rapoport's elevational rule.

4. Despite compositional similarities, the sepsid communities of the northern lowlands differed significantly from the alpine sepsid fauna. The southern lowlands were particularly differentiated in community composition due to a number of presumably thermophilic species that predominantly occur south of the Alps.

5. Relative abundances of several species were thus strongly affected by elevation and climatic variables. We illustrate the impact of elevational gradients and geography on a community of closely related, often sympatric species, and discuss potential mechanisms of niche partitioning via temporal succession, thermal adaptation and differential resource use.

Key words. Altitudinal gradients, biogeography, dispersal capacity, range size, wing morphometrics.

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Introduction

Ecological gradients in latitude or elevation, typically reflecting underlying patterns in climatic and biotic

conditions, are well known to affect the distribution of species and therefore yield valuable insights into biogeography, conservation biology and climate research (e.g. Addo-Bediako *et al.*, 2000; Deutsch *et al.*, 2008). Such research encompasses large-scale studies either of particular traits of single or multiple species (such as body size; e.g. Bergmann's or Rensch's rule: Blackburn *et al.*, 1999; Blanckenhorn & Demont, 2004; Blanckenhorn *et al.*, 2006; Klepsatel *et al.*, 2014) or of whole species assemblages (so-called macroecology: Brown & Maurer, 1989; Gaston & Blackburn, 2000; Gaston *et al.*, 2008). In general, vertebrates are better covered than invertebrates, and latitudinal studies are more abundant than altitudinal studies (Gaston & Blackburn, 2000; Blanckenhorn & Demont, 2004; Blanckenhorn *et al.*, 2006; Klepsatel *et al.*, 2014). Studies of elevational diversity gradients have received recent attention in the context of climate change and have revealed highly diverse taxon-specific distribution patterns (Rahbek, 1995; Herzog *et al.*, 2013; Zou *et al.*, 2014). One theory connecting elevation and species distribution patterns is Rapoport's elevational rule (Stevens, 1992; Gaston *et al.*, 2008), predicting that species occurring at higher elevations should show larger altitudinal ranges. This not entirely uncontroversial 'rule' (Gaston *et al.*, 1998) is based upon the assumption that high altitude habitats tend to be more variable than lowland habitats, thus species occurring at higher elevations must be able to tolerate a wider range of climatic conditions.

Due to their great ecological and economic importance, insects associated with dung decomposition have been subject to various studies focusing on ecological diversity gradients (Herzog *et al.*, 2013; Menendez *et al.*, 2014) or community ecology (Hanski & Cambefort, 1991). Most of our knowledge on temperate Palaearctic dung ecosystems is based on studying beetles, such as *Aphodius* or *Onthophagus spp.*, demonstrating complex and rapid succession in species assemblages (Hanski & Cambefort, 1991; Lee & Wall, 2006) as well as large spatio-temporal variation in species composition of the cow dung fauna (Hanski & Cambefort, 1991; Finn *et al.*, 1999; Bertone *et al.*, 2005; Lumaret *et al.*, 2007). Flies are often neglected in studies of dung ecosystems, at least partly due to the tremendous identification effort involved. Nevertheless, larvae of coprophagous diptera play an essential role in dung decomposition and more than 250 fly species have been reported to be part of the dung community in temperate regions (Hammer, 1941; Skidmore, 1991; Papp, 1992). These dung-decomposing insects fulfil an important ecosystem function all over the world and are thus of ecological relevance.

Sepsid flies (Diptera: Sepsidae) generally depend on decaying organic matter for reproduction and larval development. Many species are specialised on vertebrate dung and occur in very high numbers especially near livestock excrements (Pont & Meier, 2002). Apart from acting as an integral part of the dung fauna in many parts of the world and thus being of practical relevance in the ecotoxicology of veterinary medicine (Blanckenhorn *et al.*, 2013a, b; Puniamorthy *et al.*, 2014), sepsid flies are also rapidly

becoming model organisms in behavioural ecology, evolutionary biology and phylogenetics (Blanckenhorn *et al.*, 2000; Eberhard, 2001; Bowsher & Nijhout, 2007; Ingram *et al.*, 2008; Berger *et al.*, 2013). Yet, very little is known about their spatial distribution, community and general ecology on a local, regional and also global scale. Consequently, studies of, e.g. thermal performance in sepsids (Berger *et al.*, 2013) lack detailed faunistic and ecological information, hampering interpretation of some results.

Pont and Meier (2002) report an average of seven to eight species of sepsid flies on Central European cow pastures. Moreover, we found a surprisingly rich alpine fauna consisting of up to 12 sympatric *Sepsis* species at one single high altitude site (Lenzerheide, Graubünden), encompassing the entire *Sepsis* species richness known to Switzerland (Rohner *et al.*, 2014). Such a high extent of species sympatry appears unusual and implies elaborate and yet uninvestigated niche partitioning that begs to be scrutinised.

Switzerland is particularly well suited for studies of geographic and elevational diversity gradients in the temperate region, as it features great variation in elevation over relatively short distances and encompasses northern and southern lowlands as well as the high Alps separating Central Europe from the Mediterranean region. Using numerous ethanol collections from various Swiss institutions, this study aims to document the geographic distribution of sepsids at a broad spatial landscape scale in an ecological context. We investigate elevational diversity gradients in the Swiss Alps, test Rapoport's elevational rule and correlate estimates of dispersal capability based on morphometric measurements (wing loading, wing aspect ratio) with elevational distributions. We further compare species composition of the three main biogeographic regions in Switzerland, the lowlands north and south of the Alps and the alpine region.

Materials and methods

Species records

The ethanol samples examined in this study stem partly from private collections of Swiss entomologists gathered over the years (Bächli, Rohner), or from field experiments and biodiversity surveys (Obrist & Duelli, 2010; Jochmann, Pollini). Sepsids are typically by-catch in collections and therefore represent a random snapshot of the general sepsid diversity in the periphery of, but sometimes far away from typical breeding sites such as livestock pastures. In total, more than 5000 male individuals from 116 locations in Switzerland were identified, largely based on their characteristic foreleg and genital morphology (Hennig, 1949; Pont, 1979; Pont & Meier, 2002; Ang *et al.*, 2013). Females were not considered due to their lack of unambiguous characters for identification. A list of all locations and collecting times can be found in Table S1. The samples cover an altitudinal range from 200 to 2000 m a.s.l., with samples from higher elevations

containing no sepsids. This is probably due to the sharp decrease in cattle grazing above the tree line, presumably leading to a sudden decrease in population densities of sepsids and the corresponding decrease in collection effort, as collecting at very high altitudes is costly and complicated. The samples used in this study are stored at the Museo Cantonale di Storia Naturale (MCSN) in Lugano (leg. Pollini) and the University of Zurich (all remaining samples). All faunistic records are deposited at the Swiss Biological Records Center (CSCF).

Diversity estimates: local scale

When estimating relative abundances of sepsids, only samples with more than 20 individuals were considered, reducing the number of locations to 65. As estimates of diversity, the first three Hill numbers were calculated: 0D (species richness), 1D (evenness) and 2D (diversity weighted by relative abundance) (Gotelli & Chao, 2013). All analyses were conducted using the package *vegan* (Dixon, 2003) in R version 3.0.3.

Diversity estimates: elevational belts

Given that the area of elevational belts usually decreases with elevation, which is especially dramatic in mountainous regions, the correction of regional species richness for area is essential when studying elevational gradients (Rahbek, 1995). Following Rahbek (1997), we counted the number of species that were recorded in each elevational belt as an approximation of regional species richness (S), subdividing the elevational range covered by our samples into belts of 200 m. The area of each elevational belt was estimated using BIOCLIM data (Hijmans *et al.*, 2005) in QGIS version 2.2 (QGIS Development Team, 2009). We used the world catalogue of the Sepsidae (Ozerov, 2005) to estimate the slope of the species–area relationship (SAR) (z) in log–log space for Europe (see Table S2), which was used to correct regional species richness for area. The slope of the SAR of sepsids in Europe amounts to $z = 0.28$. Since the SAR can vary at different geographic scales, we repeated the area correction with z -values of 0.25 and 0.3. We only used constant z -values due to the lack of information on potential variation in SARs with elevation. We thus divided regional species richness by the area of the elevational belt to the power of z [rearrangement of the power function: Arrhenius (1921), see also Karger *et al.* (2011)], yielding the area-corrected species richness (S_{cor}). We multiplied S_{cor} by an arbitrary constant (here eight: cf. Pont & Meier, 2002) as suggested by McCain (2007) to receive realistic values. The absolute scale of species richness is, however, irrelevant here, since we investigate the shape of the relationship, not the amplitude.

Pearson's correlation coefficient r was used to describe the relationship between the elevational mid-point and the

altitudinal range size of 16 of the 19 species present in the data set (dropping three rare ones) to test for Rapoport's rule. Whenever the data were non-normally distributed, Spearman's rank correlation r_s is reported instead.

To estimate dispersal capability, we dissected and photographed 2 (for rare species) to (usually) 20 male individuals per species and measured thorax length (distance between the head basis and the tip of the scutellum), wing length (humeral cross vein to apex) and wing width (distance between the distal end of radius R_1 and CuA_1). Wing aspect ratio (wing length/wing width) and wing loading (thorax length/wing area) were subsequently calculated.

Community structure

Analysis of similarities (ANOSIM) [Clarke (1993); R-package *vegan* (Dixon, 2003)] was performed to assess differences in community composition among the three major geographic regions in Switzerland. ANOSIM compares Bray–Curtis dissimilarities between versus within assigned groups. Group allocations were permuted 999 times to obtain standard errors and to determine the probability of a given geographic group assignment. We used Kruskal's non-metric multidimensional scaling (NMDS) [Cox and Cox (2000); R-package *MASS* (Venables & Ripley, 2002)] of abundance data to illustrate the dissimilarities of community compositions.

The alpine region was defined as locations with an elevation of at least 900 m a.s.l., although valleys within the Central Alps were also considered as alpine. Lower sites north and south of the alpine region were considered as northern and southern lowlands. Various temporal samples from the same location were pooled, as the haphazard nature of the collections did not permit systematic investigation of temporal (e.g. seasonal) variation.

Due to the lack of climatic microhabitat information, we used BIOCLIM raster data (Hijmans *et al.*, 2005) to estimate current annual mean temperature and precipitation for all locations. Especially in mountainous regions, raster data may not be very accurate due to high elevational variation. The three main variables of interest, namely, altitude, temperature and precipitation naturally are strongly correlated (altitude and temperature: $r = -0.86$, $P < 0.001$; altitude and precipitation: $r = 0.55$, $P < 0.001$). As this leads to uninformative results, we did not perform multiple regression analyses. Nevertheless, due to this high degree of covariance, the relationship between relative species abundance and altitude mirrors more or less the relationship between abundance and temperature.

Results

Species records

Of the 26 species of Sepsidae ever recorded in Switzerland (Haenni, 1998; Merz *et al.*, 2001), 19 species were

present in the data set (we do not consider records of *Sepsis setulosa* Duda, 1926, due to its questionable taxonomic status: Pont & Meier, 2002). All native genera (*Nemopoda*, *Themira*, *Saltella*, *Meroplus* and *Sepsis*) were represented with at least one species. Absence/presence of species (116 locations) is shown in Fig. 1, and their relative abundances as a function of altitude and latitude, thus reflecting the relief of the country, are shown in Fig. 2 (65 locations).

Biogeographic comparison of community structure

The ANOSIM revealed significant differences in species composition among all three geographic regions ($R = 0.171$, $P = 0.001$, $n = 65$). Pairwise comparisons between the northern and southern lowlands ($R = 0.390$, $P = 0.014$, $n = 34$) and between the northern and the alpine region ($R = 0.078$, $P = 0.006$, $n = 60$) were also significant. Multidimensional scaling (Fig. 3) illustrates the southern samples as being clearly separated in the lower right corner, as some rarer species exclusively or predominantly occurred only there (*Meroplus*, *Nemopoda* and *Themira*; Figs 1 and 2). The northern and alpine communities overlap entirely along the NMDS axis 1, whereas axis 2 shows some separation of the northern lowland communities in the upper right and lower left corners of Fig. 3, due to some rare species almost exclusively occur-

ring in the northern lowlands (*Sa. nigripes*, *S. nigripes* and *T. annulipes*; Figs 1 and 2; Table S3). Also, note that the widespread *Sepsis punctum* predominantly occurs in the lowlands north and south of the Alps, whereas other common species such as *Sepsis cynipsea*, *S. fulgens* or *S. orthocnemis* occur all over (Fig. 2).

Altitudinal patterns of species diversity: local scale

The first two Hill numbers correlate positively with altitude (0D (species richness): $r_s = +0.32$, $P = 0.017$; 1D (evenness): $r_s = +0.29$, $P = 0.020$; 2D (diversity weighted by relative abundance): $r_s = +0.22$, $P = 0.087$; Fig. 4). As expected, there is a strong correlation between sample size and number of species per site ($r_s = +0.8$, $P < 0.001$), indicating an effect of sampling effort on the presence of rare species. There is no correlation between sample size and altitude, however ($r_s = +0.11$, $P = 0.245$).

Altitudinal patterns of species diversity: elevational belts

Both uncorrected and area-corrected regional species richness increase with elevation. The asymptotic exponential function produced the best fit ($r^2_{\text{exponential}} = 0.79$, $r^2_{\text{quadratic}} = 0.71$, $r^2_{\text{linear}} = 0.49$; Fig. 5).

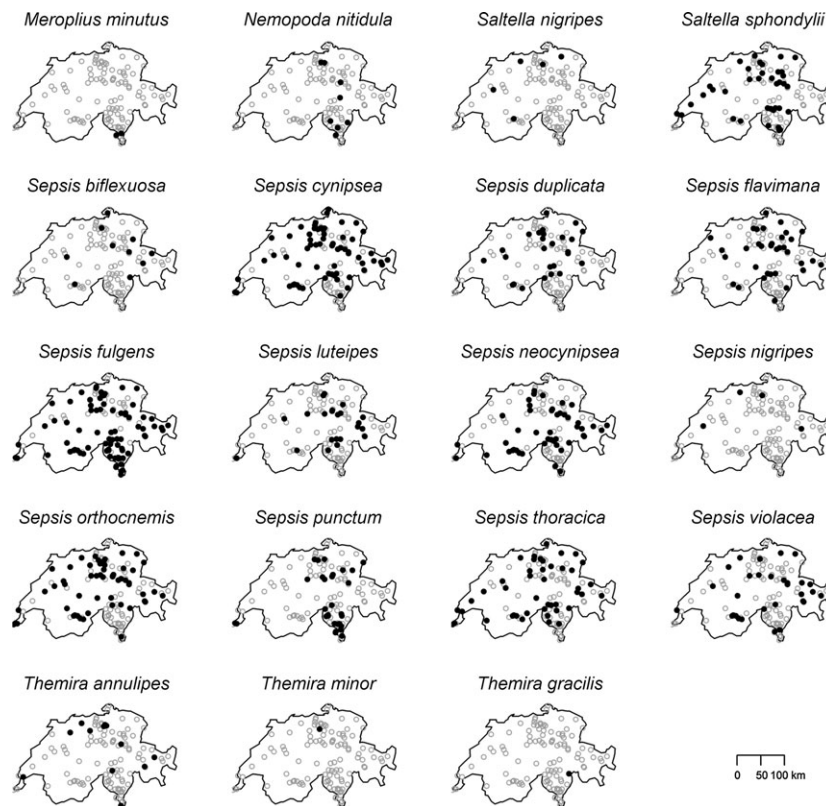


Fig. 1. Species records for 19 sepsid species at 116 locations in Switzerland. Black dots indicate the presence of the species, whereas open circles indicate locations where the species was not detected.

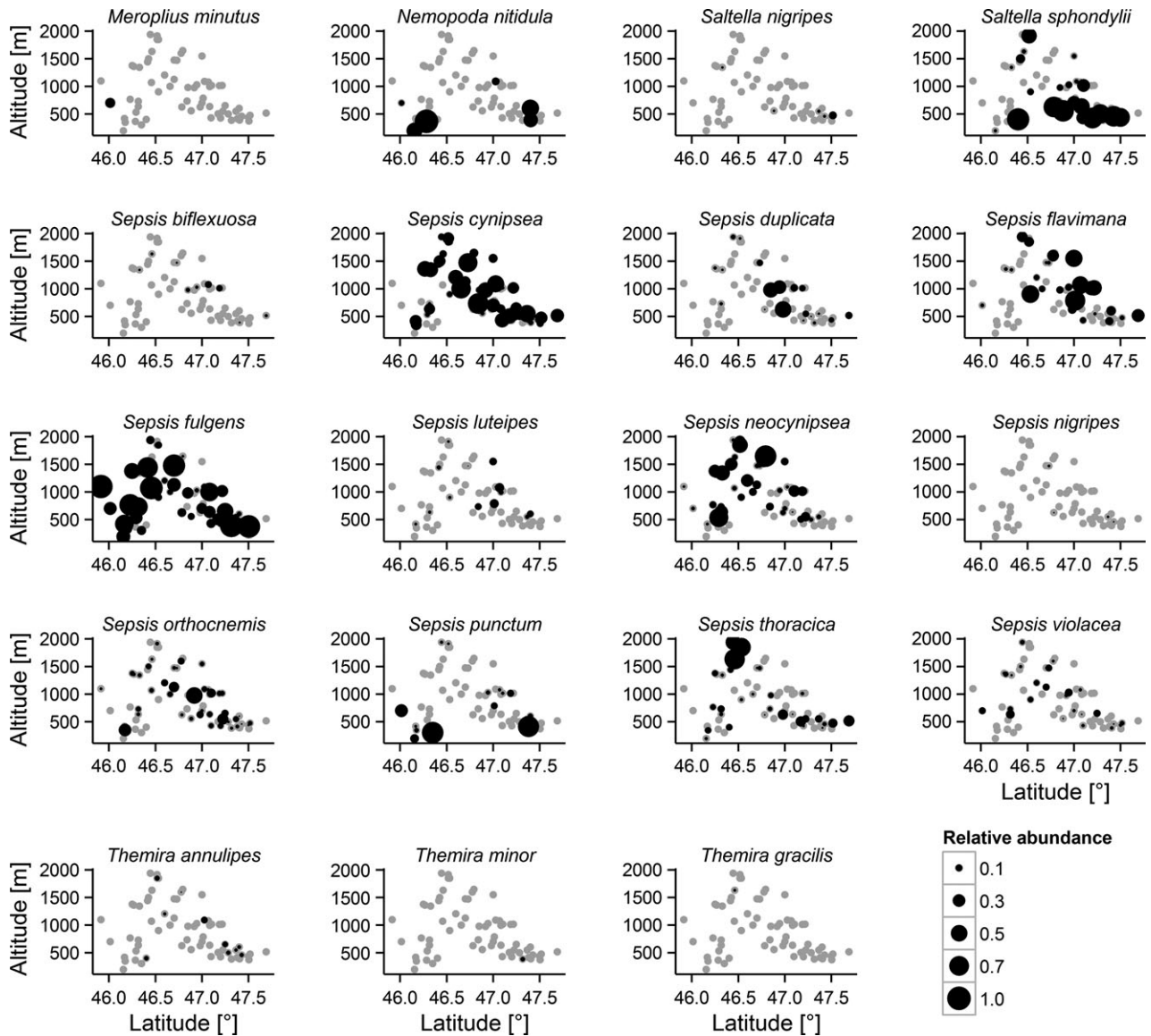


Fig. 2. Relative abundance of 19 sepsid species at 65 locations in Switzerland as a function of altitude and latitude, reflecting the relief of the country. Black dots indicate the presence of the species and are scaled to their relative abundance. Grey dots indicate locations where the species was not detected.

The species' elevational range sizes correlate positively with their elevational mid-point ($r = +0.59$, $P = 0.017$; Fig. 6), supporting Rapoport's rule. Wing loading correlates negatively with the mid-point of the elevational distribution of sepsid species ($r = -0.55$, $P = 0.028$; Fig. 6), but not quite significantly with its elevational range ($r = -0.44$, $P = 0.086$; data not shown). Wing aspect ratio does not correlate with either elevational range ($r = 0.04$, $P = 0.881$) nor mid-point ($r = 0$, $P = 1$).

Most of the 19 species show no altitudinal pattern. Upon excluding zero occurrences, only few species (*N. nitidula*, *Sa. sphondylii* and *S. punctum*) clearly favour low altitude habitats (negative correlations in Fig. S1), while

S. neocynipsea is the only species favouring high altitudes (positive correlation when including zero occurrences). Quadratic patterns, e.g. species favouring intermediate altitudes, are only indicated when the quadratic fit is better than the linear fit based on AIC: this was the case for *Sepsis biflexuosa*, *S. cynipsea*, *S. thoracica* and *S. duplicata* (Fig. S1).

Discussion

Our biogeographical analyses of sepsid flies originating from 116 locations, sampled over a large elevational

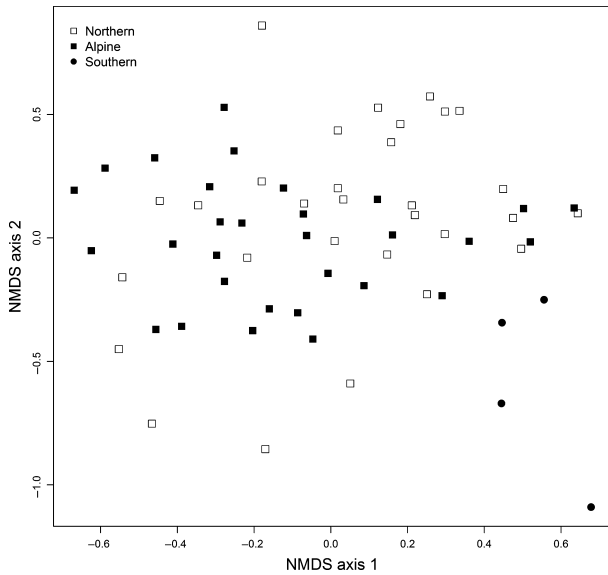


Fig. 3. Non-metric multidimensional scaling (NMDS) was used to visualise the similarity of samples based on species composition. The smaller the distance between two samples, the higher the similarity of the two species assemblages. Sampling locations are depicted as squares and circles, and their shading indicates the corresponding biogeographic area.

gradient, lead us to three main conclusions. First, the three biogeographic regions of the fauna show distinct species assemblages. Second, there are significant altitudinal gradients in terms of species richness and evenness, both of which increase with elevation; when controlled for area, regional species richness also increases with elevation. Third, species inhabiting high altitudes also have a broader elevational range, supporting Rapoport's rule. In the following, we first discuss these findings in the context of ecological adaptation and niche partitioning, and then further examine their implications for potential temporal

succession and differential foraging tactics enabling coexistence of sympatric species. We close by discussing proximate mechanisms that may underlie Rapoport's rule in sepsid flies across the study area.

The sepsid community south of the Alps clearly differs from northern communities due to a number of rare species exclusively or predominantly occurring in the south (*M. minutus*, *N. nitidula*, *T. annulipes*, *Sa. sphondylii* and *S. punctum*: Figs 1 and 2), indicating thermal niche differentiation. The northern lowland (*Mittelland*) and alpine communities overlap much more, although some separation is evident as some rare species almost exclusively occur in the lowlands (*Sa. nigripes*, *S. nigripes* and *T. annulipes*: Figs 1 and 2). This geographic differentiation relates to the altitudinal gradient discussed next, as some species, such as the common *S. punctum*, predominantly occur in the lowlands both north and south of the Alps, while the majority of the other common *Sepsis* species abound equally at alpine sites (Fig. 2).

We found an overall increase of species richness (0D) and evenness (1D) with altitude; also diversity (2D) is close to significance (Fig. 3). When correcting for the profound impact of area on species richness of elevational belts, an asymptotic exponential model fits the data best (Fig. 5). This is a rather unexpected pattern, since diversity peaks at intermediate elevations are the most often observed pattern when correcting elevational diversity gradients for area (Rahbek, 1995; Karger *et al.*, 2011; Herzog *et al.*, 2013). We suspect that if we were to increase sampling effort at even higher elevations, species diversity would and should eventually decrease again to support a hump-shaped, quadratic relationship. Being small, multi-voltine insects with short development times of about 2 weeks at room temperature (see Blanckenhorn *et al.*, 2013a), season length limitations should play a relatively minor role in limiting sepsid distributions at high altitudes and latitudes (Blanckenhorn & Demont, 2004), although at each species' specific low temperature threshold the development time will eventually become prohibitively

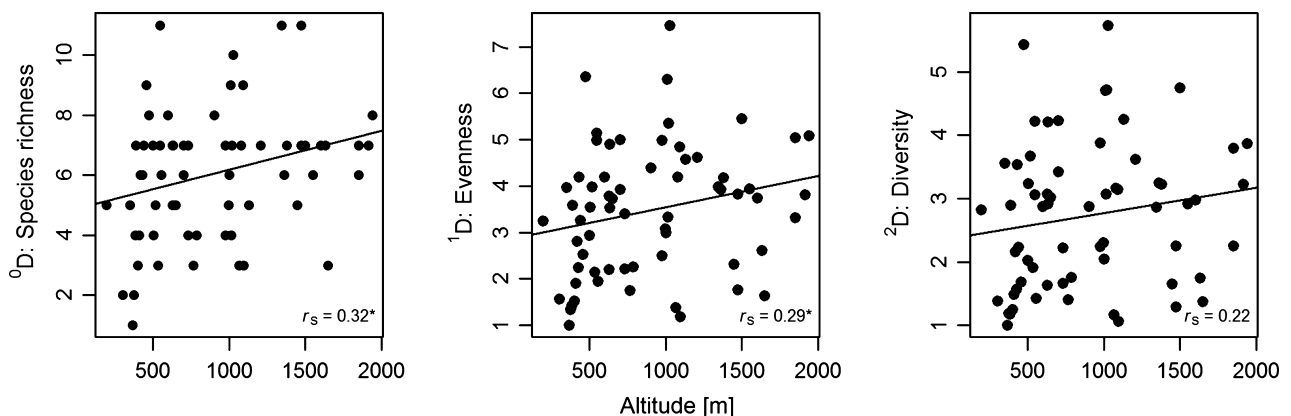


Fig. 4. Overall 0D (species richness), 1D (evenness) and 2D (diversity) for sepsid flies at all locations as a function of altitude ($n = 65$ locations with ≥ 20 specimens).

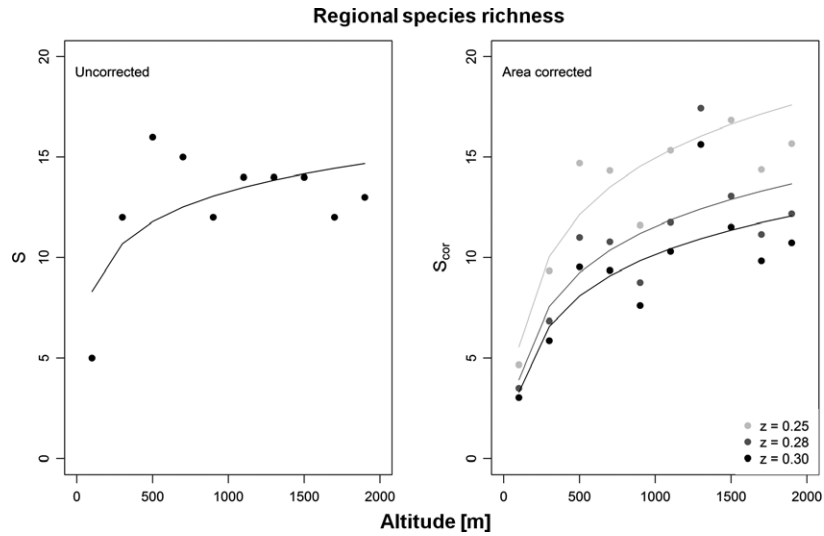


Fig. 5. Species richness per elevational belt of 200 m width follows an asymptotic exponential function (left). When correcting for area this pattern remains. Shading indicates three different values of assumed z (right) based on data for Europe (see Table S2).

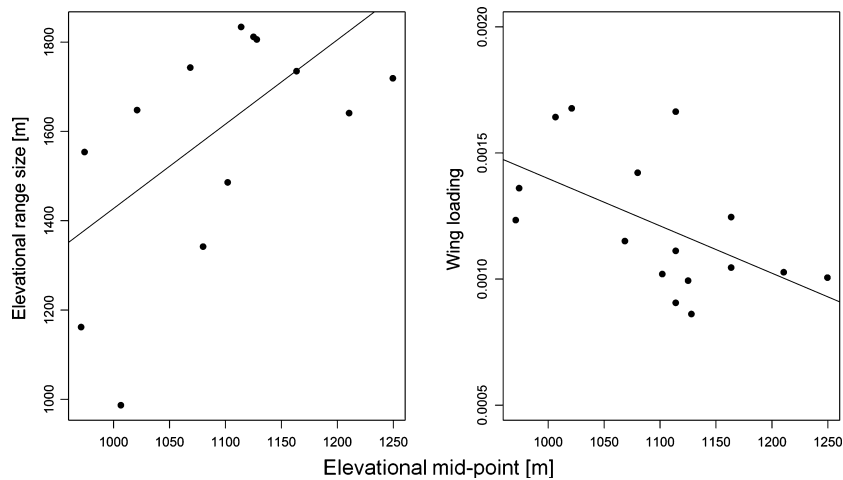


Fig. 6. Relationships of the elevational range size (left) and wing loading (ratio of thorax length to wing area; right) to the mid-point of the elevational distribution for sixteen species of Sepsidae.

long. Thus, cold temperatures and the type and/or lack of oviposition substrate will be most important in reducing species richness at high altitudes. The mechanisms leading to the particular pattern for sepsids observed here remain unclear, but could be mediated by low temperatures at high elevations and/or low humidity at low elevations (Rahbek, 1995).

In general, the diversity and availability of breeding substrates at a given location certainly limits the number of co-occurring species. There is great variation in the degree of substrate specialisation between sepsids. Ruminant dung is used for reproduction by all native *Sepsis* and *Saltella* species, although within the highly derived *Sepsis* clade (Zhao *et al.*, 2013) some specialist species almost exclusively breed on cow and sheep dung, whereas

other generalist species are unselective and reproduce in various kinds of vertebrate dung, sewage and rotting vegetation (Pont & Meier, 2002). Ruminant and especially cow dung is characterised by large amounts of resources per patch and typically small distances between dung pats on pastures. Nonetheless, for many species dung only remains suitable for reproduction during a short period of time, some species preferring fresh and others drier dung. This implies a certain degree of temporal niche partitioning, but may still force sympatric species to breed at the same time (Hanski & Cambefort, 1991; Püchel, 1993), thus creating high inter- and intra-specific competition for food and space. For instance, the sister species *S. cynipsea* and *S. neocynipsea* almost exclusively breed on fresh cow and sheep dung (Pont & Meier, 2002). On the other hand,

the small and slowly growing *S. duplicata* only visits old, crusty dung pats, using beetle tunnels to reach the moist interior of the dung pat for oviposition (Hammer, 1941). Such temporal separation of oviposition certainly represents niche differentiation enabling co-occurrence. Another partitioning mechanism within the same dung pat could relate to differential feeding behaviour. Internal filter organs of larvae strongly suggest that sepsid larvae feed on small particles such as bacteria or fungi (Pont & Meier, 2002). The actual food source, however, remains unknown, but leaves much potential for partitioning of larval foraging niches. Overall, the sympatric occurrence of up to 12 species around cow pastures remains puzzling and calls for further studies at the level of resource use, temporal succession and fine-scale spatial distribution.

Besides the general diversity increase with altitude, we found a significant positive relationship between the altitudinal range size and the distributional mid-point of sepsid species in Switzerland, supporting Rapoport's elevational rule (Stevens, 1992). Rapoport's rule is presumably mediated by climatic conditions of high altitude habitats being more variable, hence species occurring at high altitudes should be adapted to a broader range of environments, which enables them to occupy a wider elevational band. In contrast, species inhabiting lower elevations are presumably less selected to withstand strong climatic fluctuations and are therefore restricted to a narrow elevational band. Even though the term 'rule' is debatable (Gaston *et al.*, 1998), recent studies of other invertebrates indeed found evidence for Rapoport's rule (ants: Sanders, 2002; butterflies: Fleishman *et al.*, 1998; spiders: Chatzaki *et al.*, 2005; dung beetles: Herzog *et al.*, 2013).

Wing loading, but not wing aspect ratio, both used here as proxies for the dispersal capacity of our specimens, tends to decrease with elevation across species (Fig. 6). This supports the conclusion that sepsid species occurring at higher elevations might be better dispersers due to greater wing areas relative to body size (Angelo & Slansky, 1984). Yet, at the same time, the elevational range size seems uncorrelated with wing aspect ratio or wing loading. Good dispersal capacity should have an adaptive value in a highly variable environment, especially if the resource is characterised by a patchy distribution. Nevertheless, our approach used here cannot separate effects of wing morphology on local versus long-term dispersal, and requires further investigation.

To our knowledge, sepsids are far from being threatened by extinction, except perhaps for some species, such as *M. minutus*, that may suffer from the high hygienic standards in Central Europe (van der Goot, 1987). Nevertheless, sepsid flies are key members of the ruminant dung community and thus regularly exposed to residuals of veterinary medications (Floate *et al.*, 2005; Lumaret *et al.*, 2007; Jochmann *et al.*, 2011; Blanckenhorn *et al.*, 2013a). In the long term, such anthropogenic substances might contribute to a reduction in overall species diversity of this group and impede its ecosystem function (Blanckenhorn *et al.*, 2013a,b).

Here, we documented an elevational gradient in diversity, demonstrating that the assemblages of sepsid flies are characterised by a high degree of sympatry, especially at high altitudes. The actual niche partitioning mechanisms are poorly understood, yet differentiation of assemblages in major geographic regions and elevational abundance gradients of some species suggest involvement of thermal adaptation (Berger *et al.*, 2013). Furthermore, species occurring at higher altitudes appear to be better dispersers, which might be adaptive in a highly patchy environment. Subsequent studies on the temporal succession of sympatric species should yield further valuable insight into the factors driving niche differentiation in this group of flies.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12114:

Figure S1. Prevalent (negative, positive, or curvilinear) relationship of the relative abundance with altitude for 17 sepsid species in Switzerland. Grey dots indicate locations where the species was not detected, and are not included when fitting the line and calculating the linear correlation coefficients given in the upper right corner.

Table S1. List of all samples treated in this study including the corresponding coordinates, bioclimatic variables and the assigned biogeographical region. Locations of samples with 20 or more male individuals are marked with an asterisk.

Table S2. Species richness of sepsid flies per European country, data extracted from Ozerov (2005).

Table S3. Mean relative abundance of 19 sepsid species in the three main biogeographic regions of Switzerland.

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