

Article

# Preliminary Analysis of European Small Mammal Faunas of the Eemian Interglacial: Species Composition and Species Diversity at a Regional Scale

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**Abstract:** Small mammal remains obtained from the European localities dated to the Eemian (Mikulino) age have been analyzed for the first time at a regional scale based on the present biogeographical regionalization of Europe. The regional faunas dated to the warm interval in the first part of the Late Pleistocene display notable differences in fauna composition, species richness, and diversity indices. The classification of regional faunal assemblages revealed distinctive features of small mammal faunas in Eastern and Western Europe during the Eemian (=Mikulino, =Ipswichian) Interglacial. Faunas of the Iberian Peninsula, Apennine Peninsula, and Sardinia Island appear to deviate from the other regions. In the Eemian Interglacial, the maximum species richness of small mammals ( $\geq 40$  species) with a relatively high proportion of typical forest species was recorded in Western and Central Europe and in the western part of Eastern Europe. The lowest species richness (5–14 species) was typical of island faunas and of those in the north of Eastern Europe. The data obtained make it possible to reconstruct the distribution of forest biotopes and open habitats (forest-steppe and steppe) in various regions of Europe. Noteworthy is a limited area of forests in the south and in the northeastern part of Europe. In these regions, it seems likely that under conditions of relatively high temperatures characteristic of the Last Interglacial and an insufficient moisture supply there could exist open forest stands or forest-steppe landscapes, as suggested by the presence of species indicative of forest-steppe and steppe north of the forest zone. The results obtained are useful in modeling changes in the mammal faunas as well as environmental changes in entire Europe due to global climatic changes (including the global warming recorded at present).

**Keywords:** small mammals; Europe; the Eemian Interglacial; species composition; species diversity; regional aspects; reconstructions

## 1. The History of Investigation of the Eemian Interglacial

The Eemian Interglacial was first recognized from boreholes in the vicinity of Amersfoort town, the Netherlands, by Harting [1] and named after the local Eems River. In the parastratotype of the Eemian Interglacial in the Amsterdam-Terminal section it was dated by infrared stimulated luminescence at  $118 \pm 6.3$  ka BP [2].

In the north of Eastern Europe similar dates were obtained by  $^{230}\text{Th}/\text{U}$  for the Mikulino Interglacial deposits studied in Cheremoshnik key section (the Upper Volga drainage basin, Russia):  $114.2 + 11.6 / - 9.2$  ka BP and  $115.5 + 15.8 / - 11.6$  ka BP [3].

In the south of Eastern Europe, a lagoon and marine sequence including Karangatian mollusks and small mammal fauna has been described in the Eltigen section (eastern Crimea, Russia) and dated

by  $^{230}\text{Th}/\text{U}$  to  $127 \pm 8.9$  ka BP (cycle I) and  $107 \pm 7.7$  ka (cycle II) [4]. The paleomagnetic measurements performed on those layers revealed a reverse polarity event identified as the Blake Event that correlates with the Eemian interglacial.

The unique drilling on the Greenland ice in 2007–2012—North Greenland Eemian Ice Drilling, NEEM-site (North-West Greenland,  $77.45^\circ$  N,  $51.06^\circ$  W) [5]—provided data on the duration (130–115 ka BP) of the Eemian Interglacial and on the chronological position of its optimum (126 ka BP). The interglacial is correlated with marine isotope stage (MIS) 5e.

As follows from abundant paleontological evidence (pollen assemblages, diatoms, mollusks, mammal fauna, etc.), the climate of the Eemian Interglacial was warmer than that of the recent Holocene interglacial. According to the scenario developed by Bakker et al. [6], the July temperature in the Northern Hemisphere could be 0.3 to 5.3 K above that of the present day. The warming also exerted an effect on the global (eustatic) sea level that was 5.5–9 m above that of today [7].

The interglacial is known as the Ipswichian in Great Britain, Riss-Würm in the Alps, and Sangamonian in North America. Specialists differ considerably in their estimates of the environments of that time. Some are of opinion that at the Eemian maximum ( $\sim 126$  ka BP) forests were widely spread over Europe as far north as North Cape (Norway,  $71.16^\circ$  N,  $25.78^\circ$  E) and the Barents Sea coast in Eastern Europe, including regions that are now covered with tundra vegetation [8]. According to other reconstructions [9], the most densely forested regions in the Northern Hemisphere (>60% of the total area) occurred approximately between  $60^\circ$  and  $70^\circ$  N. During Eemian optimum hippopotamus inhabited the Rhine and Thames river basins; this indicates a climate considerably warmer than today.

In Eastern Europe the interglacial is known as Mikulinian named after the Mikulino settlement in the Rudnya district, Smolensk Region, Russia ( $55.034^\circ$  N,  $31.108^\circ$  E). The interglacial deposits located near the abovementioned Mikulino settlement, the city of Gadyach and Borok village near Bezhetsk are intercalated between two glacial tills—Dnieper and Valday; they were described by Markov [10]. The name “Mikulinian Interglacial” was suggested by Moskvitin [11].

## 2. Materials and Methods

There are voluminous data accumulated on the composition of local mammal faunas in Europe attributable to the Eemian (Mikulinian) Interglacial. Over the last 30 years the authors of this paper collected a huge amount of data with detailed information on the Pleistocene mammal localities in Europe and northern Asia. The remains of small mammals found in the Mikulino localities on the East European Plain were collected in the field and analyzed by the first author [12].

The studies provided data on the taxonomy of the European mammal faunas attributed to the Eemian Interglacial and revealed certain patterns in the spatial variability of the species composition in local faunas. They permitted to outline paleogeographical regions and to reconstruct paleoclimate and paleoenvironment in various regions of Europe based on paleontological information.

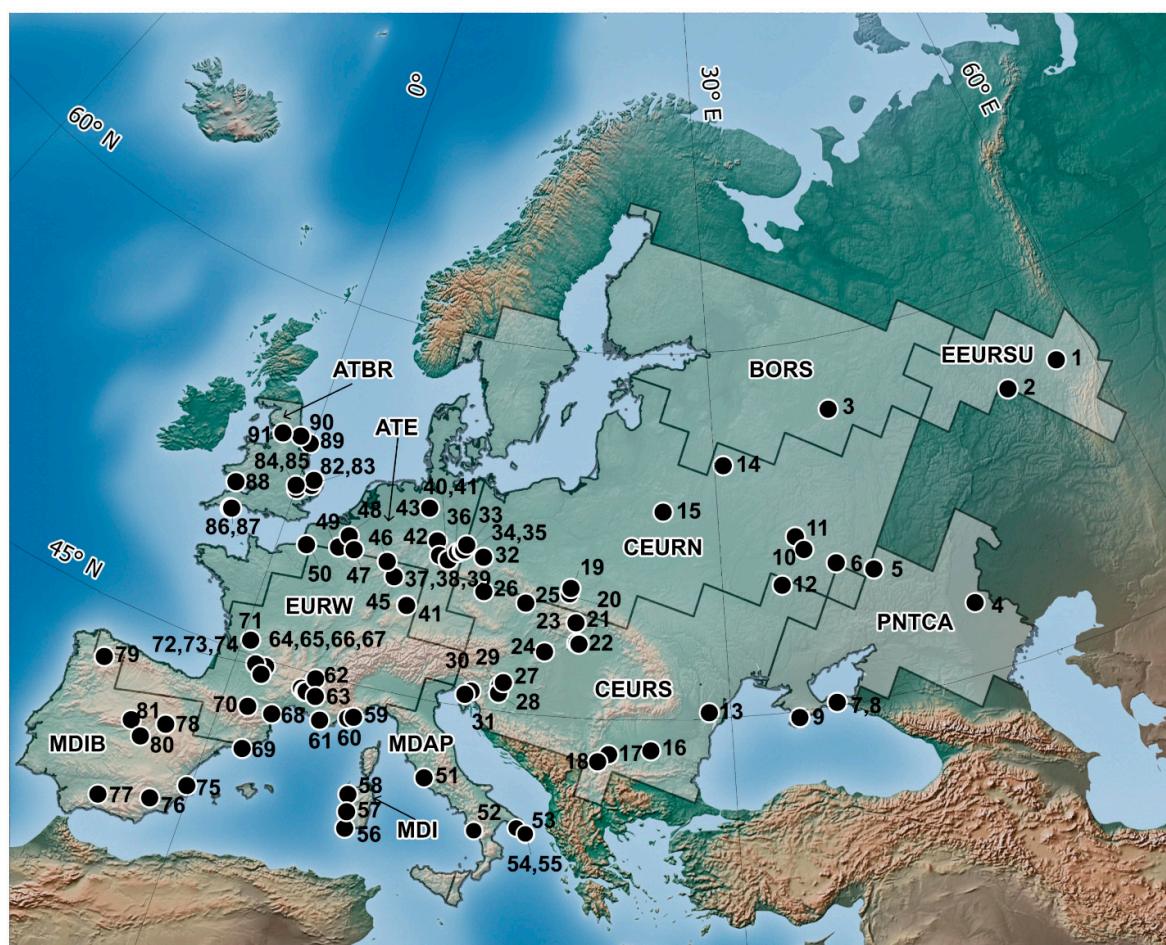
There are certain difficulties in dating the Eemian Interglacial faunas. Some of the recently studied faunas are dated with a high accuracy, using, for example,  $^{230}\text{Th}/\text{U}$  or infrared stimulated luminescence. Unfortunately, quite often the fauna localities attributed to that warm interval were dated only by geological, palynological, and archeological methods, undoubtedly giving less precise results. It should be noted, however, that the data on the small mammals attributed to the Eemian Interglacial usually display morphological and ecological characteristics (in particular taxonomic composition) that are clearly different from faunas dated to the preceding and succeeding glacial epochs.

The present work summarizes data from 91 small mammal localities (Figure ??; Table S1), including 51 localities with absolute dates and 40 ones with relative dates. In some cases the dates obtained on one locality vary over a wide range which hinders the fauna attribution to a certain interval.

When describing the faunal variability, the sites were grouped on the basis of their geographical location: Western Europe, Central Europe, Eastern Europe (including the East European Plain, Crimea, and the Urals), and the Mediterranean region (the Iberian Peninsula, Apennine Peninsula, and Sardinia

Island). To describe the small mammal species diversity in more detail, the data were aggregated in smaller spatial units.

The biogeographical zones used in this study are based on modern terrestrial mammal distribution [13], combined with general approaches that have been described in literature [14,15]. All data on species ranges (presence (1), absence (0)) were aggregated on cell grid  $150 \times 150$  km. The matrix of pairwise dissimilarities of grid cells was calculated using the Jaccard coefficient as the distance metric. Then, for the purpose of the cell ordination, the matrix was processed by means of nonmetric multidimensional scaling. Four first axes are used for cell clustering using the dichotomy of k-means clustering algorithms in order to form clusters of similar grid cell. At the 7th level of clustering, there are 12 European bioregions, which include Eemian Interglacial localities used in this study. The bioregions characterized here are as follows (Figure ??): Mediterranean Islands (MDI), Mediterranean Iberian (MDIB), Mediterranean Apenninian (MDAP), Ponto-Caspian (PNTCA), West European (WEUR), Atlantic East (ATE), Atlantic Britain (ATBR), Central European South (CEURS), Central European North (CEURN), East European South (EEURS), Boreal South (BORS), and East European Southern Ural (EEURSU).



**Figure 1.** Map of the Last Interglacial small mammal localities discussed in this paper and European bioregions (for more details see Table S1): 1-Bobylek (Russia) [16], 2-Krasnyi Bor (Russia) [17], 3-Cheremoshnik (Russia) [3,18], 4-ChernyYar (Russia) [19,20], 5-Shkurlat (Russia) (Shkurlat layers) [21], 6-Chernianka (Russia) [21], 7-El'tigen (Russia) [22], 8-Beglitsa (Russia) [23], 9-Kabazi II (Russia) [24,25], 10-Malutino (Russia) [26], 11-Mikhailovka 5 (Russia) [27], 12-Gadiach (Ukraine) [21], 13-Novonekrasovka (Ukraine) [28], 14-Borisova Gora (Belarus) [29], 15-Timoshkovichi (Belarus) [30], 16-Vârtop casa de Piatra (Romania) [31], 17-Kozarnika (Bulgaria) [32], 18-Mala Balanica (Serbia) [33], 19-Bišník Cave (Poland) [34],

20-Nietoperzowa Cave (Poland) [35], 21-Gánovce-Hrádok (Slovenia) [36], 22-Kalman Lambrecht Cave (Hungary) [37], 23-Horváti-lik (Hungary) [38], 24-Süttő Travertine Complex (Hungary) [39], 25-Za Hájovnou Cave (Czech Republic) [40], 26-Chlupá čova sluj (Czech Republic) [41], 27-Vindija Cave (Croatia) [42,43], 28-Veternica (Croatia) [42,43], 29-Krapina (Croatia) [44], 30-Betalov podmol (Slovenia) [43], 31-Caverna degli Orsi (Italy) [45], 32-Schönenfeld (Germany) [46], 33-Gröber I (Germany) [46,47], 34-Grabschütz (Germany) [46], 35-Rabutz (Germany) [46], 36-Neumark-Nord 2/2 (Germany) [46,48], 37-Burgtonna I (Germany) [46], 38-Burgtonna II (Germany) [46], 39-Burgtonnal-III (Germany) [46], 40-Taubach (Germany) [49], 41-Weimar-Ehringsdorf (Germany) [50–52], 42-Einhornhöhle (Unicorn Cave) (Germany) [44], 43-Lehringen (Germany) [47,53], 44-Biedermann travertine (Germany) [51,52], 45-Wallertheim (Germany) [53,54], 46-Tönchesberg (Germany) [53], 47-Sladina, Sclayn (Belgium) [55,56], 48-Zemst, Bosvan Aa (Belgium) [57], 49-Mesvin IV (Belgium) [58,59], 50-Caours (France) [60], 51-Castel di Guido (Italy) [61,62], 52-Grotta Grande of Scario (Italy) [63], 53-Avetrana (Italy) [64], 54-Cava Nuzzo (Italy) [65,66], 55-San Sidero 3 (Italy) [67,68], 56-Grotta dei Fiori (Italy) [69], 57-San Giovanni di Sinis (Italy) [70], 58-Dragonara Cave (Italy) [71], 59-Grotta del Principe (Monako) [72], 60-Lazaret (France) [73,74], 61-Cèdres (France) [75,76], 62-La Baume Moula-Guercy (France) [77,78], 63-Le Grand Abri aux Puces (France) [79], 64-Saint-Marcel (d'Ardeche) (France) [80], 65-Orgnac 3 (France) [81,82], 66-Baume Flandin (France) [83,84], 67-Abri-des-Pêcheurs (France) [85,86], 68-Grotte des Ramandils (France) [87,88], 69-Cova del Rinoceront (Spain) [89], 70-Grotte du Portel (France) [90,91], 71-Abri Bourgeois-Delaunay, La Chaise (France) [92], 72-Coudoulous I (France) [93], 73-Vaufrey (France) [94,95], 74-Bramefond (France) [96,97], 75-Bolomor (Spain) [98,99], 76-Cueva Negra (Spain) [100–102], 77-Cueva del Angel (Spain) [103], 78-Ambrona (Spain) [104,105], 79-Cova Eirós (Spain) [106,107], 80-Arenero de Arriaga (Spain) [108,109], 81-Villacastín (Spain) [110,111], 82-Swanton Morley (U.K.) [112], 83-Shropshire Gravel Pit (U.K.) [113], 84-Barrington Chalk Pit (U.K.) [113], 85-Woolpack Farm beds (U.K.) [114], 86-Tornewton Cave (U.K.) [115,116], 87-Joint Mitnor Cave (U.K.) [117,118], 88-Bacon Hole (U.K.) [114,118,119], 89-Sewerby cliff (U.K.) [120,121], 90-Kirkdale Cave (U.K.) [122,123], and 91-Victoria Cave (U.K.) [113,124]. Bioregions: Mediterranean Islands (MDI), Mediterranean Iberian (MDIB), Mediterranean Apenninian (MDAP), Ponto-Caspian (PNTCA), West European (WEUR), Atlantic East (ATE), Atlantic Britain (ATBR), Central European South (CEURS), Central European North (CEURN), East European South (EEURS), Boreal South (BORS), and East European Southern Ural (EEURSU).

For each bioregion, the number of species, Shannon (H) diversity index, and evenness (E) index were calculated. We used a permutation test [125] for testing the difference between diversity-indices yielded from any pairs of bioregions. All the statistical analyses were carried out using package PAST v. 3.12 (<https://folk.uio.no/ohammer/past/>) [126].

### 3. Results

#### 3.1. The East European Plain, Crimea and the Urals

The small mammal data from Eastern Europe have been collected and studied by different paleontologists. The Eemian (Mikulinian) small mammal fauna data from Eastern Europe collected until the late 20th century have been summarized by A.K. Markova [12].

New data resulted in a revision of the stratigraphic status of the fauna from the Cherny Yar locality (Russia), formerly identified as a Middle Pleistocene Khozarian faunal assemblage [127,128]. New dates obtained using optically stimulated luminescence (OSL) techniques suggest a younger Mikulinian age of the locality [128]. The enamel thickness differentiation quotient (SDQ) of the water voles *Arvicola* in the Cherny Yar complex also permits a correlation of the faunal assemblages with Mikulinian faunas [129].

Absolute dates have been obtained for several localities with a Mikulino age, including Eltigen (Russia), Cheremoshnik (Russia), and Kabazi II (Russia). Most important among them are the dates

obtained for the Cheremoshnik locality, which provided the corroborative evidence for its attribution to the Mikulinian Interglacial [3].

Detailed studies of the Paleolithic sites in Crimea performed by a team of Ukrainian archeologists proved an early age of the lowermost cultural layers in the multilayer site Kabazi II dated to the Middle Paleolithic [130]. The earliest layer of the site (Unit VI) with rich fauna of small mammals was attributed to the Mikulino Interglacial on the basis of its geological context and paleopedological data [23]. The absolute dates confirmed the stratigraphic position of the fauna.

The species composition of the East European small mammal faunas dated to the Mikulino Interglacial is given in Tables S2–S6.

It should be noted that the studied localities are widely spread and positioned in different natural zones than today; the appearance of small mammal faunas dating to the Mikulino age seems also to be affected by the diversified environments of that time. The interglacial fauna provides the possibility of reconstructing the natural zonality of the East European Plain and permits the identification of specific features of the environments in Crimea. The northernmost localities (Timoshkovichi (Belarus), Borisova Gora (Belarus), Konevich (Belarus), Niyatesos (Lithuania), Cheremoshnik (Russia), and Krasny Bor (Russia)) yielded a wide assortment of small mammal species (Eurasian red squirrel *S. vulgaris*, wood mouse/yellow necked mouse *Apodemus ex gr. sylvaticus-flavicollis*, bank vole *Clethrionomys glareolus*, field vole *Microtus agrestis*, and others) indicative of the forest zone. Steppe species are present in a small number. The Borisova Gora locality yielded remains of collared lemming *Dicrostonyx torquatus*. Motuzko [30] attributes their presence to the fact that the fauna belongs to the very beginning of the interglacial, being actually transitional from the preceding (Dnieper) glaciation.

Farther south, in Malyutino, Chernyanka, Mikhailovka 5, and Gadyach forest species are also present, for example wood mouse *Apodemus* sp., bank vole *Cl. glareolus*, *Microtus* (*Terricola subterraneus*), and the field vole *Microtus agrestis*. Steppe dwellers are also well represented (steppe pika *Ochotona pusilla*, ground squirrel *Spermophilus* sp., mole rat *Spalax*, yellow steppe lemming *Eolagurus*, steppe lemming *Lagurus*, narrow-headed vole *Lasiopodomys (Stenocranius) gregalis*, and others). This kind of assemblage indicates a forest-steppe environments [26,131].

In the southeast of Eastern Europe, Shkurlat (Russia), Eltigen (Russia), Beglitsa, Mezin paleosol complex (Russia), and Cherny Yar are completely devoid of forest species. We consider, as an example, the Shkurlat stratotype locality (the recovered mammal remains formed the basis of the Shkurlat faunal complex corresponding to the Mikulino Interglacial [26]). Among small mammals the complex includes remains of steppe pika *Ochotona pusilla*, little ground squirrel *Spermophilus pygmaeus*, *Pygerethmus (Alactagulus.) acontion*, yellow steppe lemming *Eolagurus luteus*, and steppe lemming *Lagurus lagurus* [132]. The Cherny Yar fauna is also dominated by steppe animals: little ground squirrel *S. pygmaeus*, Northern mole-vole *Ellobius talpinus*, yellow steppe lemming *E. luteus*, and the steppe lemming *L. lagurus* [133]. Some species found in the localities prefer humid environments among them are the water vole *Arvicola terrestris* and the tundra vole *Microtus oeconomus*. The water voles from the Mikulino localities are characterized by their advanced (progressive) morphology, with SDQ values of ~100 [12,130].

The Mikulinian (Eemian) layers of the multilayered Middle Paleolithic site Kabazi II (Unit VI) in Crimea, dated by using absolute dating methods, include abundant small mammal remains characterized by the different environmental conditions [24]. The fossil record includes remains of forest species: forest dormouse *Dryomys nitedula*, yellow-necked mouse *A. flavicollis*, pine vole *M. (T.) subterraneus*, and water vole *A. ex gr. terrestris* a species that indicates wet habitats. Steppe species are represented by *S. pygmaeus*, *Spalax microphthalmus*, Northern mole-vole *Ellobius talpinus*, yellow steppe lemming *E. luteus*, and the narrow-headed vole *L. (Stenocranius) gregalis*. This group is dominated by Altaian vole *Microtus obscurus* an inhabitant of meadow and steppe biotopes. The species composition of this particular fauna suggests highly diversified environments in the Crimean Mountains.

Layers 4 and 6 of the Bobylek Paleolithic site (Middle Urals), tentatively attributed to the Mikulino Interglacial (no absolute date is available), yielded small mammals of various environmental preferences: forest (*Apodemus* sp., *Cl. ex gr. rutilus-glareolus*, and *M. agrestis*), steppe pika *Ochotona* sp., ground squirrel *Spermophilus* sp., great jerboa *Allactaga major*, lesser fat-tailed jerboa *Pygeretmus* (A.) *pumilio*, black-bellied hamster *Cricetus cricetus*, narrow-headed vole *L. (S.) gregalis*, and inhabitants of wet areas (water vole *A. ex gr. terrestris* and tundra vole *M. oeconomus*) [134]. The fact of ecologically different species being found together is explained by the environmental diversity of the mountainous area and the altitudinal zonation. The remains were accumulated in the form of pellets from predatory birds hunting small animals within a few kilometers from the site at slopes varying in exposure and belonging to different altitudinal zones.

Materials of considerable importance were obtained from the Novonekrasovka site in the Danube drainage basin. The small mammal fauna were recovered from lagoonal and marine sediments of the Black Sea attributed to the Karangatian transgression (correlated with the Mikulino Interglacial and MIS 5e) based on the evidence retrieved mollusk fauna [28]. The SDQ index and size of the water vole *Arvicola* teeth agree with the data from other Mikulino localities [12]. The mammal fauna from the Eltigen section (eastern Crimea) is also confined to the Black Sea lagoonal-marine sediments and, in common with the Novonekrasovka sequence, includes Karangatian mollusk shells along with small mammal remains. That locality was dated by  $^{230}\text{Th}/\text{U}$ . In addition, paleomagnetic measurements revealed the presence of the Blake Event correlated with the Mikulino Interglacial [4].

The results obtained from the small mammal faunas of Eastern Europe indicate a natural zonation existence of the East European Plain, with clearly recognizable forest, forest-steppe, and steppe zones. The geographical position of the zones hardly differs from the present zonation, which may be attributed to the specificity of the dominant air mass transport from the Atlantic. Faunas of the Crimea mountains and the Urals suggest highly diversified environments within the mountain regions.

### 3.2. Central Europe

A considerable number of small mammal localities discovered in Central Europe are confidently correlated with the Eemian Interglacial. The species composition of a number of faunas is presented in Table S2. Various dating methods (U/Th), electron spin resonance dating (ESR), optically stimulated luminescence (OSL), and thermoluminescence dating (TL) have been applied. Many localities yielded remains of forest dwellers: European mole *Talpa europaea*, common shrew *Sorex araneus*, pygmy shrew *Sorex minutus*, Eurasian red squirrel *S. vulgaris*, bank vole *Cl. glareolus*, wood mouse *A. sylvaticus*, European pine vole *M. (T.) subterraneus*, and field vole *M. agrestis*. The species composition strongly suggests widely spread forest and shrub biotopes in the vicinities of the sites.

The paleo-landscapes of Central Europe dating to the Eemian Interglacial display a certain zonality in their spatial distribution. The sites located at latitudes  $\sim 48\text{--}51^\circ \text{ N}$  including Taubach (bed 11), Weimar-Eringsdorf (Upper Travertine), Burgtonna (lower layer in section Cm), Bišník cave (layers 13 and 12), and some others yielded a considerable number of forest species: western hedgehog *Erinaceus europaeus*, European mole *T. europaea*, common shrew *S. araneus*, pygmy shrew *S. minutus*, bicoloured shrew *C. leucodon*, common white-toothed shrew *Crocidura russula*, lesser white-toothed shrew *C. suaveolens*, Eurasian beaver *Castor fiber*, fat dormouse *Glis glis*, forest dormouse *D. nitedula*, wood mouse *A. sylvaticus*, bank vole *Cl. glareolus*, and the European pine vole *M. (T.) subterraneus* [46,135,136]. A few small mammals found in those localities prefer open landscape habitats (*Spermophilus citellus*, *Al. major*, *L. lagurus*, and *L. (S.) gregalis*). Forest environments undoubtedly dominated in Central Europe at those latitudes.

Further east the Central European localities (Kozarnika, layers 9a–9b (Bulgaria), Kalman Lambrecht cave (Hungary), Horvati-lik and Za Hájovnou cave (Czech Republik), Vârtop casa de Piatra (Romania), and others) feature a noticeable presence of the open landscape species (steppe pika *O. pusilla*, ground squirrel *Spermophilus* sp., yellow steppe lemming *E. luteus*, steppe lemming *L. lagurus*, and the narrow-headed vole *L. (S.) gregalis*. Less common are golden hamster *Mesocricetus auratus*,

Newton' medium hamster *Mesocricetus newtoni*, hamster *Allocricetus bursae*, and the gray dwarf hamster *Cricetulus migratorius* (e.g., [32,37,38]). Remains of those steppe species are usually found together with forest and eurytopic species. Specific species (water vole *Arvicola*, tundra vole *M. oeconomus*, Russian desman *Desmana moschata*, and the Eurasian water shrew *Neomys fodiens*) prefer wet biotopes; they were widely distributed over the European subcontinent. The obtained data suggest forest-steppe environments in the regions, both on the plains and in mountains.

Remains of a tundra species collared lemming *Dicrostonyx gulielmi* were described in two localities in Hungary and Poland (Horvati-lik and Bišník cave, layers 12 and 13) [38,136]. The possibility must not be ruled out that those remains were redeposited from earlier layers dated to the Saale glaciation.

Of interest are findings of porcupine remains (*Hystrix brachyura vinogradovi*) in a few localities (Burgtonna, lower layer (Germany); Taubach, bed 11 (Germany); Weimar–Eringsdorf, upper travertine (Germany); Kalman-Lambrecht cave (Hungary)) [135,137–140]. That mammal is thermophilic and occurs nowadays mostly in subtropical areas. Its presence in the Eemian layers supports the view of the Eemian Interglacial climate was warmer than the present-day interglacial. Unlike the East European faunas, remains of arid open space inhabitants (such as pygmy ground squirrel *S. pygmaeus*, greater mole rat *Spalax microphthalmus*, Northern mole rat *E. talpinus*, fat-tailed jerboa *P. (A.) pumilio*, as well as Altaiian vole *M. obscurus*) have not been found in Central Europe. Their absence may be attributed to specific features of the fauna evolution there.

In summary, it can be stated that the composition of the Eemian faunas in Central Europe suggests a forest and forest-steppe landscape in the area. Steppe biotopes, widely spread over the southeast of Eastern Europe, are practically absent in the central regions of Europe.

### 3.3. Western Europe and the British Isles

In Western Europe there are two main groups of small mammal localities dated to the Eemian Interglacial. The localities in the northern part of the region (Biedermann travertine and Tönchesberg, Zemst layer IIB (Germany), Sladina and Mesvin IV (Belgium), Caours (France)), mostly north of 47° N, yielded remains of *Erinaceus* sp., *T. europaea*, *S. araneus*, *S. caecutiens*, *S. minutus*, *Crocidura leucodon*, *Lepus* sp., *O. pusilla* (Biedermann travertine locality), *Sciurus vulgaris*, *Marmota marmota*, *Sicista betulina* (Biedermann travertine locality), *C. cricetus*, *C. major*, *A. bursae*, *G. glis*, *A. sylvaticus*, *Cl. glareolus*, *A. terrestris-cantianus*, *M. (T.) subterraneus* (Sladina I, locality 1.5), *M. agrestis* and *M. arvalis* (e.g., [46,56,59,60,141,142] (Tables S4 and S5). Most of the localities have direct datings. The ecological characteristics of the fauna indicate a dominance of forest biotopes; species of open landscapes (pika and hamsters) are present in insignificant quantities. Some data must be verified, for example, the attribution of water vole from Tönchesberg locality to *A. cantianus*, which is characteristic for the Middle Pleistocene faunas [141].

Quite different in composition are faunas recovered from localities farther south (Baune Flandin (France), Cèrdes (France), Grotte Vaufrey, layer IV (France); Orgnac 3, layer 5a (France); Saint-Marcel, layer U (France); La Baume Moula-Guercy, layer XV (France); Lazaret (layers: C III 7-265, 236, CII 17-326) (France); Le Grand Abri aux Puces L. 2 (France), Grotte de Portel, L, K (France); Coudoulus I (France), Abri-des-Pêcheurs, ensemble 1 (France), Grotta del Principe (Monaco), etc.) [70,76–78,84,90,143–148]. The faunas of those localities, along with *c. Talpa europea*, *Sorex* sp., *C. leucodon*, *C. russula*, *Lepus* sp., *S. vulgaris*, *A. bursae*, *G. glis*, *A. sylvaticus*, *Cl. glareolus*, *M. (T.) subterraneus*, *L. (S.) gregalis* (Grotte Vaufrey, layer IV; Orgnac 3, layer 5a, Moula, La Baume Moula-Guercy; Le Grand Abri aux Puces), and *M. arvalis* and *M. agrestis*, include also the southwestern water vole *A. sapidus* (the species characteristic of the Iberian Peninsula and the south of Western Europe), the vole *Pliomys coronensis* (a species extinct from Eastern and Central Europe as early as the beginning of the Middle Pleistocene), Cabrera's vole *Microtus (Iberomys) cabrerae brecciensis* typical also of the Iberian Peninsula; voles *Microtus (Terricola) duodecimcostatus* and *M. (T.) pyrenaicus* (also commonly found on the Iberian Peninsula). La Baume Moula-Guercy [77,78,146] yielded remains of Balkan snow vole *Dinaromys bogdanovi*, the only representative of the Pliomyini tribe persisting today.

It may be concluded that the southern faunas of Western Europe are unique in having endemic species present and they are undoubtedly closely correlated to faunas of the Iberian Peninsula. Based on species composition, the region was dominated by forest and bush communities alternating with communities that inhabit open areas. The latter are characterized by steppe biotope species: *A. bursae*, *L. (Stenocranius) gregalis*, and *L. lagurus* (Orgnac 3, layer 5a [83]). A wide occurrence of marmots *M. marmota* is recorded in mountains.

On the whole, the Eemian faunas of Western Europe point to mild climate, which enabled the forest landscapes to expand widely on the continent. Only a few species recovered from the Eemian localities are inhabitants of open biotopes. Cold-tolerant animals were completely absent.

Few species of small mammals have been recovered from Eemian (Ipswichian) localities in the British Isles (U.K.), 15 taxa of Eulipotyphla, Lagomorpha, and Rodentia have been described in Bacon Hole, Barrington Chalk Pit, Joint Minor cave, Kirkdale Cave, Shropshire Gravel Pit, Swanton Morley, Tornewton Cave (*Hyaena stratum*), Victoria cave, Woolpack Farm beds, and some others (Table S6) (e.g., [112–119,122–124]). Most of the species are inhabitants of forest and forest-steppe biotopes (*T. europaea*, *Sorex araneus*, *S. minutus*, *A. sylvaticus*, *Cl. glareolus*, and *M. agrestis*). There are also some wet biotope dwellers (*Castor fiber*, *N. fodiens*, *A. terrestris-cantianus*, and *M. oeconomus*). Evidently, the small mammal fauna of the British Isles dated to the last interglacial suggests a mild climate beneficial for the expansion of forest biotopes. No cold-tolerant species are present. Among large mammal fauna there are some thermophilic species, such as *Hippopotamus amphibius* and *Palaeoloxodon antiquus* [149].

### 3.4. The Iberian Peninsula, Apennine Peninsula, and Sardinia Island

Small mammal faunas that inhabited the Mediterranean during the Eemian Interglacial were of a specific kind. The mammal remains of that age were recovered in Italy from Castel di Guido [63,64], Grotta Grande of Scario (Salerno) [63], Cava Nuzzo (Salento region) [65,66], and Avetrana (Taranto) (Table S6, Figure ??) [62]. The Castel di Guido fauna includes only a few small mammal species: *Lepus europaeus*, *Lepus* sp., and *Castor* sp. The remains of *E. europaeus*, *L. europaeus*, *Oryctolagus cuniculus*, and *Microtus (Terricola) savii* (Table S6) recovered from Cava Nuzzo, in the southeast Apennine Peninsula, suggest the prevalence of open biotopes. In the same region animal bones identified as *E. europaeus*, *M. (T.) savii*, Pleistocene porcupine *H. b. vinogradovi* were found in the Avetrana karst cavity (Table S6) [64]. The authors assigned that fauna to the last interglacial. It is extremely rare that Pleistocene porcupine remains are found in the deposits of that warm interval in Italy [150]. A considerable number of large and small mammals were recovered from Grotta Grande of Scario (Table S6), including *M. (T.) cf. savii*, *A. terrestris*, *G. glis*, and *Crocidura suaveolens*, three species of *Talpa* (*T. caeca*, *T. romana*, and *T. europaea*) and many others. The abundance of *M. (Terricola) cf. savii* seems to indicate open arid biotopes in the immediate vicinity of the site. The presence of *Cl. glareolus*, *A. sylvaticus*, and *Eliomys quercinus* and some other species of the same environmental preference suggests forest and shrub communities near the site. In the authors' opinion, human presence at the site may be assigned to the Eemian Interglacial (before its optimum).

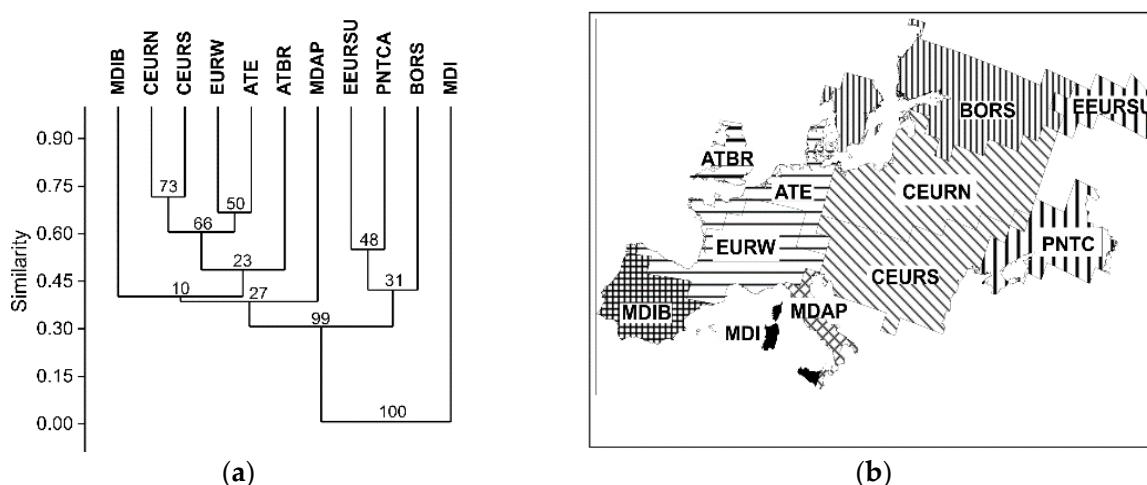
Eemian localities yielding small mammals are found in abundance on the Iberian Peninsula (in Spain): Cueva del Angel (layer I–XIII), Arenero de Arriaga (layer I.I), Ambrona (layer AS1), Cueva Negra del Estrecho (layer 15), Villacasin, Bolomor (layer II), Cova del Rinoceront (layers III a, b, c); Cova Eiros (layer 3) (Table S6, Figure ??). The southernmost faunas of the peninsula (Cueva del Angel, Cueva Negra del Estrecho, Bolomor) include *E. europaeus*, *T. europaea*, *Sorex minutissimus*, *Neomys* sp., *Galemys* sp., *Prolagus* sp., *S. vulgaris*, *A. bursae*, *E. quercinus*, *A. sylvaticus*, *Arvicola sapidus*, and *M. (I.) cabrerae brecciensis*. Specific features of the faunas are the presence of an Iberian Peninsula endemic—Pyrenean desman *Galemys* sp., southern water vole *A. sapidus*, as well as Cabrera vole *M. (I.) cabrerae brecciensis*, all occurring in the southern Mediterranean and on the Iberian Peninsula. Dominant in the fauna are small mammals, inhabitants of forest and shrub landscapes, those of wet biotopes are also present.

Some of the above-listed animals—*E. europaeus*, *T. europaea*, *Neomys* sp., *Galemys* sp., *A. bursae*, *A. sapidus*, and *M. (I.) cabrerae brecciensis*—occur farther north as well, at the center of the peninsula, in the localities (Spain) Ambrona, Arenero de Arriaga, and Villacastin (Figure ??). Additionally, there are *S. minutus*, bicoloured shrew *C. leucodon*, European rabbit *O. cuniculus*, porcupine *Hystrix* sp., *Clethrionomys* sp., and *M. (T.) duodecimcostatus*, which have not been found in the south [104,108,110]. *Pliomys coronensis* has not been found as yet in the local faunas of that period, though it has been recorded in the earlier and later Pleistocene faunas, as well as in layers dated to other stages of MIS 5 in the localities Valdegoba, Teixoneres cave, and Lezetxiki (Spain) [151–153].

The small mammals described in Cova Eiros locality ( $42.7^{\circ}$  N), in the mountain region of Galicia in the NW of the peninsula (Figure ??), include *E. europaea*, Spanish mole *Talpa occidentalis*, wood mouse *A. sylvaticus*, Southern water vole *A. sapidus*, European snow vole *Chionomys nivalis*, Lusitanian pine vole *M. (T.) lusitanicus*, and *M. arvalis* [106]. The fauna is noted for the presence of endemic species, Spanish mole *T. occidentalis*, and Lusitanian pine vole *M. (T.) lusitanicus*. The snow vole *C. nivalis* is typical of the European mountains. The data available at present suggest forest and shrubland biotopes to be dominant in the low mountains of Galicia.

There are three localities attributable to the last interglacial described on Sardinia Island, namely San Giovanni di Sinis, Dragonara Cave, and Grotta dei Fiona. The small mammals described include only a few species: Sardinian mole *Talpa tyrrhenica*, Sardinian shrew *Episoriculus similis*, Sardinian pika *Prolagus sardus*, large field mouse *Rhagamus orthodon*, and Tyrrhenian vole *M. (Tyrrhenicola) henseli* [69,70,81], all of them being endemic to Sardinia, which suggests a long-term isolation of the island from the continent. Abundant materials on the Plio-Pleistocene theriofaunas of Sardinia Island were summarized by Palombo [151].

The above overview shows essential differences in small mammal faunas of the bioregions. In the dendrogram (Figure 2a) there is a distinctly outlined insular bioregion MDI, its fauna consists entirely of endemics of Sardinia dominated by *M. (Tyrrhenicola) henseli* (Table 1).



**Figure 2.** (a) Bioregion classification based on the composition of the small mammal faunas (method: unweighted pair group method with arithmetic mean clustering (UPGMA); similarity: Sorenson coefficient; bootstrap support values (%; 1000 repeats) are shown at the branch nodes); (b) the sketch map of bioregions' clustering.

**Table 1.** Dominant and subdominant taxa of bioregions.

Bioregion	Dominants	Subdominants
MDI	<i>Microtus (Tyrrhenicola) henseli</i>	<i>Episoriculus similis</i> and <i>Rhagamus orthodon</i>
MDAP	<i>Lepus corsicanus</i> (South of the Apennine peninsula) or <i>L. europaeus</i>	<i>Erinaceus europaeus</i> and <i>Microtus (Terricola) savii</i>
MDIB	<i>Apodemus sylvaticus</i>	<i>Arvicola sapidus</i> and <i>Microtus (Iberomys) cabrerae brecciensis</i>
ATBR	<i>Arvicola terrestris</i>	<i>Apodemus sylvaticus</i> and <i>Microtus agrestis</i>
ATE	<i>Talpa europaea</i> , <i>Castor fiber</i>	<i>Sorex araneus</i> , <i>Microtus (Terricola) subterraneus</i> and <i>Microtus arvalis</i>
EURW	<i>Apodemus sylvaticus</i>	<i>Talpa europaea</i> , <i>Eliomys quercinus</i> and <i>Microtus agrestis</i>
CEURN	<i>Microtus agrestis</i>	<i>Talpa europaea</i> , <i>Sorex araneus</i> , <i>Clethrionomys glareolus</i> and <i>Arvicola terrestris</i>
CEURS	-	<i>Spermophilus citellus</i> , <i>Clethrionomys glareolus</i> , <i>Lagurus lagurus</i> and <i>Microtus arvalis</i>
BORS	-	-
EEURSU	-	<i>Apodemus flavicollis</i> , <i>Cricetus cricetus</i> , <i>Microtus agrestis</i> and <i>Arvicola terrestris</i>
PNTCA	-	<i>Spermophilus pygmaeus</i> , <i>Lagurus lagurus</i> , <i>Eolagurus luteus</i> , <i>Arvicola terrestris</i> and <i>Lasiopodomys (Stenocranius) gregalis</i>

MDI = Mediterranean Islands; MDIB = Mediterranean Iberian; MDAP = Mediterranean Apenninian; PNTCA = Ponto-Caspian; WEUR = West European; ATE = Atlantic East; ATBR = Atlantic Britain; CEURS = Central European South; CEURN = Central European North; EEURSU = East European South; BORS = Boreal South; EEURSU = East European Southern Ural.

The ensuing analysis permits recognition of a cluster of bioregions in the east of Europe, of these the regions EEURSU and PNTCA being closest to each other. A common feature of the two regions consists in a considerable proportion of xerophilous species (*C. cricetus*, *S. pygmaeus*, *L. lagurus*, *E. luteus*, and *L. (S.) gregalis*). The dominance of these is most pronounced in the SSE of Europe, in the PNTCA bioregion. At the same time, a wide occurrence of yellow-necked mouse (*A. flavicollis*) in the EEURSU regional fauna suggests widespread broadleaf forests in the Southern Urals during the Last Interglacial.

Boreal South region is rather close to the EEURSU in the fauna composition. In spite of its position farther north (57.12° N; Figure 2b), forest-steppe and steppe species are present including marmot (*Marmota*), mole rat (*Spalax*), hamster (*C. cricetus*), narrow-headed vole (*L. (S.) gregalis*), yellow steppe lemming (*E. luteus*), etc.

The southern Mediterranean bioregions (MDAP and MDIB) appear to differ considerably from each other in the fauna composition. The small mammal faunas of the Iberian and Apennine peninsulas are also distinctly different from those of continental Europe. As our materials show, the most common species in the MDAP region are Apennine hare *Lepus corsicanus* and/or *L. europaeus*, Savi's pine vole *M. (T.) savii*, and *M. (T.) brachycercus* [154]. The most widespread in MDIB bioregion was *A. sylvaticus*, with *A. sapidus* and *M. (Iberomys) cabrerae brecciensis* as its codominants.

East European bioregions (CEURN and CEURS) differ distinctly enough from West European ATE and EURW. It is quite possible that the demarcation between them during the Last Interglacial was close to its present position. Dominant in the CEURN fauna was the field vole (*M. agrestis*), its co-dominants *T. europaea*, *Cl. glareolus*, and others (Table 1). In the southern bioregion CEURS small mammal assemblages seem to be polydominant. Along with species typical of forest, forest-steppe and meadows (*Cl. glareolus* and *M. arvalis*), the proportion of xerophilous species of open biotopes (*S. citellus* and *L. lagurus*) was considerable. The European mole (*T. europaea*) and beaver (*Castor fiber*) occur most often in the localities in the north and northwest of Western Europe (ATE region), with *Sorex araneus*, *M. (T.) subterraneus*, and *M. arvalis* as codominants.

The small mammal fauna of the British Isles is similar to continental fauna in species composition, though the number of species is insignificant. The most common animals are the water vole (*A. terrestris*), wood mouse (*A. sylvaticus*), and the field vole (*M. agrestis*), no specific taxa has been recorded.

There is an essential difference in the species richness of individual bioregions (Table 2). Faunas of the three regions (EURW, CEURN, and CEURS) include at least 40 species. This is lower in the ATE region (~29 species), as well as in regions MDIB and PNTCA (no less than 24 taxa). The “Island effect” makes itself evident in a low diversity of faunas; that may be clearly seen in the faunas of the Apennine Peninsula (MDAP, at least 17–19 taxa), Great Britain (ATBR, 14 taxa), and Sardinia Island (MDI, 5 taxa). A low diversity index denotes the East European bioregion BORS.

**Table 2.** Species richness and diversity indices (Shannon diversity index (H) and evenness diversity index (E)) of bioregions and their approximate 95 percent confidence intervals computed with a bootstrap procedure.

Bioregion	Number of Taxa	H, Nit	95 Percent Confidence Intervals	E	95 Percent Confidence Intervals
MDI	5	1.52	1.34	0.917	0.799
MDAP	17–19	2.68	2.42	0.856	0.763
MDIB	24	2.95	2.81	0.794	0.712
ATBR	14	2.34	2.20	0.738	0.633
ATE	29	3.15	3.03	0.808	0.727
EURW	46	3.57	3.49	0.774	0.717
CEURN	40	3.51	3.42	0.832	0.776
CEURS	41	3.55	3.47	0.846	0.789
BORS	9	2.20	1.89	1.000	0.931
EEURSU	16	2.72	2.48	0.947	0.885
PNTCA	24	2.95	2.82	0.799	0.723

The diversity indices (H, E) display specific features of species occurrence, including the degree of individual taxa predominance (Tables 2 and 3). The Shannon index varies regularly from 3.57 (EURW) to 1.52 (MDI). Higher values of the H index are typical for the regions marked with high species richness (CEURN and CEURS). A low diversity of small mammal fauna is characteristic, apart from the Sardinia Island fauna, also for Great Britain (ATBR), as well as the BORS and MDAP bioregions. Relatively high dominance of a few taxa (index E) have been documented in faunas with a high (EURW) and a low (ATBR) species richness. The interregional differences of the Shannon index are statistically more significant than the differences revealed by the evenness index (Table 2).

**Table 3.** Pairwise comparisons Shannon diversity index (above diagonal) and evenness diversity index (under diagonal) using permutation test (probability of a no difference).

	MDI	MDAP	MDIB	ATBR	ATE	EURW	CEURN	CEURS	BORS	EEURSU	PNTCA
MDI		0.03	0.05	0.35	0.02	0.00	0.00	0.00	0.00	0.00	0.04
MDAP	0.51		0.77	0.30	0.48	0.18	0.10	0.13	0.98	0.88	0.77
MDIB	0.66	0.77		0.00	0.17	0.95	0.00	0.00	1.0	0.99	0.95
ATBR	0.42	0.19	0.44		0.00	0.00	0.00	0.00	0.99	0.37	0.00
ATE	0.84	0.77	0.79	0.35		0.04	0.02	0.03	0.96	0.87	0.29
EURW	0.94	0.92	0.00	0.95	0.71		0.91	0.81	0.91	0.71	0.03
CEURN	0.93	0.97	0.47	0.43	0.60	0.59		0.85	0.63	0.37	0.00
CEURS	0.96	0.99	0.41	0.29	0.55	0.05	0.79		0.69	0.59	0.01
BORS	0.08	0.01	0.16	0.07	0.19	0.26	0.35	0.36		0.60	0.89
EEURSU	0.55	0.01	0.12	0.04	0.24	0.32	0.55	0.73	0.38		0.92
PNTCA	0.67	0.59	0.88	0.41	0.83	0.92	0.56	0.69	0.14	0.02	

#### 4. Summary and Conclusions

This work presents the first overview of the small mammal faunas of Europe dating to the last (Mikulinian/Eemian/Ipswichian) interglacial at a sub-continent scale. The wide spatial coverage of the studies revealed principal differences in the faunas, most probably resulting from the nonuniform climate in various regions of Europe, as well as from the geographic position of the regions, their physiographic characteristics, and the degree of isolation (the most important in the case of island faunas).

The analysis of the small mammal faunas revealed a considerable number of geographical variants, each with its own specificity in species composition and species richness. A distinct geographic zonation is reflected in the fauna composition, species richness, and the widespread dominance of species.

The faunas of Eastern Europe (in the south of the East European platform and in Crimea), include, in addition to forest species, a considerable number of inhabitants of open landscapes. Typically, xerophilous species of Asian provenance are dominant (or present to a considerable degree) in the south, east, and even in the north of Eastern Europe. These data give evidence for reconstructing a zonal pattern: forest landscapes were spread over the CEURN bioregion (Figure 2b) and most probably including mixed and broadleaf forests; farther south (bioregion CEURS and particularly PNTCA) there were forest-steppe and steppe (including dry steppe) environment. Xero- to mesophytic forest-steppe landscapes existed in the north and northeast of Eastern Europe up to the Urals. The Southern Ural Mountains were covered by montane broadleaf and coniferous-broadleaf forests and forest-steppe and steppe in the forelands. On the whole, such a zonation differs essentially from the modern zonality; in all probability it was related to the specific distribution of rainfall in the region combined with the relatively high mean annual temperatures. It should be noted that, judging from palynological data, open forests and xerophytic forest-steppes developed in the north of the East European Plain during the Last Interglacial, probably due to the absence of conditions for the tundra zone formation.

The paleo-landscapes of Central Europe also display a certain zonation. Small mammal sites located at ~48–51° N indicate forest environments in the north (bioregions ATE and CEURN). Localities in the east of Central Europe (bioregion CEURS) are noted for a noticeable amount of open landscape species, though forest animals are also present. The data suggest forest-steppe environments in these regions.

The micromammal materials from the northern and central regions of Western Europe (bioregions ATE and EURW) strongly suggest the dominance of forest ecosystems. Judging from the dominant mammal species, the landscapes were mostly mixed coniferous-broadleaf forests. In the south they gave way to broadleaf forests (except for mountains). The wide occurrence of *M. arvalis* in the north (bioregion ATE) suggests a predominance of open habitats including meadows.

The local faunas of the West European south show a noticeable influence from the Mediterranean fauna. Some West European relicts were present; one of them, *P. coronensis*, should be mentioned. The species became extinct in Central and Eastern Europe as early as the beginning of Middle Pleistocene.

Few species have been identified in the small mammal assemblages from the British Isles. In species composition those faunas are similar to (though much poorer than) those of continental Europe (bioregion ATE); no endemic species are found. The fauna is dominated by inhabitants of forest and wet biotopes.

The small mammal fauna of the Iberian Peninsula, with exception of its northernmost part (bioregion MDIB), was distinct from the fauna of the EURW bioregion bordering MDIB on the north. The dominance of *A. sylvaticus* and the wide occurrence of typical species such as the southwestern water vole (*A. sapidus*) and the Cabrera's vole (*M. (I.) cabrerae brecciensis*) are indicative of a mild climate with sufficient moisture supply; the aridity increased gradually from north to south. The faunal composition suggests the predominance of forest and shrub vegetation alternating with open sites, the proportion of the latter increasing southwards. Specific features of the MDIB bioregion fauna are the

presence of Pyrenean desman (*Galemys pyrenaicus*), Pyrenean pine vole (*Microtus (Terricola) pyrenaicus*), Mediterranean pine vole (*M. (T.) duodecimcostatus*), and some others.

The fauna of Sardinia Island differs from faunas of all the other regions. The Eemian localities of the island contain only endemic forms of small mammals, indicative of a long-term isolation of the island from the continent during the Pleistocene.

The micromammal fauna of the Apennine Peninsula (bioregion MDAP) is not highly diversified in composition. The notable presence of endemic Savi's pine vole species (at least in the south of peninsula) suggests the wide occurrence of open and relatively arid landscapes.

All the Mikulinian (Eemian, Ipswichian) faunas in Europe show signs of a considerably warmer climate. Under those conditions the rainfall could be important for the development of forests. The climate was favorable for the territorial afforestation in the west of Europe and over a considerable part of Central and Eastern Europe. At the same time the south of Central Europe, as well as considerable areas in the south, southeast, and east of Eastern Europe, could suffer from insufficient moisture supply, which accounts for wide distribution of open xerophytic steppes and mesophytic forest-steppes. In contrast, the southwestern margins of Europe received precipitation in greater abundance in the Last Interglacial than at present and the forest assemblages were widespread in the region, in its middle part in particular. A similar situation presumably existed on the Apennine Peninsula, though this hypothesis cannot be tested as yet due to insufficient data on the small mammals in its northern part. By analogy, we may assume rather arid conditions and open biotope prevalence over a greater part of the Balkan Peninsula at the considered time interval.

To obtain more detailed regional characteristics of the faunas we used the data on the European regions based on the modern ranges of mammal species. Those biogeographic units appear to be distinctly differentiated with respect to the composition of local small mammal faunas of the Last Interglacial age forming "natural" well-interpretable clusters. This is an argument in support of a relative stability of biogeographic units during the Late Pleistocene as had been suggested on the basis of the analysis of mammal species ranges in MIS 3–MIS 1 [155].

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/2571-550X/1/2/9/s1>. Table S1: The list of localities used in this work, Table S2: The Eemian small mammals faunas of Eastern Europe, Table S3: The Eemian small mammal faunas of Central Europe, Table S4: The Eemian small mammal faunas of Western Europe, Table S5: The Eemian small mammal faunas of the British Isles, Table S6: The Eemian small mammal faunas of Northern Mediterranean (Apennine and Iberian Peninsulas and Sardinia Island).

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