

# Modelling habitat-suitability using museum collections: an example with three sympatric *Apodemus* species from the Alps

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## Abstract

**Aim, Location** Although the alpine mouse *Apodemus alpicola* has been given species status since 1989, no distribution map has ever been constructed for this endemic alpine rodent in Switzerland. Based on redetermined museum material and using the Ecological-Niche Factor Analysis (ENFA), habitat-suitability maps were computed for *A. alpicola*, and also for the co-occurring *A. flavicollis* and *A. sylvaticus*.

**Methods** In the particular case of habitat suitability models, classical approaches (GLMs, GAMs, discriminant analysis, etc.) generally require presence and absence data. The presence records provided by museums can clearly give useful information about species distribution and ecology and have already been used for knowledge-based mapping. In this paper, we apply the ENFA which requires only presence data, to build a habitat-suitability map of three species of *Apodemus* on the basis of museum skull collections.

**Results** Interspecific niche comparisons showed that *A. alpicola* is very specialized concerning habitat selection, meaning that its habitat differs unequivocally from the average conditions in Switzerland, while both *A. flavicollis* and *A. sylvaticus* could be considered as 'generalists' in the study area.

**Main conclusions** Although an adequate sampling design is the best way to collect ecological data for predictive modelling, this is a time and money consuming process and there are cases where time is simply not available, as for instance with endangered species conservation. On the other hand, museums, herbariums and other similar institutions are treasuring huge presence data sets. By applying the ENFA to such data it is possible to rapidly construct a habitat suitability model. The ENFA method not only provides two key measurements regarding the niche of a species (i.e. marginality and specialization), but also has ecological meaning, and allows the scientist to compare directly the niches of different species.

## Keywords

Alps, *Apodemus*, Ecological-Niche Factor Analysis, Geographic Information System, habitat suitability model, museum data, presence data.

## INTRODUCTION

Although museums store large amounts of material in the form of either herbariums, collections or list of observations,

this information is generally not used for quantitative studies. Such data suffer from several drawbacks that make them unsuitable for most statistical analyses. These drawbacks include: (1) a global sampling design is lacking, which makes observation biases unknown but highly probable and (2) accuracy regarding specimen measurement, determination and/or spatial localization is generally both variable and unverified. Nevertheless, museum collections, provided that

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their deficiencies are recognized and coped with, can offer by their sheer number invaluable insights into a species spatial distribution and ecology. In the particular case of habitat suitability models, classical approaches (GLMs, GAMs, discriminant analysis, etc. see Guisan & Zimmermann, 2000) generally require both presence and absence data. In this paper, we apply Ecological-Niche Factor Analysis (ENFA, Hirzel *et al.* 2002) which requires only presence data, to build a habitat-suitability map of three species of *Apodemus* on the basis of museum skull collections.

The ENFA computes a habitat suitability model by comparing in the ecogeographical variables (EGVs) space the distribution of the locations where the species has been detected to that of all locations of the study area (Hirzel *et al.*, 2002). This approach is recommended when absence data are not available (most data banks), unreliable (most cryptic or rare species) or meaningless (invaders) (Hirzel *et al.*, 2001b). Thus, an application of the method could be interesting in many domains: landscape management for endangered species, better knowledge of unknown or inaccessible areas, or also better knowledge of 'new' species' ecology and/or distribution. In our case, we focused on the 'newly' discovered alpine mouse *Apodemus alpicola* whose ecology and distribution in the Alpine arc still remains unclear.

Mice of the genus *Apodemus* are amongst the most widely distributed rodents in Europe (Niethammer, 1978). Three species occur in the Alps: the wood mouse, *Apodemus sylvaticus* (Linnaeus, 1758), the yellow-necked mouse, *A. flavicollis* (Melchior, 1834), and the alpine mouse, *A. alpicola* Heinrich, 1952. The alpine mouse is endemic to Europe, where it is, to our knowledge, confined to the Alps of France, Switzerland, Germany, Italy, and Austria (Storch & Lütt, 1989; Spitzenberger & Englisch, 1996; Storch, 1999).

In Switzerland *A. sylvaticus* is widespread and common from the plains to 1800 m above sea level (Vogel, 1995). While the number of registrations in museum collections of *A. flavicollis* is smaller than that of *A. sylvaticus*, their distribution areas are very similar (Vogel, 1995). The situation for *A. alpicola* is more complex. The alpine mouse was considered, till 1989, as a high-altitude subspecies of the yellow-necked mouse (Heinrich, 1951, 1952). Its interpretation as a separate species (Storch & Lütt, 1989) was based on the occurrence of three morphologically distinct syntopic forms in the German and Austrian Alps. The specific status of the alpine mouse was later confirmed biochemically by Vogel *et al.* (1991) and Filippucci (1992). Thus, it is highly probable that a certain part of the species assignment for *A. flavicollis* in Switzerland between 1400 and 2000 m refers effectively to *A. alpicola* (Vogel, 1995).

The habitat of *A. sylvaticus* is extremely variable, including suburban or inner city areas where parkland is available, cultivated areas (Kikkawa, 1964; Pollard & Relton, 1970; Green, 1979; Pelikan & Nesvadbova, 1979; Angelstam *et al.*, 1987), hedgerows (Pollard & Relton, 1970; Boone & Tinklin, 1988; Kotzageorgis & Mason, 1997), oldfields (Montgomery, 1981), moors, forestry plantations

and woodlands of all kinds (Kikkawa, 1964; Flowerdew, 1985; Gorman *et al.*, 1993; Pucek *et al.*, 1993; Canova *et al.*, 1994). The habitat of *A. flavicollis* is restricted to mature deciduous and mixed forest zone (Pucek, 1981) as well as coniferous forest, but occurs occasionally in parks and hedges. The habitat of *A. alpicola* is not yet very well studied but appears to include a combination of debris and rocks, water and grassy spots, mostly in the mountainous woodland zone (Storch & Lütt, 1989; Spitzenberger & Englisch, 1996; Storch, 1999). In Switzerland, the alpine mouse was recorded between 550 and 2000 m above sea level (Vogel, 1995).

The aims of this study were: (1) to establish new distribution maps for the three sympatric species in Switzerland, particularly for the yellow-necked and alpine mouse, as no previous maps existed for them; and (2) to investigate how habitat-suitability maps could be modelled on the basis of reclassified museum material.

## MATERIAL AND METHODS

The habitat-suitability maps were computed by the ENFA (Hirzel *et al.*, 2002). Given a set of ecogeographical predictors, the ENFA compares their distribution for a presence data set consisting in locations where the species has been detected, to their distribution on the whole area. Like Principal Component Analysis, ENFA summarizes all predictors into a few uncorrelated factors retaining most of the information. But in this case, the factors have an ecological meaning: the first factor represents the marginality, i.e. those variables for which the species niche mostly differs from the available conditions in the global area. The other factors represent successively decreasing amount of information about specialization, i.e. how restricted is the species niche as compared with the available habitat. As a large part of the information is accounted for by a few of the first factors, only those shown significant by comparison with MacArthur's Broken-stick distribution (Hirzel *et al.*, 2002) were included in further analyses.

The correlations of these factors with the original predictors give precious information about the ecological niche of the studied species. Global marginality and specialization coefficients, although they depend on the study area, can be used to compare several species studied in the same region. Finally, the species distribution on the factors is used to compute a habitat-suitability map.

The study area comprised the whole of Switzerland. All analyses were performed within a raster-map data structure based on the Swiss Coordinate System (plane projection, with a 100 × 100-m resolution).

The first type of data needed by the ENFA is a list of locations where the studied species has been detected. The *Apodemus* presence data sets originated from various Swiss museum collections and from the Institute of Ecology's (University of Lausanne, Switzerland) own material. The species of most of the individuals was determined by skull morphometry (Reutter *et al.*, 1999), biochemical (Vogel *et al.*, 1991; Reutter *et al.*, 2001) or genetic (Reutter *et al.*,

2002) analysis. A total of 2237 individuals (1640 *A. sylvaticus*, 469 *A. flavicollis*, and 128 *A. alpicola*) were included in this study, each one attached to a set of geographic coordinates. The latter were used to locate the individuals on a raster presence map. Several locations occurred in the same grid cell but, because of the unreliability of the sampling design, we could not make use of this 'abundance' information and had to reduce it to 'presence' only. As a consequence, the final sample size was 406 for *A. sylvaticus*, 202 for *A. flavicollis*, and eighty-two for *A. alpicola*.

The second type of data needed by the ENFA is a set of quantitative raster maps describing the environment. Fifty-five ecogeographical variables (Table 1) were derived from governmental databases (Table 2). Among them, topo-

graphical data (altitude, slope and aspect) were directly quantitative. Land-cover qualitative data (occurrence of permanent snow, rocks, meadow, forest, building, etc.) were transformed into frequency and distance variables. Distance variables express the distance between the focal cell and the closest cell belonging to a given category. Frequency variables describe the proportion of cells from a given category within a circle of 300 m radius around the focal cell. This radius was reflecting the home range size of *Apodemus* species which varies from 3000 to 16000 m<sup>2</sup> depending on sex, breeding season and habitat (various woodlands, arable land, etc.) (Wilson *et al.*, 1993; Canova *et al.*, 1994).

In a multivariate niche as defined in Hutchinson's (1957) concept of the ecological niche an index of marginality and specialization can be quantified on any of its dimensions.

**Table 1** List of the fifty-five ecogeographical variables (EGV) included into the Ecological-Niche Factor Analysis (ENFA). FQ are frequency and DIST distance variables

Code	EGV	Code	EGV
ALBUSH_F	Alpine meadows-bushy-FQ	FOFRA_D	Forest-fragmented-DIST
ALMOW_F	Alpine meadows-mowed-FQ	FOAGRI_D	Forest-agriculture-DIST
ALFAV_F	Alpine meadows-favourable-FQ	SNOW_D	Snow-DIST
ALROC_F	Alpine meadows-rocky-FQ	LAKES_D	Lakes-DIST
ALHAY_F	Alpine meadows-hay-FQ	MBUSH_D	Meadows-bushy-DIST
BUSH_F	Bushes-FQ	MLOCA_D	Meadows-local-DIST
BHUM_F	Biotopes-humid-FQ	FRUPLA_D	Fruit plantations-DIST
HEDGE_F	Hedgerows-FQ	GRASS_D	Grass-DIST
EXPO_COS	Exposition-cos	ROCKS_D	Rocks-DIST
RIVERS_F	Rivers-FQ	VEHERB_D	Vegetation-herb-DIST
ALTITUDE	Altitude	VESHOR_D	Vegetation-shore-DIST
SD_ALT	SD Altitude	VILLAG_D	Villages-DIST
ALBUSH_D	Alpine meadows-bushy-DIST	RAIL_D	Railway-DIST
ALMOW_D	Alpine meadows-mowed-DIST	WOSPA_F	Wooden spaces-FQ
ALFAV_D	Alpine meadows-favourable-DIST	FOBUSH_F	Forest-bushy-FQ
ALROC_D	Alpine meadows-rocky-DIST	FOOPEN_F	Forest-open-FQ
ALHAY_D	Alpine meadows-hay-DIST	FONOR_F	Forest-normal-FQ
BUSH_D	Bushes-DIST	FOFRA_F	Forest-fragmented-FQ
BUILD_D	Buildings-DIST	FOAGRI_F	Forest-agriculture-FQ
BANKS_D	Banks, shores-DIST	MBUSH_F	Meadows-bushy-FQ
BHUM_D	Biotopes-humid-DIST	MLOCA_F	Meadows-local-FQ
HEDGE_D	Hedgerows-DIST	FRUPLA_F	Fruit plantations-FQ
RIVERS_D	Rivers-DIST	GRASS_F	Grass-FQ
WOSPA_D	Wooden spaces-DIST	ROCKS_F	Rocks-FQ
FOOTH_D	Forest-other-DIST	EXPO_SIN	Exposition-sin
FOBUSH_D	Forest-bushy-DIST	SLOPE	Slopes
FOOPEN_D	Forest-open-DIST	VEHERB_F	Vegetation-herb-FQ
FONOR_D	Forest-normal-DIST		

**Table 2** Nature and source of the fifty-five ecogeographical variables included into the Ecological-Niche Factor Analysis (ENFA) of *Apodemus* distribution. LT is the Swiss Federal Office of Topography, and BFS the Swiss Federal Office of Statistics

Official data base	Source	EGV derived from it
AS85R (cover use)	BFS	Rock, snow, forests, meadows, etc. frequency and distance
DHM (topography)	BFS	Altitude, slope, aspect, SD altitude
GWN (hydrography)	BFS	Distance to rivers and lakes
Vector 200 (land map)	LT	Villages, railways, etc. distance
<i>Apodemus</i> data sets	Museums	Calibrating and validating presence data set

These dimensions are often highly correlated between them and some of them are obviously more interesting than others; this is why a factor analysis is introduced.

The ENFA computes for each species a global marginality coefficient, expressing how, on all the EGVs, the species average differs from the global average, and a global specialization coefficient, expressing the ratio of global variance to species variance. The global marginality is generally between zero and one (although the value can exceed one) (Hirzel *et al.*, 2002). Large values indicate that the focal species lives in a very particular habitat in relation to the reference area (here, Switzerland). The global specialization coefficient varies from one to infinite. More tractable, however, is the tolerance value – inverse of specialization – which varies from 0 to 1. Intuitively, a species showing a tolerance close to one inhabits a wider niche than a species with a tolerance close to zero.

Model validation was achieved through a jack-knife cross-validation process (Fielding & Bell, 1997) as follows: for each species, the presence points were partitioned into ten subsets of equal sizes. Nine of them were used to calibrate the habitat-suitability map and the last one was used to evaluate the result; by replicating this process ten times, each subset being used in turn for validation purpose, it was possible to compute mean and standard deviation of the accuracy assessment.

All these operations, including ENFA, were performed using the software *Biomapper* (Hirzel *et al.*, 2001a).

In the ENFA, the niche dimensions permitting a segregation in syntopic co-occurrence (spatial, temporal and trophic behaviour) are not included.

## RESULTS

### *Apodemus alpicola*

*Apodemus alpicola* had a global marginality of 1.04 and a global tolerance value of 0.25 (Table 4), showing that its habitat differs unequivocally from the average conditions in Switzerland. The seven factors retained according to the Broken-stick rule (of the fifty-five computed) accounted for 100% of the total marginality and 80.3% of the total specialization (Table 3). The marginality factor alone accounted for 34% of the total specialization, meaning that the alpine mouse displays a restricted range on those conditions for which it mostly differs from the average conditions in Switzerland.

Marginality coefficients (Table 3) showed that *A. alpicola* is essentially linked to open forests (less dense forests with a cover of 20–60%) (distance =  $-0.25$ , frequency = 0.23), bushy forests (with *Alnus viridis*, *Pinus mugo* and *Corylus avellana*, exclusively in alpine areas) (distance =  $-0.23$ ), rivers (frequency = 0.25, distance =  $-0.22$ ) and mowed alpine meadows (situated in the alpine region, used for dry foraging) (distance =  $-0.21$ , frequency = 0.17). On the other hand, *A. alpicola* tends to avoid shore vegetation (lake and river reed vegetation). The large eigenvalue (34%) attributed

to this first factor shows that *A. alpicola* is quite sensitive to shifts from its optimal conditions on this axis. The next factors account for some more specialization, mostly regarding altitude, distance to woody spaces (groups of trees in the alpine region), rocky alpine meadows, rocks and rocky slopes (second factor).

A suitability map was constructed from the first five factors for the whole of Switzerland (Fig. 1). As shown in Fig. 4, presence cells are largely higher than those of the global distribution; this shows that the model assigns higher suitability values to cells inhabited by *A. alpicola*. According to Jack-knife cross-validation, predicted suitability exceeds 0.5 in 68.6% of the validation cells (SD = 0.17).

### *Apodemus flavicollis*

*Apodemus flavicollis* showed a global marginality value of 0.83 and a global tolerance value of 0.57 (Table 4). The yellow-necked mouse lives in habitats that differ less from average conditions in Switzerland than does *A. alpicola*. Six factors (of the fifty-five computed) were retained (Broken-stick) and accounted for 58% of the total specialization and 100% of the total marginality (Table 3). The marginality factor alone accounted for 31% of this total specialization, meaning that the yellow-necked mouse also displays a restricted range on these conditions for which it mostly differs from the Swiss average.

Marginality coefficients (Table 3) showed that *A. flavicollis* is essentially linked to hedgerows (distance =  $-0.25$ , frequency = 0.22), grassland (suitable for cultivation, poor and dry meadows) (distance =  $-0.23$ , frequency = 0.21) fragmented forests (distance =  $-0.22$ ), and buildings (distance =  $-0.24$ ). *Apodemus flavicollis* seems to avoid rocks and rocky slopes (frequency =  $-0.20$ ). Furthermore, the yellow-necked mouse preferentially inhabits altitudes below the Swiss average (1311 m above sea level, distance =  $-0.27$ ).

The suitability map was built from the first six factors for all of Switzerland (Fig. 2). The difference between the global and the species distribution is not as drastic as found in *A. alpicola*, graphically showing that the former lives in less marginal conditions than the latter (Fig. 4). The Jack-knife cross-validation shows that predicted suitability exceeds 0.5 in 75.6% of the validation cells (SD = 0.08).

### *Apodemus sylvaticus*

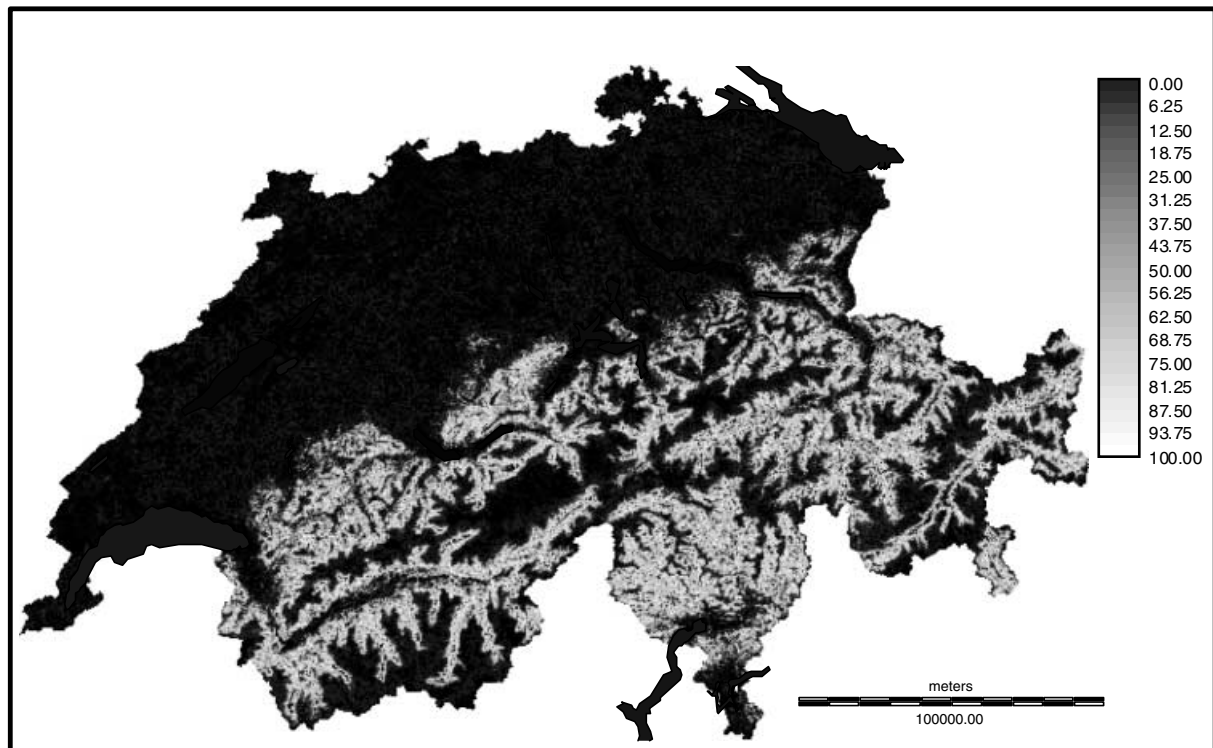
The global marginality (0.80) and tolerance (0.62) values (Table 4) of *A. sylvaticus* are similar to those of *A. flavicollis*. In contrast to *A. alpicola*, the other two *Apodemus* species do not seem to be very attached to special regions in Switzerland. The three factors (Broken-stick) retained (of the fifty-five computed) accounted for 46% of the total specialization and 100% of the total marginality (Table 3). The marginality factor alone accounted for 11% of this total specialization.

**Table 3** Variance explained by the first four (of fifty-five) ecological factors, and coefficient values for the thirteen most important variables for *Apodemus alpicola* (a), *A. flavicollis* (b), and *A. sylvaticus* (c). Positive values on the marginality factor mean that *A. alpicola* prefers locations with higher values on the corresponding ecogeographical variable (EGV) than the Swiss average. The signs of the specialization coefficients have no meaning. The amount of specialization accounted for is given between parentheses

EGV	Marginality (34%)	EGV	Factor 2 (17%)	EGV	Factor 3 (9%)	EGV	Factor 4 (7%)
(a)							
RIVERS_F	0.25	ALTITUDE	0.49	FOBUSH_D	0.62	ALROC_D	0.63
FOOPEN_D	-0.25	WOSPA_D	0.41	VESHOR_D	0.32	RIVERS_D	0.29
FOBUSH_D	-0.23	ALROC_D	0.34	ALTITUDE	0.32	ALTITUDE	0.26
FOOPEN_F	0.23	ROCKS_D	0.30	WOSPA_D	0.27	ALBUSH_D	0.22
VESHOR_D	0.22	FONOR_D	0.23	ALROC_D	0.20	ALHAY_F	0.20
RIVERS_D	-0.22	SNOW_D	0.22	FOFRA_D	0.20	BUSH_D	0.19
ALMOW_D	-0.21	FOAGRI_D	0.21	FOOTH_D	0.19	FOBUSH_D	0.18
BUSH_D	0.20	FONOR_F	0.19	FONOR_D	0.18	SNOW_D	0.18
WOSPA_D	-0.20	VEHERB_D	0.17	VEHERB_D	0.16	ALMOW_D	0.18
SNOW_D	-0.18	ALFAV_D	0.17	ALHAY_F	0.14	LAKES_D	0.17
WOSPA_F	0.18	SD_ALT	0.12	VILLAG_D	0.13	GRASS_D	0.15
ALMOW_F	0.17	RAIL_D	0.11	EXPO_SIN	0.12	ALFAV_F	0.15
VEHERB_D	-0.17	LAKES_D	0.11	ALROC_F	0.10	EXPO_SIN	0.13
EGV	Marginality (31%)	EGV	Factor 2 (8%)	EGV	Factor 3 (7%)	EGV	Factor 4 (6%)
(b)							
ALTITUDE	-0.27	ALHAY_F	0.46	ALBUSH_F	0.415	ALHAY_F	0.49
HEDGE_D	-0.25	ALROC_F	0.43	FOFRA_D	0.366	ALROC_F	0.41
BUILD_D	-0.24	GRASS_D	0.36	ALMOW_D	0.316	ALBUSH_F	0.38
GRASS_D	-0.23	ALBUSH_F	0.28	ALHAY_D	0.301	GRASS_D	0.29
HEDGE_F	0.22	FOFRA_D	0.25	ROCKS_F	0.248	VEHERB_F	0.25
FOFRA_D	-0.22	FOBUSH_D	0.24	ALTITUDE	0.247	FONOR_D	0.22
GRASS_F	0.21	SNOW_D	0.23	GRASS_D	0.224	FOFRA_D	0.21
ROCKS_F	-0.20	ALBUSH_D	0.22	SNOW_D	0.205	ALFAV_D	0.17
FRUPLA_D	-0.20	ALMOW_D	0.19	ALHAY_F	0.195	ALROC_D	0.16
VILLAG_D	-0.19	ALROC_D	0.17	ALBUSH_D	0.193	WOSPA_F	0.14
RIVERS_F	0.19	ALFAV_D	0.11	HEDGE_D	0.181	VEHERB_D	0.13
RAIL_D	-0.18	SD_ALT	0.11	FONOR_D	0.146	HEDGE_D	0.13
FOAGRI_D	-0.18	SLOPE	0.11	GRASS_F	0.145	SLOPE	0.12
EGV	Marginality (11%)	EGV	Factor 2 (29%)	EGV	Factor 3 (6%)	EGV	Factor 4 (4%)
(c)							
BUILD_D	-0.25	ALHAY_F	0.90	SNOW_D	0.57	ALROC_F	0.55
GRASS_D	-0.24	FOFRA_D	0.23	ALHAY_F	0.40	ALFAV_D	0.39
ALTITUDE	-0.24	GRASS_D	0.19	FONOR_D	0.31	ALBUSH_F	0.34
HEDGE_D	-0.23	ALROCK_F	0.14	ALFAV_D	0.30	ALROC_D	0.34
RAIL_D	-0.23	ALBUSH_F	0.14	FOBUSH_D	0.23	ALBUSH_D	0.28
VILLAG_D	-0.22	FONOR_D	0.13	ALFAV_F	0.19	ALTITUDE	0.20
GRASS_F	0.21	SNOW_D	0.09	HEDGE_D	0.19	ALFAV_F	0.20
FRUPLA_D	-0.21	FONOR_F	0.07	ALROC_F	0.16	SLOPE	0.12
FOFRA_D	-0.21	FOFRA_F	0.07	ALBUSH_D	0.13	MLOCA_D	0.11
RIVERS_F	0.20	GRASS_F	0.07	GRASS_D	0.11	ALHAY_F	0.11
HEDGE_F	0.19	FOBUSH_F	0.06	EXPO_COS	0.11	MBUSH_D	0.10
MLOCA_D	-0.19	ALROCK_D	0.04	FONOR_F	0.11	ALMOW_D	0.10
ALFAV_F	-0.18	EXPO_COS	0.04	VESHOR_D	0.11	VEHERB_D	0.09

Marginality coefficients (Table 3) showed the wood mouse to be more synanthropic than the two other species (distance to buildings = -0.25, distance to villages = -0.22, distance to railway = -0.23, distance to grassland = -0.24, frequency of grassland = 0.21, distance to fruit planta-

tions = -0.21). The wood mouse is also linked to hedgerows (distance = -0.23, frequency = 0.19) as well as to fragmented forests (distance = -0.21), rivers (frequency = 0.20), and local meadows (used by cattle, sheep and goats) (distance = -0.19). *Apodemus sylvaticus* occurs mostly



**Figure 1** Habitat-suitability map for *Apodemus alpicola* in Switzerland, as computed by Ecological-Niche Factor Analysis (ENFA). The scale on the right shows the habitat suitability values presented by each shade in the map.

**Table 4** Global marginality, specialization and tolerance values for the three *Apodemus* species, computed for Switzerland

	<i>A. alpicola</i>	<i>A. flavicollis</i>	<i>A. sylvaticus</i>
Marginality	1.04	0.83	0.80
Specialization	3.98	1.75	1.6
Tolerance	0.25	0.57	0.62

below the average altitude of Switzerland and tends to avoid favourable alpine meadows (used by cattle but limited by rocks, rocky slopes and bushes, frequency =  $-0.18$ ).

The first three factors were taken in consideration to build the habitat-suitability map of *A. sylvaticus* for the whole of Switzerland (Fig. 3). Comparison of suitability distribution between global and species validation values (Fig. 4) showed a pattern similar to the one observed also by *A. flavicollis*. Predicted suitability exceeds 0.5 in 71.5% of the validation cells (SD = 0.1).

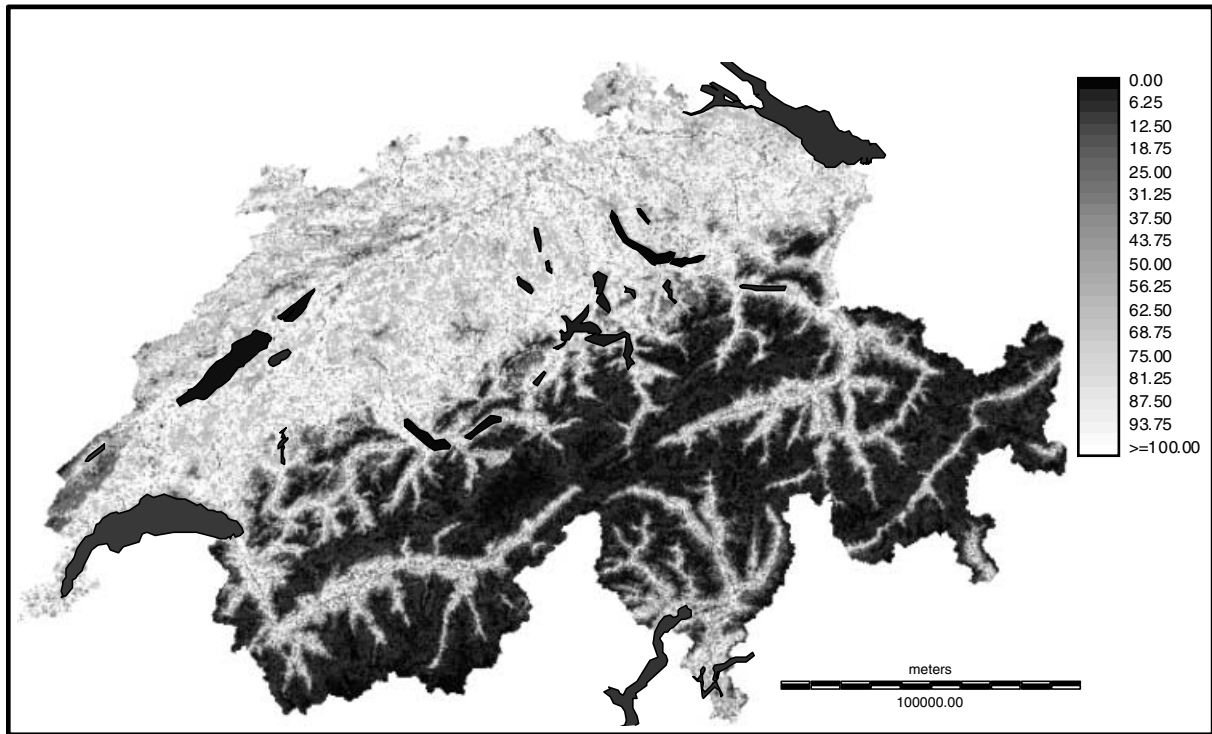
## DISCUSSION

*Apodemus flavicollis* and *A. sylvaticus* are closely related species living in Switzerland in perfect sympatry. Both species show almost the same global marginality coefficients (0.83 and 0.80, respectively), which was also observed by Vogel (1995) following the procedure of Hausser (1995), although

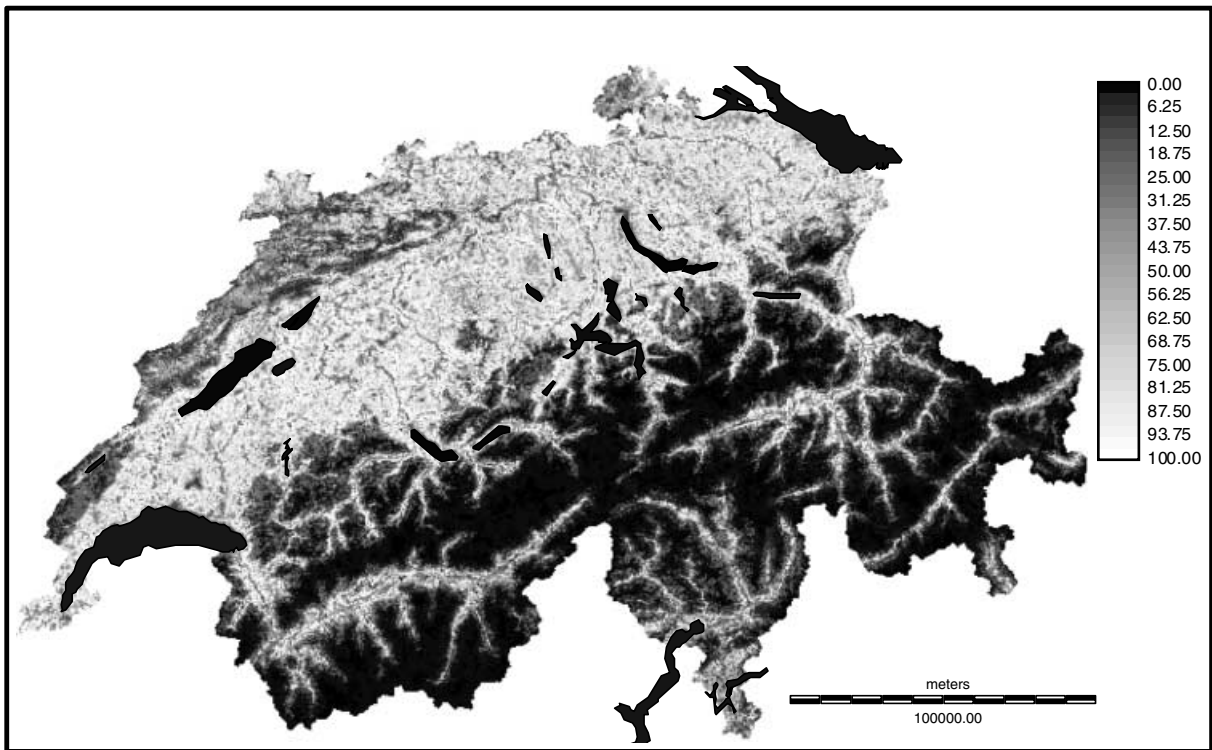
his results (0.5) differed from ours. This difference is due to the fact that we did not use exactly the same ecological parameters as did Hausser (1995) for the Swiss Atlas of Mammals. They were derived from thirty-four EGVs transformed into frequency variables with a square-kilometre resolution.

In contrast, the optimal habitat of *A. alpicola* differs drastically from the Swiss average, which means that the alpine mouse prefers to inhabit extreme regions of Switzerland, namely the Alps. The ecological difference between *A. alpicola* and the two other species is clearly greater than that between *A. flavicollis* and *A. sylvaticus*, strengthening its specific status, as determined by Storch & Lütt (1989).

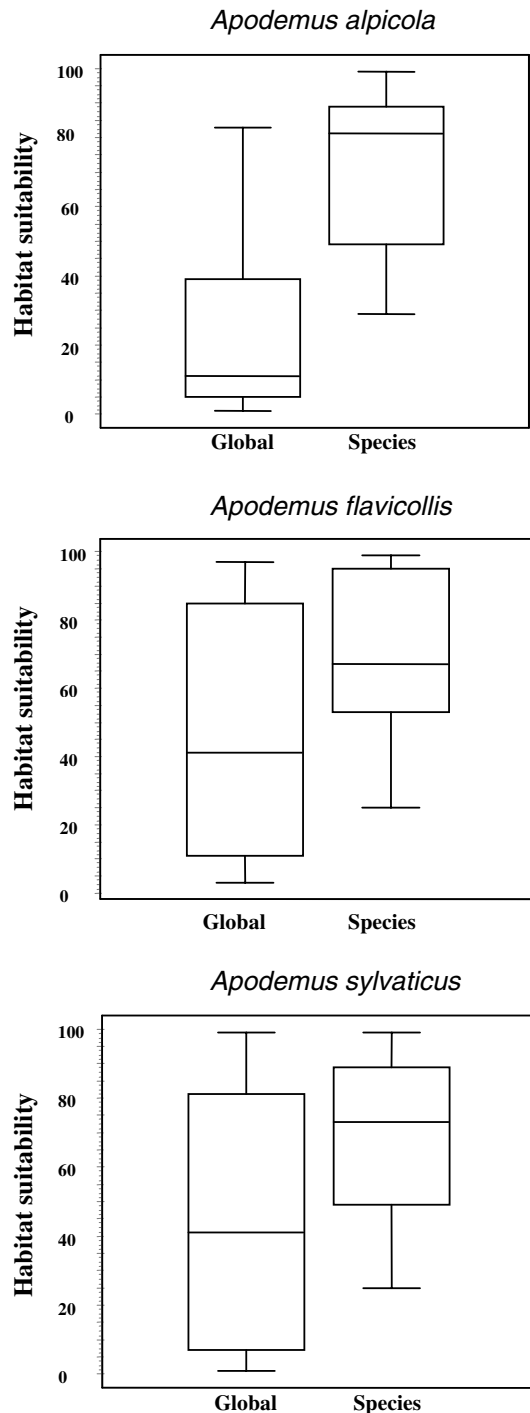
Interspecific comparisons among the marginality coefficients show interesting differences for all EGVs related to altitude. While *A. flavicollis* and *A. sylvaticus* are mostly observed lower than the Swiss average (1311 m), *A. alpicola* prefers to inhabit higher altitudes. In addition, the presence of the yellow-necked mouse and wood mouse is correlated with human factors (grassland, buildings, villages, fruit plantations, railway etc.), whereas the presence of the alpine mouse is linked to less dense and bushy forests, bushes, alpine meadows (mowed, rocky), rivers and permanent snow. Interpretation of the factors in terms of EGVs turns out to be very consistent with the experience of field specialists. Therefore, our results could be considered as additional information to the few habitat descriptions



**Figure 2** Habitat-suitability map for *Apodemus flavicollis* in Switzerland, as computed by Ecological-Niche Factor Analysis (ENFA). The scale on the right shows the habitat suitability values presented by each shade in the map.



**Figure 3** Habitat-suitability map for *Apodemus sylvaticus* in Switzerland, as computed by Ecological-Niche Factor Analysis (ENFA). The scale on the right shows the habitat suitability values presented by each shade in the map.



**Figure 4** Box-plots presenting the distributions of the habitat-suitability values for the whole set of cells (left) and the validation subset (right). Boxes delimit the interquartile range, the middle line indicating the median. Whiskers encompass the 90% confidence interval.

known for *A. alpicola* (Storch & Lütt, 1989; Spitzenberger & Englisch, 1996; Storch, 1999). In general, we can conclude that all three species prefer 'open' landscape elements:

hedgerows, grasslands and fragmented forests in the cases of *A. flavicollis* and *A. sylvaticus*, and less dense forests, bushy forests and alpine meadows in the case of *A. alpicola*. Thus they live in similar habitats differing only in altitude. Grasslands and alpine meadows are probably not a real habitat for *Apodemus*, but in the mosaic like landscape of Switzerland, they are often admixed with the suitable structures.

The global tolerance values were observed to decrease from *A. sylvaticus* (0.62), *A. flavicollis* (0.57) to *A. alpicola* (0.25), meaning that the first two species are not very specialized concerning their ecological niche, and that they are able to inhabit large parts of Switzerland with only altitude as a limiting factor. In contrast, *A. alpicola* seems to be quite specialized.

The habitat-suitability maps graphically display our numeric results. They show a low specialization (or a high tolerance) for the yellow-necked mouse and the wood mouse and for the alpine mouse a fixation on extreme habitats (in particular, according to the altitude).

These results show that, in spite of the inaccuracies and potential biases related to data not resulting from a cautious sampling design, it was nevertheless possible to extract highly consistent ecological information about the three focal species derived from museum data. Furthermore, besides confirming field knowledge, the ENFA produced accurate predictive models resulting in informative habitat suitability maps. This analysis bases itself on what is known with a quite high level of reliability – namely species presence – discarding all more dubious data from the calibration process – as generally are absences. It can, therefore, extract relevant information from museum data, while coping with false absence biases (Hirzel *et al.*, 2001b). Nevertheless, it must be kept in mind that detection biases are difficult to remove from habitat analyses: actually, presence data depend not only on species behaviour but also on observers' behaviour, as well as on a habitat-dependent detectability factor. Although the former bias can be removed by carefully designing a sampling plan, the latter is much more difficult to handle. Moreover, museum data may suffer from another kind of bias, particularly with flag-species and plants: observations may be concentrated along the borders of a species range, making abundance modelling totally illusory and absences particularly misleading. However, with the ENFA, this effect is weakened when data are numerous enough to assure coverage of all possible suitable habitats.

Although an adequate sampling design is the best way to collect ecological data for predictive modelling, this is a time- and money-consuming process and there are cases where time is simply not available, as for instance with endangered species conservation. On the other hand, museums, herbariums and other similar institutions are treasuring huge presence data sets. By applying the ENFA to such data it is possible to rapidly construct a habitat suitability model. The ENFA method provides not only two key measurements regarding the niche of a species, namely those of marginality and of specialization, but also it has intuitive ecological meaning, and allows the scientist to compare directly the



niches of different species, as far as the study is applied to the same variables and in the same area.

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