**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2015

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

Rohner, Patrick T ; Bächli, Gerhard ; Pollini Paltrinieri, Lucia ; Duelli, Peter ; Obrist, Martin K ;
Jochmann, Ralf ; Blanckenhorn, Wolf U

Abstract: 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. Sepsidae are a family of acalyptrate 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. 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. 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. 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.

DOI: <https://doi.org/10.1111/icad.12114>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-111886>

Journal Article

Accepted Version

Originally published at:

Rohner, Patrick T; Bächli, Gerhard; Pollini Paltrinieri, Lucia; Duelli, Peter; Obrist, Martin K; Jochmann, Ralf; Blanckenhorn, Wolf U (2015). Distribution, diversity gradients and Rapoport's elevational rule in the black scavenger flies of the Swiss Alps (Diptera: Sepsidae). *Insect Conservation and Diversity*, 8(4):367-376.

DOI: <https://doi.org/10.1111/icad.12114>

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

Patrick T. Rohner¹, Gerhard Bächli², Lucia Pollini Paltrinieri³, Peter Duelli⁴, Martin K. Obrist⁴, Ralf Jochmann^{1,5}, Wolf U. Blanckenhorn^{1,2}

¹ Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

² Zoological Museum, University of Zurich, Karl Schmid-Strasse 4, CH-8006 Zurich, Switzerland

³ Museo Cantonale di Storia Naturale, Viale Carlo Cattaneo 4, CH-6901 Lugano, Switzerland

⁴ Swiss Federal Research Institute WSL, CH-8903, Birmensdorf, Switzerland

⁵ University of Bielefeld, Department of Evolutionary Biology, D-33615 Bielefeld, Germany

Insect Conservation and Diversity (2015) doi: [10.1111/icad.12114](https://doi.org/10.1111/icad.12114)

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 is 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 acalyptrate flies strongly associated with decaying organic matter and vertebrate dung, and characterized 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 meters were available in ethanol collections of various Swiss museums.

3. Nineteen species encompassing all native genera (*Meroplius*, *Nemopoda*, *Saltella*, *Sepsis*, *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.

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 (Blanckenhorn & Demont, 2004; Blanckenhorn *et al.*, 2006; Gaston & Blackburn, 2000; 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 (Herzog *et al.*, 2013; Rahbek, 1995; Zou *et al.*, 2014). One theory that connects elevation and species distribution patterns is Rapoport's elevational rule (Gaston *et al.*, 2008; Stevens, 1992), predicting that species occurring at higher elevations should show larger altitudinal ranges. This not entirely uncontroversial "rule" (Gaston *et al.*, 1998) bases 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 palaeartic dung ecosystems is based on studies of 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 (Bertone *et al.*, 2005; Finn *et al.*, 1999; Hanski & Cambefort, 1991; 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; Papp, 1992; Skidmore, 1991). These dung-decomposing insects fulfil an important ecosystem function all over the world and are therefore of ecological relevance.

Sepsid flies (Diptera: Sepsidae) generally depend on decaying organic matter for reproduction and larval development. Many species are specialized on vertebrate dung and occur in very high numbers especially near livestock excrements (Pont & Meier, 2002). Aside from being an integral part of the fauna breaking down the dung in many parts of the world, and thus of practical relevance in the ecotoxicology of veterinary medical products (Blanckenhorn *et al.*, 2013a, 2013b; Puniamoorthy *et al.*, 2014), sepsid flies are also rapidly becoming model organisms in behavioural ecology, evolutionary biology, and phylogenetics (Berger *et al.*, 2013; Blanckenhorn *et al.*, 2000; Bowsher & Nijhout, 2007; Eberhard, 2001; Ingram *et al.*, 2008). Yet very little is known about their spatial distribution, community and general ecology on a local, regional but 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 & 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 twelve 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 scrutinized.

Switzerland is particularly well suited for studies of geographic and elevational diversity gradients in the temperate region, because 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 (Ang *et al.*, 2013; Hennig, 1949; Pont, 1979; Pont & Meier, 2002). 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 Appendix A1. The samples cover an altitudinal range from 200 to 2000 meters above sea level, 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, with a corresponding decrease in collection effort because 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 will be 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 total sample to 65 locations. 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 meters. 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 (z) in log-log space for Europe (see Appendix A2), which was used to correct regional species richness for area. The slope of the species-area relationship of sepsids in Europe amounts to $z = 0.28$. Since the species-area relationship (SAR) may differ 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. However, the absolute scale of species richness is 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 midpoint and the altitudinal range size of sixteen of the nineteen species present in the dataset (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 (depending on the amount of available specimens) 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 between the three major geographic regions in Switzerland. ANOSIM compares Bray-Curtis dissimilarities between vs. 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 meters above sea level, although valleys within the Central Alps were also considered alpine. Lower sites north and south of the alpine region were considered 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. Because the three main variables of interest altitude, temperature and precipitation naturally are strongly correlated (altitude and temperature: $r = -0.86$, $P < 0.001$; altitude and precipitation: $r = 0.55$, $P < 0.001$), leading 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

Out of the twenty-six species of Sepsidae ever recorded in Switzerland (Haenni, 1998; Merz *et al.*, 2001), nineteen species were present in the dataset (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*, *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, in Fig. 2 (65 locations).

Biogeographic comparison of community structure

The analysis of similarities (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 (*Meroplius*, *Nemopoda*, *Themira*; Figs. 1 & 2). The northern and alpine communities overlap entirely along NMDS axis 1, while 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 occurring in the northern lowlands (*Sa. nigripes*, *S. nigripes*, *T. annulipes*; Figs. 1 & 2; Appendix A3). Note also 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 could be 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. However, there is no correlation between sample size and altitude ($r_s = +0.11$, $P = 0.245$).

Altitudinal patterns of species diversity: elevational belts

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

The species' elevational range sizes correlate positively with their elevational midpoint ($r = +0.59$, $P = 0.017$; Fig. 6), supporting Rapoport's rule. Wing loading also correlates negatively with the midpoint of the elevational distribution of sepsid species ($r = -0.55$, $P = 0.028$; Fig. 6), but not quite significantly with its elevational range ($r = -0.44$, $P = 0.086$; not shown). Wing aspect ratio does not correlate with either elevational range ($r = 0.04$, $P = 0.881$) or midpoint ($r = 0$, $P = 1$).

Most of the 19 species show no altitudinal pattern. When excluding zero occurrences (grey dots), only few species (*N. nitidula*, *Sa. sphondylii*, *S. punctum*) clearly favour low altitude habitats (negative correlations in supplementary Fig. 7), while *S. neocynipsea* is the only species favouring high altitudes (positive correlation when including zero occurrences). Quadratic patterns, i.e. 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* (Supplementary Fig. 7).

Discussion

Our biogeographic analyses of sepsid flies originating from 116 locations sampled over a large elevational 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 increased 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*, *S. punctum*: Figs. 1 & 2), indicating thermal niche differentiation. The northern lowland (*Mittelland*) and alpine communities overlap much more, although some separation is also evident in that some rare species almost exclusively occur in the lowlands (*Sa. nigripes*, *S. nigripes*, *T. annulipes*: Figs. 1 & 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 (Figs. 2).

We found an overall increase of species richness (0D) and evenness (1D) with altitude, with diversity (2D) also 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 (Herzog *et al.*, 2013; Karger *et al.*, 2011; Rahbek, 1995). However, we suspect that if we would increase sampling effort to find sepsids 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 two 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 development time will eventually become prohibitively 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 lower temperatures at high elevations and/or lower 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 sepsid species. Ruminant dung is used for reproduction by all native *Sepsis* and *Saltella*, 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 not choosy and reproduce in various kinds of vertebrate dung, sewage and rotting vegetation (Pont & Meier, 2002). Ruminant and especially cow dung is characterized by large amounts of resource per patch and typically small distances between dung pats on pastures. However, for many species dung only remains suitable for reproduction during a short time period, some preferring fresh and others drier dung. This implies some 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). However, the actual food source remains unknown but leaves much potential for partitioning of larval foraging niches. Overall, the sympatric occurrence of up to twelve species around cow pastures remains puzzling and calls for further studies at the level of resource use, temporal succession and fine-scale spatial distribution.

Along with 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, enabling 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 such evidence for Rapoport's rule (ants: Sanders, 2002; butterflies: Fleishman *et al.*, 1998; spiders: Chatzaki *et al.*, 2005; dung beetles: Herzog *et al.*, 2005) .

Wing loading, but not wing aspect ratio, both used here as proxies for 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 (although a slight negative trend was also evident). Good dispersal capacity should have adaptive value in a highly variable environment, especially if the resource is characterized by a patchy distribution. However, in the end our approach here cannot separate effects of wing morphology on local vs. 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 (Blanckenhorn *et al.*, 2013a; Floate *et al.*, 2005; Jochmann *et al.*, 2011; Lumaret *et al.*, 2007). In the long term, such anthropogenic substances might contribute to a reduction in overall species diversity of this group and impede their ecosystem function (Blanckenhorn *et al.*, 2013a, 2013b).

We here documented an elevational gradient in diversity, demonstrating that the assemblages of sepsid flies are characterized 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

We thank the various collectors that contributed to the dataset treated here. Considering the fact that many of the samples are older than the first author, we thank the Zoological Museum Zurich, the Natural History Museum Neuchâtel and the Museo Cantonale di Storia Naturale in Lugano for storing the samples for years on end. Further, we thank Nalini Puniamoorthy and especially Martin A. Schäfer for helpful comments and vivid discussions on the manuscript. Ralf Jochmann acknowledges funding from the Velux Stiftung.

References

- Addo-Bediako, A., Chown, S.L., & Gaston, K.J. (2000) Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B-Biological Sciences*, **267**, 739-745.
- Ang, Y., Puniamoorthy, J., Pont, A.C., Bartak, M., Blanckenhorn, W.U., Eberhard, W.G., Puniamoorthy, N., Silva, V.C., Munari, L., & Meier, R. (2013) A plea for digital reference collections and other science-based digitization initiatives in taxonomy: Sepsidnet as exemplar. *Systematic Entomology*, **38**, 637-644.
- Angelo, M.J. & Slansky, F. (1984) Body Building by Insects - Trade-Offs in Resource-Allocation with Particular Reference to Migratory Species. *Florida Entomologist*, **67**, 22-41.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95-99.
- Berger, D., Postma, E., Blanckenhorn, W.U., & Walters, R.J. (2013) Quantitative genetic divergence and standing genetic (co)variance in thermal reaction norms along latitude. *Evolution*, **67**, 2385-2399.
- Bertone, M., Green, J., Washburn, S., Poore, M., Sorenson, C., & Watson, D.W. (2005) Seasonal activity and species composition of dung beetles (Coleoptera : Scarabaeidae and Geotrupidae) inhabiting cattle pastures in North Carolina. *Annals of the Entomological Society of America*, **98**, 309-321.
- Blackburn, T.M., Gaston, K.J., & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165-174.
- Blanckenhorn, W.U. & Demont, M. (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: Two ends of a continuum? *Integrative and Comparative Biology*, **44**, 413-424.
- Blanckenhorn, W.U., Muhlhauser, C., Morf, C., Reusch, T., & Reuter, M. (2000) Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea*. *Ethology*, **106**, 577-593.
- Blanckenhorn, W.U., Puniamoorthy, N., Schafer, M.A., Scheffczyk, A., & Rombke, J. (2013a) Standardized laboratory tests with 21 species of temperate and tropical sepsid flies confirm their suitability as bioassays of pharmaceutical residues (ivermectin) in cattle dung. *Ecotoxicology and Environmental Safety*, **89**, 21-28.
- Blanckenhorn, W.U., Puniamoorthy, N., Scheffczyk, A., & Rombke, J. (2013b) Evaluation of ecotoxicological effects of the parasiticide moxidectin in comparison to ivermectin in 11 species of dung flies. *Ecotoxicology and Environmental Safety*, **89**, 15-20.
- Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W., & Ashton, K.G. (2006) When Rensch meets Bergmann: Does sexual size dimorphism change systematically with latitude? *Evolution*, **60**, 2004-2011.

Bowsher, J.H. & Nijhout, H.F. (2007) Evolution of novel abdominal appendages in a sepsid fly from histoblasts, not imaginal discs. *Evolution & Development*, **9**, 347-354.

Brown, J.H. & Maurer, B.A. (1989) Macroecology - the Division of Food and Space among Species on Continents. *Science*, **243**, 1145-1150.

Chatzaki, M., Lymberakis, P., Markakis, G., & Mylonas, M. (2005) The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *Journal of Biogeography*, **32**, 813-831.

Clarke, K.R. (1993) Nonparametric Multivariate Analyses of Changes in Community Structure. *Australian Journal of Ecology*, **18**, 117-143.

Cox, T.F. & Cox, A.A. (2000) Multidimensional Scaling, Second Edition Taylor & Francis.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668-6672.

Dixon, P. (2003) VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*, **14**, 927-930.

Eberhard, W.G. (2001) Species-specific genitalic copulatory courtship in sepsid flies (Diptera, Sepsidae, Microsepsis) and theories of genitalic evolution. *Evolution*, **55**, 93-102.

Finn, J.A., Gittings, T., & Giller, P.S. (1999) Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland. *Ecological Entomology*, **24**, 24-36.

Fleishman, E., Austin, G.T., & Weiss, A.D. (1998) An empirical test of Rapoport's rule: Elevational gradients in montane butterfly communities. *Ecology*, **79**, 2482-2493.

Floate, K.D., Wardhaugh, K.G., Boxall, A.B.A., & Sherratt, T.N. (2005) Fecal residues of veterinary parasiticides: Nontarget effects in the pasture environment. *Annual Review of Entomology*, **50**, 153-179.

Gaston, K.J. & Blackburn, T.M. (2000) Pattern and Process in Macroecology Blackwell Science.

Gaston, K.J., Blackburn, T.M., & Spicer, J.I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology & Evolution*, **13**, 70-74.

Gaston, K.J., Chown, S.L., & Evans, K.L. (2008) Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, **35**, 483-500.

Gotelli, N.J. & Chao, A. (2013). Measuring and Estimating Species Richness, Species Diversity, and Biotic Similarity from Sampling Data. In Encyclopedia of Biodiversity (ed. by L. S.A.), Vol. 5, pp. 195-211. MA: Academic Press, Waltham.

Haenni, J.-P. (1998). Sepsidae. In Diptera - Checklist. Fauna Helvetica (ed. by B. Merz, G. Baechli, J.-P. Haenni & Y. Gonseth), Vol. 1, pp. 249-250. Schweizerische Entomologische Gesellschaft, Neuchâtel.

Hammer, O. (1941) Biological and ecological studies on flies associated with pasturing cattle and their excrement. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, **105**, 140-393.

Hanski, I. & Cambefort, Y. (1991) Dung Beetle Ecology Princeton University Press, Princeton.

Hennig, W. (1949). 39a. Sepsidae. In Die Fliegen der palaearktischen Region (ed. by E. Lindner), pp. 1-92. Schweizerbart, Stuttgart.

Herzog, S.K., Hamel-Leigue, A.C., Larsen, T.H., Mann, D.J., Soria-Auza, R.W., Gill, B.D., Edmonds, W.D., & Spector, S. (2013) Elevational Distribution and Conservation Biogeography of Phanaeine Dung Beetles (Coleoptera: Scarabaeinae) in Bolivia. *Plos One*, **8**.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Ingram, K.K., Laamanen, T., Puniamoorthy, N., & Meier, R. (2008) Lack of morphological coevolution between male forelegs and female wings in *Themira* (Sepsidae: Diptera: Insecta). *Biological Journal of the Linnean Society*, **93**, 227-238.

Jochmann, R., Blanckenhorn, W.U., Bussiere, L., Eirkson, C.E., Jensen, J., Kryger, U., Lahr, J., Lumaret, J.P., Rombke, J., Wardhaugh, K.G., & Floate, K.D. (2011) How to test nontarget effects of veterinary pharmaceutical residues in livestock dung in the field. *Integrated Environmental Assessment and Management*, **7**, 287-96.

458 Karger, D.N., Kluge, J., Kromer, T., Hemp, A., Lehnert, M., & Kessler, M. (2011) The effect of area on
 459 local and regional elevational patterns of species richness. *Journal of Biogeography*, **38**, 1177-1185.
 460 Klepsatel, P., Galikova, M., Huber, C.D., & Flatt, T. (2014) Similarities and differences in altitudinal
 461 versus latitudinal variation for morphological traits in *Drosophila melanogaster*. *Evolution*, **68**, 1385-
 462 98.
 463 Lee, C. & Wall, R. (2006) Distribution and abundance of insects colonizing cattle dung in South West
 464 England. *Journal of Natural History*, **40**, 1167-1177.
 465 Lumaret, J.P., Alvinerie, M., Hempel, H., Schallinass, H.J., Claret, D., & Rombke, J. (2007) New
 466 screening test to predict the potential impact of ivermectin-contaminated cattle dung on dung
 467 beetles. *Veterinary Research*, **38**, 15-24.
 468 McCain, C.M. (2007) Area and mammalian elevational diversity. *Ecology*, **88**, 76-86.
 469 Menendez, R., Gonzalez-Megias, A., Jay-Robert, P., & Marquez-Ferrando, R. (2014) Climate change
 470 and elevational range shifts: evidence from dung beetles in two European mountain ranges. *Global*
 471 *Ecology and Biogeography*, **23**, 646-657.
 472 Merz, B., Bächli, G., & Haenni, J.-P. (2001) Erster Nachtrag zur Checkliste der Diptera der Schweiz.
 473 *Mitteilungen der Entomologischen Gesellschaft Basel*, **51**, 110-140.
 474 Obrist, M.K. & Duelli, P. (2010) Rapid biodiversity assessment of arthropods for monitoring average
 475 local species richness and related ecosystem services. *Biodiversity and Conservation*, **19**, 2201-2220.
 476 Ozerov, A.L. (2005) World catalogue of the family Sepsidae (Insecta: Diptera). *Zoologicheskie*
 477 *issledovania (Zoological Studies)*, **8**, 1-74.
 478 Papp, L. (1992) Fly Communities in Pasture Dung - Some Results and Problems (Diptera). *Acta*
 479 *Zoologica Hungarica*, **38**, 75-88.
 480 Pont, A.C. (1979) Sepsidae. Diptera Cyclorrhapha, Acalyptrata. *Handbooks for the Identification of*
 481 *British Insects*, **10**, 1-35.
 482 Pont, A.C. & Meier, R. (2002) The Sepsidae (Diptera) of Europe. *Fauna Entomologica Scandinavica*,
 483 **37**, 1-221.
 484 Püchel, F. (1993) Untersuchungen über die Besiedlung von Kuhdung durch Sepsiden (Diptera),
 485 Universität Bielefeld, Bielefeld.
 486 Puniamoorthy, N., Schäfer, M.A., Römbke, J., Meier, R., & Blanckenhorn, W.U. (2014) Ivermectin
 487 sensitivity is an ancient trait affecting all ecdysozoa but shows phyloge-netic clustering among sepsid
 488 flies. *Evolutionary Applications* **7**, 548-554.
 489 QGIS Development Team. (2009) *QGIS Geographic Information System*. Open Source Geospatial
 490 Foundation Project.
 491 Rahbek, C. (1995) The Elevational Gradient of Species Richness - a Uniform Pattern. *Ecography*, **18**,
 492 200-205.
 493 Rahbek, C. (1997) The relationship among area, elevation, and regional species richness in
 494 neotropical birds. *American Naturalist*, **149**, 875-902.
 495 Rohner, P.T., Ang, Y., Lei, Z., Puniamoorthy, N., Blanckenhorn, W.U., & Meier, R. (2014) Genetic data
 496 confirm the species status of *Sepsis nigripes* Meigen (Diptera : Sepsidae) and adds one species to the
 497 Alpine fauna while questioning the synonymy of *Sepsis helvetica* Munari. *Invertebrate Systematics*,
 498 **28**, 555-563.
 499 Sanders, N.J. (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport's
 500 rule. *Ecography*, **25**, 25-32.
 501 Skidmore, P. (1991) *Insects of the British Cow-Dung Community*. Richmond Publishing, Slough,
 502 United Kingdom.
 503 Stevens, G.C. (1992) The Elevational Gradient in Altitudinal Range - an Extension of Rapoport
 504 Latitudinal Rule to Altitude. *American Naturalist*, **140**, 893-911.
 505 van der Goot, V.S. (1987) *Meroplus minutus* (Wiedemann)(Dipt. Sepsidae) extinct in the Low
 506 Countries. *Entomologist's monthly Magazine*, **123**.
 507 Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S* Springer.

Zhao, L., Annie, A.S., Amrita, S., Yi, S.K., & Rudolf, M. (2013) Does better taxon sampling help? A new phylogenetic hypothesis for Sepsidae (Diptera: Cyclorrhapha) based on 50 new taxa and the same old mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution*, **69**, 153-64.

Zou, Y., Sang, W.G., Zhou, H.C., Huang, L.Y., & Axmacher, J.C. (2014) Altitudinal diversity patterns of ground beetles (Coleoptera: Carabidae) in the forests of Changbai Mountain, Northeast China. *Insect Conservation and Diversity*, **7**, 161-171.

Figure 1: Species records for nineteen 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.

Figure 2: Relative abundance of nineteen 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.

Figure 3: Non-metric multidimensional scaling (NMDS) was used to visualize 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.

532

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

535

536

537

538 **Figure 5:** Species richness per elevational belt of 200m width follows an asymptotic exponential (left). When correcting for area this
 539 pattern remains. Colours indicate three different values of assumed z (right) based on data for Europe (see Appendix A2).

540

541 **Figure 6:** Relationships of the elevational range size (left) and wing loading (ratio of thorax length to wing area; right) to the midpoint
 542 of the elevational distribution for sixteen species of Sepsidae.

543

544

545 **Supplementary Data**

546 **Table A1:** Description of the entire data set. Locations of samples with 20 or more male individuals are marked with an asterisk.

Location	Collection	Year	Kanton	Latitude	Longitude	Altitude	Geography	Number of subsamples	Precipitation (mm)	Annual mean temperature (°C)
Airolo*	Pollini	1991, 1992	TI	46.533	8.617	1850	alpine	9	1386	6.1
Alptal*	Duelli	2000	SZ	47.083	8.717	996	alpine	1	1332	6.8
Alptal*	Jochmann	2008	SZ	47.067	8.712	1080	alpine	1	1342	6.7
Alt St. Johann*	Jochmann	2007, 2008	SG	47.187	9.275	1011	alpine	2	1237	6.7
Aquacalda*	Bächli	2001	TI	46.533	8.833	902	alpine	1	1546	2.8
Astano*	Pollini	1991, 1992	TI	46.013	8.817	700	southern	11	1304	9.8
Äugst am Albis	Jochmann	2007	ZH	47.288	8.489	767	northern	1	1171	8.4
Beatenberg*	Duelli	2000, 2001, 2004	BE	46.700	7.783	1129	alpine	3	1614	2.9
Benken	Jochmann	2008	SG	47.190	9.008	534	northern	1	1103	9.7
Beringen*	Jochmann	2007	SH	47.690	8.570	516	northern	1	994	8.9
Bernex*	Bächli	2000	GE	46.167	6.067	420	northern	1	967	9.9
Biasca*	Bächli	1995, 1997	TI	46.350	8.967	303	southern	2	1260	11.1
Biasca	Pollini	2009	TI	46.350	8.967	303	southern	1	1257	11.2
Biberburg*	Bächli	2011	SZ	NA	NA	NA	alpine	1	NA	NA
Bignasco	Pollini	1991, 1992	TI	46.333	8.600	1410	alpine	2	1316	7.4
Bolle di Magadino	Bächli	1995	TI	46.156	8.865	196	southern	2	1269	11.7
Bolle di Magadino*	Pollini	2000	TI	46.164	8.920	194	southern	5	1284	11.7
Brunnadern	Jochmann	2008	SG	47.314	9.132	905	alpine	1	1237	7
Bürchen*	Bächli	1993, 2001	VS	46.267	7.817	1360	alpine	2	1401	4.1
Camorino	Pollini	1992, 1993, 2009	TI	46.167	9.000	223	southern	1	1298	11.7

Cartigny*	Bächli	2000	GE	46.175	6.020	350	northern	1	956	10
Castaneda	Pollini	1992	GR	46.258	9.140	1495	alpine	4	1289	10.6
Cerentino	Bächli	1997	TI	46.305	8.550	981	alpine	1	1273	8.2
Cevio	Pollini	2010	TI	46.317	8.602	421	southern	1	1212	10.2
Chancy	Bächli	2004	GE	46.150	5.967	360	southern	1	925	10.4
Changins*	Duelli	2001, 2004	VD	46.400	6.233	403	northern	2	965	9.9
Chironico*	Pollini	1992	TI	46.417	8.850	1445	alpine	4	1320	7.9
Courlevon*	Duelli	2001, 2005, 2000	FR	46.883	7.100	556	northern	5	929	8.5
Cudrefin	Duelli	2000	VD	46.950	7.017	434	northern	1	909	9
Dierikon*	Duelli	2001	LU	47.097	8.372	432	northern	1	1109	9.5
Dietikon*	Bächli	1989, 1991, 1995	ZH	47.406	8.404	388	northern	5	1055	9.4
Dischmatal*	Bächli	1990, 1991, 1992	GR	46.776	9.870	1600	alpine	8	992	3.2
Einsiedeln*	Jochmann	2007	SZ	47.103	8.733	1019	alpine	1	1313	7
Elm (Wichlen)*	Bächli	2001	GL	46.917	9.167	977	alpine	1	1263	7.1
Felsberg*	Jochmann	2008	GR	46.842	9.450	732	northern	1	1149	9.2
Ftan*	Bächli	1996	GR	46.794	10.249	1648	alpine	1	872	3.2
Fusio	Bächli	1997	TI	46.433	8.650	1234	alpine	1	1412	5.4
Glarus	Bächli	1991, 1995	GL	47.033	9.067	1102	alpine	2	1207	8.5
Gordola	Pollini	2009	TI	46.179	8.865	222	southern	1	1274	11.5
Greppen	Jochmann	2008	LU	47.057	8.446	886	northern	1	1307	7.1
Guttannen*	Bächli	1993	BE	46.656	8.287	1000	alpine	1	1327	6.4
Guttet-Feschel*	Bächli	1993	VS	46.327	7.665	1345	alpine	2	1434	3.9
Hönggerberg*	Bächli	1989, 1991, 1994, 1995, 1997	ZH	47.400	8.500	601	northern	10	1071	9.4
Jeizinen * (Gampel-Bratsch)	Bächli	1999, 2001, 2004	VS	46.315	7.740	634	northern	4	883	8.8
Kaltbrunn*	Jochmann	2007, 2008	SG	47.225	9.012	548	northern	2	1143	8.8
Köniz	Jochmann	2007	BE	46.921	7.385	683	northern	1	954	8.3

Künten*	Jochmann	2007	AG	47.383	8.325	413	northern	1	1033	9.6
La Dole*	Bächli	2004	VD	46.425	6.100	1500	alpine	1	1689	4.1
La-Chaux-des-Breuleux*	Bächli	2001	JU	47.217	7.033	1016	alpine	1	1284	6.1
Landquart	Bächli	1980	GR	46.950	9.567	563	northern	1	1121	9.2
Lenk*	Bächli	1996	BE	46.457	7.443	1068	alpine	1	1113	6.4
Lenzerheide	Bächli	1994, 1998	GR	46.729	9.557	1473	alpine	1	1141	4.6
Lenzerheide*	Rohner	2013	GR	46.729	9.557	1473	alpine	1	1141	4.6
Leuk-Platten*	Bächli	1996, 2004	VS	46.317	7.633	731	northern	2	987	7.4
Lommis*	Bächli	2007	TG	47.517	8.983	475	northern	1	1023	9.3
Losone	Pollini	1991, 1992	TI	46.167	8.780	275	southern	5	1245	11.5
Luzern	Bächli	2006	LU	47.083	8.267	436	northern	1	1123	9.2
Männedorf	Jochmann	2007	ZH	47.264	8.696	579	northern	1	1140	8.9
Matt*	Jochmann	2007	GL	46.945	9.169	1028	alpine	1	1247	7.4
Medeglia	Pollini	1991, 1993	TI	46.117	8.967	945	alpine	2	1309	8.7
Merishausen	Bächli	1992	SH	47.761	8.609	533	northern	1	1031	8.1
Mondte San Giorgio*	Bächli	1995	TI	45.914	8.950	1097	alpine	1	1287	8.6
Monteggio	Pollini	2009	TI	45.995	8.808	420	southern	1	1305	10.8
Mörel	Bächli	2010	VS	46.367	8.033	746	northern	1	1499	3.5
Müllingen	Jochmann	2008	AG	47.454	8.232	459	northern	1	1031	9.3
Niedermuhlern*	Jochmann	2007	BE	46.850	7.440	978	alpine	1	1097	7
Nuvilly*	Duelli	2000, 2001, 2004	FR	46.783	6.831	629	northern	5	1015	8
Oberalppass	Bächli	1991	GR	46.659	8.671	2044	alpine	1	1818	0.2
Oberriet	Jochmann	2008	SG	47.336	9.576	465	northern	1	1120	9.1
Oetwil	Bächli	1996	ZH	47.431	8.394	410	northern	1	1074	9.1
Olivone	Pollini	1991, 1992, 1993	TI	46.530	8.942	1760	alpine	5	1318	7.5
Origlio	Bächli	1988	TI	46.050	8.950	452	southern	2	1326	10
Osco	Pollini	1991, 1992	TI	46.494	8.781	1700	alpine	5	1394	5.9
Osogna	Pollini	1991, 1993	TI	46.317	8.983	1705	alpine	2	1266	11.3

Othmarsingen	Jochmann	2008	AG	47.395	8.224	653	northern	1	1037	9.3
Pian Segna	Pollini	1991, 1992, 1993	TI	46.199	8.639	1175	alpine	5	1265	9.3
Piora*	Pollini	2010	TI	46.519	8.705	1850	alpine	1	1430	5.2
Pragelpass*	Bächli	1991	SZ	46.999	8.869	1548	alpine	1	1541	3.8
Quinto*	Pollini	1992	TI	46.519	8.705	1815	alpine	13	1430	5.2
Rapperswil-Jona	Jochmann	2008	SG	47.226	8.909	503	northern	1	1112	9.4
Robiei*	Bächli	2008	TI	46.446	8.517	1940	alpine	1	1705	0.9
Roggwil*	Duelli	2000, 2001, 2004, 2005	TG	47.500	9.383	440	northern	4	1065	9
Romoos*	Jochmann	2008	LU	47.013	8.027	786	northern	1	1147	7.9
Rothenbrunnen	Bächli	1996	GR	46.770	9.423	625	northern	1	1160	9.2
Rottenschwil*	Bächli	2008	AG	47.317	8.367	387	northern	1	1063	9.5
Rovio	Pollini	2009	TI	45.934	8.987	497	southern	1	1306	10.1
Rümlingen*	Duelli	2001, 2002, 2004	BE	47.426	7.850	459	northern	3	960	9.1
Ruswil*	Duelli	2001, 2005	LU	47.083	8.117	634	northern	4	1142	8.3
S. Bernardino*	Pollini	1991, 1992	GR	46.462	9.192	1630	alpine	18	1338	4.1
Saas	Bächli	2012	GR	46.917	9.800	988	alpine	1	1039	5.1
Savognin*	Bächli	1988	GR	46.598	9.600	1207	alpine	1	1089	6.4
Schänis	Duelli	2005	SG	47.150	9.050	420	northern	1	1145	9.1
Schlossrued*	Duelli	2000, 2001, 2004, 2005	AG	47.283	8.083	499	northern	4	1126	8.2
Schwändital*	Duelli	2001	SG	47.000	9.067	701	northern	1	1184	9.1
Sedrun	Bächli	1991	GR	46.680	8.775	1405	alpine	1	1463	4.7
Senarclens	Duelli	2004	VD	46.601	6.488	582	northern	1	1030	8.7
Siders*	Bächli	1996	VS	46.292	7.534	533	northern	1	764	9.2
Someo*	Bächli	1997	TI	46.283	8.667	366	southern	1	1233	10.5
Stabio	Pollini	2009	TI	45.850	8.940	352	southern	1	1300	11.1
Steinhausen*	Duelli	2000, 2005	ZG	47.200	8.467	427	northern	2	1113	9.3
Sumvitg	Bächli	1991	GR	46.730	8.933	1056	alpine	1	1328	6.9
Sursee*	Bächli	2004	LU	47.174	8.108	504	northern	1	1078	8.9

Susch	Bächli	1996	GR	46.750	10.067	1438	alpine	1	997	2.2
Tinizong-Rona	Bächli	2007	GR	46.583	9.617	1350	alpine	1	1113	3.6
Troistorrents*	Bächli	2004	VS	46.227	6.915	765	northern	1	1041	7.3
Uitikon*	Duelli	2001, 2004, 2005	ZH	47.367	8.467	550	northern	3	1148	8.4
Untersiggenthal*	Bächli	1991	AG	47.506	8.253	375	northern	1	1004	9.5
Visp	Duelli	2001	VD	46.283	7.867	658	northern	1	1242	5.8
Visperterminen*	Bächli	1998, 2004	VS	46.250	7.900	1378	alpine	2	1328	4.9
Vitznau	Jochmann	2007	LU	47.014	8.503	1121	alpine	1	1385	6.2
Vorauen*	Bächli	1991, 1995	GL	47.026	8.944	1090	alpine	2	1327	6.6
Weissenstein*	Bächli	2006	SO	47.250	7.533	650	northern	1	1204	6.7
Wohlen*	Jochmann	2007	BE	46.976	7.352	629	northern	1	968	8.2
Würenlingen	Bächli	1991	AG	47.533	8.261	370	northern	1	1024	9.2
Zernez*	Bächli	1996	GR	46.700	10.100	1474	alpine	2	847	4.7
Zürich	Bächli	1993	ZH	47.379	8.541	408	northern	1	1079	9.3

547 **Table A2:** National species richness of Sepsidae, data extracted from Ozerov
548 (2005).

Country	Area (km²)	log(Area)	S	log(S)
Albania	28748	4.46	3	0.48
Austria	83858	4.92	22	1.34
Belarus	207600	5.32	7	0.85
Belgium	30510	4.48	20	1.30
Bulgaria	110910	5.04	9	0.95
Croatia	56542	4.75	5	0.70
Cyprus	9251	3.97	5	0.70
Czech Republic	78866	4.90	26	1.41
Denmark	43094	4.63	22	1.34
Estonia	43094	4.63	11	1.04
Finland	338145	5.53	30	1.48
France	551695	5.74	22	1.34
Germany	357050	5.55	28	1.45
Great Britain	244820	5.39	28	1.45
Greece	131940	5.12	12	1.08
Hungary	93030	4.97	23	1.36
Iceland	103000	5.01	2	0.30
Ireland	84420	4.93	18	1.26
Italy	301318	5.48	29	1.46
Kazakhstan	150000	5.18	7	0.85
Latvia	64589	4.81	18	1.26
Liechtenstein	160	2.20	5	0.70
Lithuania	65200	4.81	15	1.18
Luxemburg	2586	3.41	1	0.00
Macedonia	25333	4.40	7	0.85
Malta	316	2.50	3	0.48
Moldova	33843	4.53	4	0.60
Netherlands	41526	4.62	15	1.18
Norway	385155	5.59	24	1.38
Poland	312685	5.50	17	1.23
Portugal	91568	4.96	4	0.60
Romania	238392	5.38	21	1.32
Russia	3960000	6.60	34	1.53
Slovakia	48845	4.69	24	1.38
Spain	505992	5.70	17	1.23
Sweden	449964	5.65	31	1.49
Switzerland	41290	4.62	24	1.38
Turkey	24378	4.39	16	1.20
Ukraine	603628	5.78	23	1.36

549

Table A3: Mean relative abundance of nineteen sepsid species in the three main biogeographic regions of Switzerland.

Species	Author	Northern lowlands	Alpine region	Southern lowlands
<i>Meroplius minutus</i>	(Wiedemann, 1830)	-	-	0.049
<i>Nemopoda nitidula</i>	(Fallén, 1820)	0.031	0.004	0.378
<i>Saltella nigripes</i>	Robineau-Desvoidy, 1830	0.006	-	-
<i>Saltella sphondylii</i>	(Schränk, 1803)	0.230	0.047	0.005
<i>Sepsis biflexuosa</i>	Strobl, 1893	0.001	0.009	-
<i>Sepsis cynipsea</i>	(Linnaeus, 1758)	0.176	0.200	-
<i>Sepsis duplicata</i>	Haliday, 1838	0.027	0.038	-
<i>Sepsis flavimana</i>	Meigen, 1826	0.055	0.131	0.007
<i>Sepsis fulgens</i>	Meigen, 1826	0.250	0.220	0.205
<i>Sepsis luteipes</i>	Melander & Spuler, 1917	0.013	0.014	-
<i>Sepsis neocynipsea</i>	Melander & Spuler, 1917	0.060	0.167	0.007
<i>Sepsis nigripes</i>	Meigen, 1826	0.001	-	-
<i>Sepsis orthocnemis</i>	Frey, 1908	0.043	0.059	-
<i>Sepsis punctum</i>	(Fabricius, 1794)	0.033	0.007	0.323
<i>Sepsis thoracica</i>	(Robineau-Desvoidy, 1830)	0.050	0.076	0.005
<i>Sepsis violacea</i>	Meigen, 1826	0.015	0.022	0.021
<i>Themira annulipes</i>	Meigen, 1826	0.007	0.006	-
<i>Themira gracilis</i>	(Zetterstedt, 1847)	-	0.001	-
<i>Themira minor</i>	(Haliday, 1833)	0.001	-	-
Number of locations		30	30	4

Figure 7: Prevalent (negative, positive, or curvilinear) relationship with altitude of the relative abundance for seventeen 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