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Population structure and habitat characteristics of *Arnica montana* L. in the NE Carpathians (Romania)

Populationsstruktur und Lebensraumeigenschaften von *Arnica montana* L. in den Nordost-Karpaten (Rumänien)

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Abstract

In many European countries *Arnica montana* is decreasing due to intensification or abandonment of traditional extensive land use and thus is considered endangered. In Romania the species is also decreasing due to excessive collecting for pharmaceutical and cosmetic purposes, but it is still relatively common in montane nutrient-poor grasslands and successional vegetation of forest clearings on acidic soil. In this study we analysed habitats and population structure of *A. montana* in the Romanian NE Carpathians. We asked for differences in population structure between habitat types and how population structure is related to environmental conditions. We investigated population structure and habitat characteristics in 25 populations of *A. montana* on three 1 m × 1 m-plots each (total of 75 plots). The plot-based assessment of the population structure included the numbers of rosettes (rosette density), flower heads (flower head density), flowering rosettes and flower stems per flowering rosette. From these variables we calculated the proportions of flowering and vegetative rosettes and the number of flower heads per flowering rosette. Habitats were characterised using climatic data (including elevation), land use types (grazing, mowing or abandonment), vegetation types, soil measurements (pH, several nutrient elements, organic matter content) and N supply on basis of plant indicator values. Vegetation types were defined by using hierarchical clustering and linked to phytosociological syntaxa based on diagnostic species. Observed habitat types included Mountain hay meadows, Species-rich *Nardus* grasslands and Alpine and subalpine heathlands according to the European Habitats Directive. DCA analysis was used for detecting floristic gradients, which were subsequently correlated to environmental conditions. Relationships between rosette density, proportion of vegetative rosettes, flower head density and number of flower heads per flowering rosette and environmental variables were assessed using GLMs. Five syntaxa with *A. montana* were identified: *Festuco rubrae-Agrostietum capillaris nardetosum strictae*, *Scorzonero roseae-Festucetum nigricantis*, *Violo declinatae-Nardetum strictae*, *Cetrario-Vaccinietum gaultherioidis* and *Campanulo abietinae-Vaccinietum myrtilli*. While vegetation composition was mainly correlated with altitude and soil variables such as pH and organic matter content, altitude was an important predictor for the proportion of flowering rosettes of *A. montana*, which decreased with altitude. Rosette density of *A. montana* varied between habitat types and was highest in Mountain hay meadows and lowest in plant communities dominated by tall plants with

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high cover. Organic matter content of the soil was the only important (negative) predictor for the number of flower heads per rosette, while a hump-shaped correlation was found between the density of inflorescences and the soil pH, with a maximum around pH 4.5. Grassland management was also an important factor for rosette density of *A. montana*, suggesting that maintaining and promoting traditional land use practices will be the most effective measure for the species' conservation.

Keywords: elevation, flower intensity, habitat analysis, medicinal plant, population density, threatened plant

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

In many European countries *Arnica montana* is currently strongly declining due to abandonment or intensification of traditional extensive land use. Only in few countries the populations are considered stable (FENNEMA 1992, DE GRAAF et al. 1998, LUIJTEN et al. 2000, FALNIOWSKI et al. 2011, MAURICE et al. 2012, VERA et al. 2014). Therefore, the species is listed in the fifth appendix of the Habitats Directive by the European Union. In Romania, where *A. montana* is listed as "vulnerable" in the Red List of vascular plants (OLTEAN et al 1994), excessive collecting of inflorescences for pharmaceutical and homeopathic purposes and for cosmetics is a further threat for the species (SUGIER et al. 2013). Beside this, the species is poorly valued economically in Romania, i.e., most of the collected material is exported and processed in other countries. Despite the pressure of excessive collecting, in Romania the species still occurs frequently in mesophytic montane grasslands and, to a lesser extent, in successional vegetation emerged in forest clearings on acidic and nutrient-poor soil (MICHLER 2007, STOIE & ROTAR 2009, MARDARI et al. 2015).

Analysing plant population structure is a suitable tool for gaining insight into the demographic trend of a population and can thus be used to assess its risk of extinction (KIENBERG & BECKER 2017). It is known that environmental factors mainly influence plant population structure and that data referring to the density of individuals or flowers can highlight the demographic characteristics of a population in time or along environmental gradients (HEYWOOD & IRIONDO 2003). For *A. montana* it has been shown that altitude has a positive effect on plant density and plant performance, while high nutrient content has a negative effect on population size (MAURICE et al. 2012). For clonal plants like *A. montana*, population size is difficult to estimate (LUIJTEN et al. 2000), and therefore rosette density must be used for assessing population structure (ADRIAENS et al. 2009). Also, the proportion of flowering/vegetative rosettes or density of inflorescences can be used as indicators for both constitution of populations and habitat quality of *A. montana*. In strongly resource-limited environments as e.g. nutrient-poor soils, plants may allocate their resources by shifting from sexual reproduction to more clonal growth, which enhances survival of plants (WEPPLER & STÖCKLIN 2005, HAUTIER et al. 2009, XIE et al. 2014, BILLS et al. 2015). This allocation is considered an important general plant strategy for growing in harsh environments (PLUESS & STÖCKIN 2005, VALLEJO-MARÍN et al. 2010, YE et al. 2016). A high proportion of non-flowering individuals may e.g. indicate a species' altitudinal limit (KLIMEŠOVÁ & DOLEŽAL 2011), an unfavourable management status of the habitat or population-biological characteristics like genetic erosion (DUWE et al. 2017).

Although the distribution of *A. montana* in the Romanian Eastern Carpathians is well documented, there is a lack of studies dealing with the population structure of *A. montana* and the relationships between its population structure and habitat characteristics. We studied

25 populations of *A. montana* in the NE Carpathians in Romania and asked the following questions: (1) Which population structure is typical of *A. montana* in the study area, and are there differences in population structure between sites? (2) How is the population structure of *A. montana* related to habitat characteristics such as elevation, vegetation and habitat types, land use and soil conditions?

2. Study area

The study area (Fig. 1) is located in the NE Carpathians in N Romania (46°23'–47°65' N, 25°01'–25°91' E) and includes nine geographical sub-regions: Ceahlău Massif, Bistriţei Mountains, Stânişoarei Mountains, Rarău Massif, Obcinele Bucovinei, Călimani Mountains, Suhardului Mountains, Bârgăului Mountains and Dornelor Depression. The altitude of the study sites ranges from 700 to 2100 m a.s.l. The climate is moderately temperate-continental (CHIFU et al. 2006). The mean annual temperature is 2–6 °C and the mean annual precipitation 800–1200 mm. The geology of the area is diverse and includes crystalline schists (Bistriţei and Suhardului Mountains), limestones (Ceahlău Massif, Stânişoarei Mountains, Rarău Massif, Obcinele Bucovinei), volcanic rocks (Călimani Mountains) and Pliocene deposits of sandstones, sands and clays (Dornelor Depression). Dominant soil types are spodosols, cambisols and, to a lesser extent, andosols. Potential natural vegetation includes mainly coniferous and mixed broad-leaved-coniferous forests (BOHN et al. 2004). The area

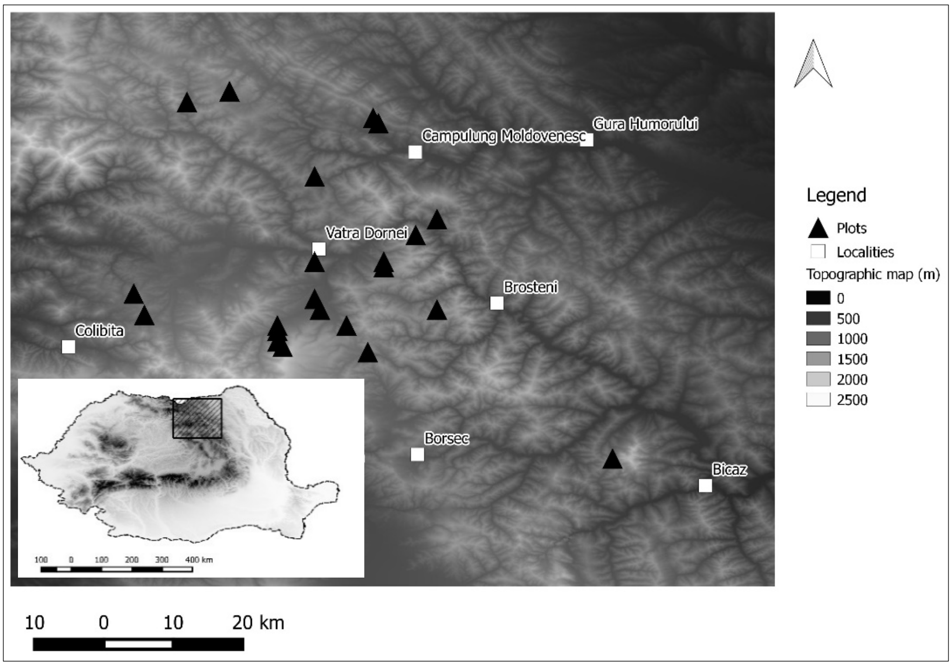

Fig. 1. Maps of the study area and its location in Romania (bottom left) and of the locations of studied *Arnica* populations. The basis of the maps was represented by the rasters downloaded from United States Geological Survey's EarthExplorer (www.earthexplorer.usgs.gov).

Abb. 1. Lage des Untersuchungsgebiets in den rumänischen Karpaten (links unten) und Lage der Untersuchungsflächen mit den untersuchten *Arnica*-Populationen.

belongs to the Carpathian Province within the Central European flora region (CIOCÂRLAN 2000). According to the Habitats Directive of the European Union, the study sites are considered part of the Alpine biogeographic region (COUNCIL OF EUROPEAN COMMUNITIES 1992).

3. Material and methods

3.1 Studied species

Arnica montana L. (*Asteraceae*) is a rosette-forming perennial mainly growing in nutrient-poor grasslands of the order *Nardetalia* within the class *Calluno-Ulicetea* (MUCINA 1997, COLDEA 2012). The species reproduces vegetatively by means of short underground rhizomes as well as sexually. Ramification of the rhizomes leads to rosette groups, which may consist of several genets if different rosette groups grow into each other (LUIJTEN et al. 1996, MAURICE et al. 2016). Flowering rosettes have one or few flower stems with up to seven yellow, nectariferous flower heads (capitula) (LUIJTEN et al. 2002); however, most rosettes do not flower. *Arnica montana* is highly self-incompatible (LUIJTEN et al. 1996) and is visited pre-dominantly by hoverflies and various bees (LUIJTEN 2002). There is no persistent seed bank (THOMPSON et al. 1997). Germination occurs either directly after seed shedding in autumn or in the following spring.

3.2 Record of population structure and vegetation

In 25 populations of *A. montana*, three 1 m × 1 m-plots each (i.e. a total of 75 plots) were selected in areas of typical and visually homogeneous vegetation with typical plant density and flower activity of *A. montana* (Fig. 2–3). Within these plots we measured the population structure of *A. montana* as the number of rosettes (rosette density), number of flower heads (flower head density), number of flowering/non-flowering rosettes and number of flower stems per flowering rosette. From these variables we calculated the proportion of flowering and vegetative rosettes per plot. The vegetation record included vascular plants and vegetation structure (cover and height of vascular plants and moss cover) according to the standard protocol by BORZA & BOȘCAIU (1965). Habitat types were defined according to the European Union (COUNCIL OF EUROPEAN COMMUNITIES 1992), and land use type was classified as “mown”, “grazed” or “unused” in the field. Nomenclature of plant species follows SÂRBU et al. (2013).

3.3 Measuring environmental variables

Altitude, slope degree and geographic coordinates were registered in the field. Soil samples were collected from the A horizon, and the Ca, Mg, Na, K, P and organic matter content as well as the soil pH were measured in the lab. As a proxy for the nitrogen content of the soil, we used unweighted mean Ellenberg indicator values for nutrients (EIV-N) (ELLENBERG et al. 1992). Climatic variables (mean annual temperature and precipitation) were extracted from the WorldClim database (HIJMANS et al. 2005). Numeric variables were checked for collinearity using Pearson correlation (Supplement E1).

3.4 Data analysis

The vegetation was classified using hierarchical agglomerative clustering (flexible ß algorithm with ß = −0.25 and Bray-Curtis distance) on square root-transformed data represented by the mid-percentage values corresponding to the Braun-Blanquet cover-abundance scale, adapted for Romanian vegetation (BORZA & BOȘCAIU 1965). The output dendrogram was cut in nine partitions with 2–10 clusters, and the optimum number of clusters was identified using the corrected Rand index and the mean Silhouette index. Diagnostic species for each cluster were identified based on their indicator value index (DUFRÊNE & LEGENDRE 1997), which is independent of the relative size of the vegetation unit.

A permutation test (DE CÁCERES & LEGENDRE 2009) allowed to observe which species were significantly associated to the clusters. The identified diagnostic species were used to relate the clusters to plant communities presented in phytosociological literature (COLDEA 2012, CHIFU 2014). Vegetation classification was carried out using the Gingko module of the VEGANA package (BOUXIN 2005).

Relationships between the floristic composition of plots and environmental variables were investigated with DCA (detrended correspondence analysis) on basis of square root-transformed data, detrending by segments and down-weighting rare species. The effect of each variable on the floristic composition was assessed via CCA (canonical correspondence analysis) with forward selection and 999 Monte Carlo test iterations (because the length of the first floristic gradient was 4.2 and thus unimodal methods were appropriate in this situation). Ordination analyses were carried out with CANOCO 5 (TER BRAAK & ŠMILAUER 2012).

Relationships between rosette density, proportion of vegetative rosettes, flower head density, number of flower heads per flowering rosette and environmental variables were modelled using generalised linear models (GLMs) with negative binomial distribution of errors (instead of Poisson distribution, usually used for count data, because of over-dispersion). Only for the analysis of the relationship between the proportion of vegetative rosettes and environmental variables, a Gaussian distribution (for arcsin-transformed data) was assumed. For each population average values (of the three plots) were used for the response variables. In order to identify the most influential environmental variables, full models including all variable combinations were constructed, but only those with ΔAICc < 2 (difference in AICc – Akaike Information Criterion corrected for small sample size – compared to the best model) were selected (BURNHAM & ANDERSON 2002). Only variables included in at least half of the selected models were subjected to single parameter GLM. Quadratic terms were inserted in single parameter GLMs in order to test if the relationship is linear, U-shaped or hump-shaped. Effects of land use and habitat type (coded as dummy variables) were also tested in GLMs. All these relationships were assessed using the MASS (RIPLEY et al. 2016) and MuMIn packages (BARTON et al. 2016) of the R software environment (version 3.2.3., R CORE TEAM 2015). Because altitude was strongly correlated with climate and soil conditions, we excluded annual temperature and precipitation as well as K and P content of the soil (which strongly depend on organic matter content and pH) from the GLMs.

Differences in total rosette number, proportion of vegetative rosettes, number of inflorescences per rosette, number of inflorescences per plot as well as environmental data depending on habitat type were analysed using non-parametric Kruskal-Wallis and Mann-Whitney post-hoc tests.

4. Results

4.1 Population and habitat characteristics

Rosette density of *Arnica montana* strongly varied both between and within populations with a minimum of 7 rosettes and a maximum of 165 rosettes per m². On average, 53 rosettes were counted per m² (Table 1). The proportion of vegetative rosettes of *A. montana* ranged from 68 to 100% (average 83%). Flower head density per m² ranged from 0 to 55 with an average of 19.5 flower heads per m². On average, a flowering rosette had 2.15 flower heads.

In the study region *A. montana* was found in an altitudinal range from 868 to 1994 m a.s.l., from almost flat terrains up to steep slopes (2–48° inclination) with different aspects on acidic and nutrient-poor soils. The mean annual temperature of the sites was 4.7 °C (ranging from 2.3 to 6.0 °C) and the mean annual precipitations 794 mm (from 701 mm in lower areas to 990 mm at higher altitudes). The pH of the A horizon of the soil ranged from 3.9 to 5.0 (with a mean pH of 4.5), the organic matter content from 5.0 to 28.5% (with a mean content of 12.8%) and the Ellenberg indicator values for nutrients from 2.2 to 3.9 (with a mean EIV-N of 3.1) (Table 1).

Table 1. Descriptive statistics of population structure and habitat characteristics of *Arnica montana* in the NE Carpathians (*n* = 75 plots).

Tabelle 1. Deskriptive Statistik der Populationsstruktur und Umweltbedingungen von *Arnica montana* in den Nordost-Karpaten (*n* = 75 Probeflächen).

Variable	Abbrev.	Mean	SD	Min	Max
Population structure of A. montana					
Rosette density per m²	–	53.1	24.2	7.0	165.0
Proportion of vegetative rosettes (%)	–	82.7	8.6	68.3	100.0
Flower head density per m²	–	19.5	14.9	0.0	55.0
No. of flower heads per flowering rosette	–	2.1	0.8	0.0	3.3
Habitat characteristics					
Altitude (m a.s.l.)	Alt	1145	288	868	1994
Slope (°)	Slop	15.1	10.0	2.0	48.0
Maximum vegetation height (cm)	Maxheight	60	15	35	105
Plant species richness per m²	Srichness	21.8	5.9	9.0	37.0
Vegetation cover (%)	Vegcov	94	6	75	100
Bryophyte cover (%)	Bryocov	14	10	3	50
Ca (meq/100 g soil)	Ca	2.6	1.7	0.4	7.0
Mg (meq/100 g soil)	Mg	0.55	0.35	0.10	1.57
Na (meq/100 g soil)	Na	0.40	0.09	0.28	0.58
K (meq/100 g soil)	K	0.65	0.32	0.31	1.41
P (meq/100 g soil)	P	0.79	0.56	0.25	2.35
Organic matter content of soil (%)	Orgmat	12.8	7.0	5.0	28.5
pH of the soil	pH	4.47	0.27	3.88	4.96
Ellenberg indicator values for nutrients	EIV-N	3.1	0.4	2.2	3.9
Mean annual temperature (°C)	Tmean	4.8	1.0	2.3	6.0
Mean annual precipitation (mm)	Precmean	794	74	701	990

4.2 Habitat types and plant communities

Arnica montana was found in the habitat types Mountain hay meadows, Species-rich *Nardus* grasslands and Alpine and subalpine heathlands. The mean herb layer cover was 94% and the mean bryophyte cover 14% (Table 1). Vascular plant species richness per m² ranged from 9 to 37 and was higher in grasslands as compared to heathlands. The vegetation classification revealed five groups, which were assigned to five associations within four alliances and three orders/classes:

Class: *Molinio-Arrhenatheretea* R. Tx. 1937
  Order: *Arrhenatheretalia* R. Tx. 1931
    All.: *Cynosurion* R. Tx. 1947
      Ass.: *Festuco rubrae-Agrostietum capillaris* Horv. 1951
        Subass.: *Festuco rubrae-Agrostietum capillaris nardetosum strictae* Oroian 1998
Class: *Calluno-Ulicetea* Br.-Bl. et R. Tx. ex Klika et Hadač 1944
  Order: *Nardetalia* Oberd. 1949
    All.: *Potentillo-Nardion* Simon 1958
      Ass.: *Scorzonero roseae-Festucetum nigrescentis* (Pușcaru et al. 1956)
      Ass.: *Violo declinatae-Nardetum strictae* Simon1966

Class: *Loiseleurio-Vaccinietea* Eggler ex Schubert 1960
Order: *Rhododendro-Vaccinietalia* Br.-Bl. in Br.-Bl. et Jenny 1926
All.: *Loiseleurio-Vaccinion* Br.-Bl. in Br.-Bl. et Jenny 1926
Ass.: *Cetrario-Vaccinietum gaultherioidis* Hadač 1956
All.: *Rhododendro-Vaccinion* J. Br.-Bl. ex G. Br.-Bl. et J. Br.-Bl. 1931
Ass.: *Campanulo abietinae-Vaccinietum myrtilli* (Buia et al. 1962) Boşcaiu 1971

60% of the vegetation plots belonged to the class *Molinio-Arrhenatheretea* (mesic grasslands), 12% to the *Calluno-Ulicetea* (grasslands and heathlands on nutrient-poor acidic soil) and 24% to the *Loiseleurio-Vaccinietea* (subalpine dwarf shrub heathlands) (Fig. 2–3, Supplement E1). *Arnica montana* had its highest density in the association *Festuco rubrae-Agrostietum capillaris* (with a mean of 61.3 rosettes per m²). The lowest density was found in the *Cetrario-Vaccinietum gaultherioidis* (18.2 rosettes per m²); in this association the proportion of non-flowering rosettes (98.2 %) was highest. Over all associations the mean number of flower heads per m² was 19.5 and the mean number of flower heads per flower stem 2.2. With 28.3 flower heads per m², the average flower head density was highest in the *Scorzonero roseae-Festucetum nigrescentis*, while it was lowest in the *Cetrario-Vaccinietum gaultherioidis* (10.2 flower heads per m²) (Supplement E1).

The plant communities were assigned to three habitat types according to the Habitats Directive of the European Union (Council of European Communities 1992): The *Festuco rubrae-Agrostietum capillaris* corresponded to the habitat type Mountain hay meadows (Fig. 2). These grasslands were secondary, mesophilic and species-rich and occurred on more nutrient-rich, less acidic soils with the lowest organic matter content within our study. Due to their higher productivity, most of these sites were mown. The sites were located in the lower mountain belt, with higher mean annual temperatures, but lower mean annual precipitations compared to subalpine areas (Table 2). The vegetation included diagnostic species of the *Arrhenatheretalia* (e.g. *Achillea millefolium*, *Campanula patula*, *Leucanthemum vulgare*, *Lotus corniculatus* and *Tragopogon orientalis*), the *Brometalia erecti* (e.g. *Anthyllis vulneraria*, *Campanula glomerata* and *Carlina acaulis*) and the *Origanetalia vulgaris* (e.g. *Origanum vulgaris*, *Stachys officinalis* and *Trifolium ochroleucon*) (Supplement E1).

The *Scorzonero-Festucetum nigricantis* and the *Violo-Nardetum* correspond to the habitat type Species-rich *Nardus* grasslands. They included secondary communities with high covers of *Festuca nigrescens* and *Nardus stricta*. In the study area *Nardus* grasslands were scattered and occurred at intermediate elevation in the Călimani, Bistriței and Rarău Mountains (Fig. 3). They were developed on nutrient-poor acidic soil with a significant content of organic matter. In the stands diagnostic species for *Nardetalia* were e.g. *Antennaria dioica*, *Hypericum maculatum* and *Thymus pulegioides* and for *Arrhenatheretalia* e.g. *Briza media*, *Prunella vulgaris* and *Trisetum flavescens* (Supplement E1).

The third habitat type was Alpine and subalpine heathlands, which ocurred in the subalpine belt of the Ceahlău, Călimani and Bistriței Mountains. These sites were characterised by low temperature and high precipitation. Soil conditions were acidic and very nutrient-poor, with high contents of organic matter. The dwarf shrub communities were dominated by *Vaccinium gaultherioides* and *V. myrtillus*. The mean shrub cover was 83% and included *Juniperus sibirica*, *Vaccinium vitis-idaea* and *Pinus mugo*. The cover of the herb layer was 15%, and the herb layer consisted of *Caricetalia curvulae* species (*Festuca supina*, *Hieracum alpinum*, *Juncus trifidus* and *Ligusticum mutellina*) or *Junipero-Pinetalia mugi* species (e.g. *Calamagrostis villosa* and *Deschampsia flexuosa*) (Supplement E1). Species-richness was low overall (Table 1–2).

Fig. 2. Plot of a Mountain hay meadow with *Arnica montana* (Photo: C. Bîrsan, 18.06.2016).

Abb. 2. Probefläche einer Berg-Heuwiese mit *Arnica montana* (Foto: C. Bîrsan, 18.06.2016).

Fig. 3. Plot of a species-rich *Nardus* grassland with *Arnica montana* (Photo: C. Bîrsan, 18.06.2016).

Abb. 3. Probefläche eines artenreichen Borstgrasrasens mit *Arnica montana* (Foto: C. Bîrsan, 18.06.2016).

Table 2. Habitat characteristics of *Arnica montana* in the Romanian NE Carpathians according to Natura 2000 habitat types (means and standard deviations). Different letters indicate significant differences (α = 0.05) according to the Mann-Whitney post-hoc test. *p*-values were derived from a non-parametric Kruskal-Wallis test. *n.s.* = not significant.

Tabelle 2. Umweltbedingungen von *Arnica montana* nach Natura 2000-Habitattypen in den rumänischen Nordost-Karpaten (Mittelwerte und Standardabweichungen). Werte mit unterschiedlichen Buchstaben unterscheiden sich signifikant (α = 0,05) nach einem Mann-Whitney Post-hoc-Test. Die *p*-Werte stammen aus Kruskal-Wallis-Tests. *n.s.* = nicht signifikant.

	Mountain hay meadows	Species-rich *Nardus* grasslands	Alpine and subalpine heaths	*p*
Population structure of A. montana				
Rosette density per m²	61.3 ± 20.7^{a}	46.7 ± 25.3^{a}	23.7 ± 11.6^{b}	0.006
Proportion of vegetative rosettes (%)	80.7 ± 6.8^{a}	81.8 ± 11.3^{a}	92.2 ± 8.1^{b}	0.001
Flower head density per m²	19.0 ± 15.0^{a}	22.8 ± 14.8^{a}	10.7 ± 10.2^{a}	*n.s.*
No. of flower heads per flowering rosette	2.4 ± 0.5^{a}	1.9 ± 0.8^{a}	1.4 ± 1.1^{b}	0.034
Habitat characteristics				
Altitude (m a.s.l.)	1023 ± 98^{a}	1202 ± 284^{a}	1607 ± 373^{b}	< 0.001
Slope (°)	14.7 ± 9.7^{a}	17.1 ± 6.9^{b}	13.8 ± 7.9^{a}	0.030
Maximum vegetation height (cm)	62.6 ± 14.3^{a}	66.3 ± 12.0^{a}	46.2 ± 8.8^{b}	< 0.001
Plant species richness per m²	23.5 ± 5.2^{a}	22.7 ± 4.7^{a}	12.6 ± 4.5^{b}	< 0.001
Vegetation cover (%)	95.2 ± 6.1^{a}	95.4 ± 4.5^{a}	85.0 ± 8.7^{b}	< 0.001
Bryophyte cover (%)	14.1 ± 10.9^{a}	14.2 ± 7.6^{a}	13.2 ± 10.2^{a}	*n.s.*
Ca (meq/100 g soil)	3.13 ± 1.45^{a}	2.06 ± 1.54^{ab}	0.62 ± 0.50^{b}	< 0.001
Mg (meq/100 g soil)	0.60 ± 0.28^{a}	0.47 ± 0.16^{ab}	0.27 ± 0.35^{c}	< 0.001
Na (meq/100 g soil)	0.40 ± 0.09^{a}	0.39 ± 0.07^{a}	0.44 ± 0.10^{a}	*n.s.*
K (meq/100 g soil)	0.56 ± 0.18^{a}	0.74 ± 0.41^{a}	0.90 ± 0.45^{a}	*n.s.*
P (meq/100 g soil)	0.63 ± 0.32^{a}	0.67 ± 0.43^{ab}	1.48 ± 0.84^{b}	0.009
Organic matter content of the soil (%)	11.0 ± 4.7^{a}	14.9 ± 7.8^{ab}	18.7 ± 9.3^{b}	0.001
pH of the soil	4.54 ± 0.19^{a}	4.51 ± 0.33^{ab}	4.16 ± 0.27^{c}	0.001
Mean annual temperature (°C)	5.2 ± 0.45^{a}	4.7 ± 0.88^{ab}	3.2 ± 1.19^{bc}	< 0.001
Mean annual precipitations (mm)	773 ± 46^{a}	771 ± 57^{ab}	897 ± 89^{c}	0.001
Ellenberg indicator values for nutrients	3.26 ± 0.35^{a}	3.10 ± 0.40^{b}	2.66 ± 0.31^{c}	< 0.001

In the DCA Mountain hay meadows and Alpine and subalpine heathlands were maximally separated, with Species-rich *Nardus* grasslands in between (Fig. 4). Alpine and subalpine heathlands were positively correlated with altitude, precipitation, organic matter content and P content of the soil. In contrast, Mountain hay meadows were mainly positively correlated with pH of the soil, nutrient indicator values, Ca and Mg content of the soil and species richness. In the CCA altitude explained most of the variation in the vegetation, followed by P content and abandonment (Table 3).

4.3 Relationships between population structure and habitat characteristics

Generalised linear models (GLMs) showed differences in the relative importance of environmental variables for rosette and flower head density and proportion of vegetative rosettes (Table 3–4, Supplement E2). In the GLM altitude had a strong linear negative effect on rosette density, a linear positive effect on the proportion of vegetative rosettes and no

Table 3. Results of the CCA ordination (forward selection) of the effects of environmental variables on the composition of vegetation with *Arnica montana*.

Tabelle 3. Ergebnisse einer CCA-Ordination (forward selection) mit den Effektstärken der Umweltvariablen auf die Artenzusammensetzung der Vegetation mit *Arnica montana*.

Variable	Explained variance (%)	Contribution (%)	Pseudo-F	*P* adj.
Altitude	9.2	24.0	7.4	0.019
Plant species richness	3.1	8.0	2.5	0.019
P content of the soil	2.5	6.6	2.1	0.012
Land use type “unused”	2.2	5.8	1.9	0.019
K content of the soil	2.0	5.3	1.7	0.019
Mean annual precipitations	1.9	5.0	1.7	0.019
Slope	1.8	4.8	1.6	0.038
Na content of the soil	1.9	4.8	1.6	0.038
Mean annual temperature	1.8	4.6	1.6	0.076
Ellenberg indicator values for nutrients	1.7	4.4	1.5	0.076
Ca content of the soil	1.6	4.2	1.4	0.247
Mg content of the soil	1.5	3.8	1.3	1.000
Organic matter content of the soil	1.5	4.0	1.4	0.342
Land use: mowing	1.5	3.8	1.3	0.950
Land use: grazing	1.5	3.8	1.3	0.836
pH of the soil	1.2	3.2	1.1	1.000
Bryophyte cover	1.1	2.8	1.0	1.000
Vegetation height	1.1	2.8	0.0	1.000
Vegetation cover	0.7	1.9	0.7	1.000

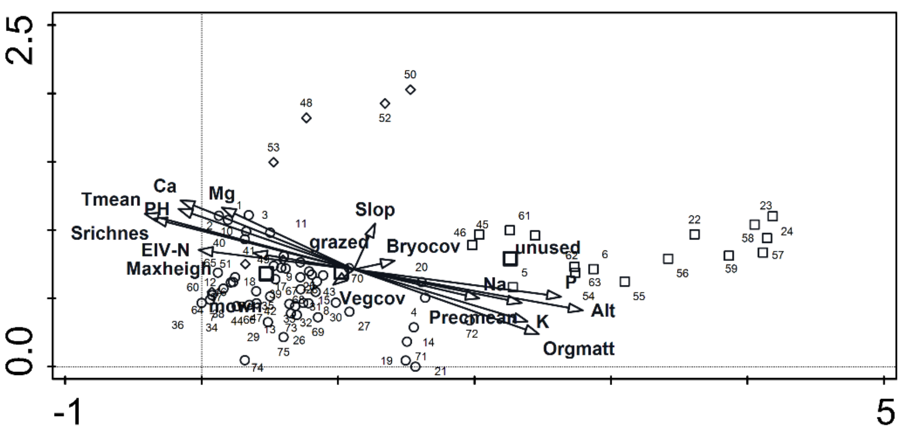

Fig. 4. DCA of the vegetation with *Arnica montana*. Eigenvalue axis 1: 0.713, axis 2: 0.234; gradient length axis 1: 4.19, axis 2: 2.03. Symbols indicate Natura 2000 habitat types: Mountain hay meadows (circles), Species-rich *Nardus* grasslands (rhombuses) and Alpine and subalpine heath lands (squares). For abbreviations see Table 1.

Abb. 4. DCA der Vegetation mit *Arnica montana*. Eigenwert Achse 1: 0,713, Achse 2: 0,234. Gradientenlänge Achse 1: 4,19, Achse 2: 2,03. Die Symbole kennzeichnen folgende Natura 2000-Lebensraumtypen: Berg-Heuwiesen (Kreise), Artenreiche Borstgrasrasen (Rauten) und Alpine und subalpine Zwergstrauchheiden (Quadrate). Für die Abkürzungen s. Tabelle 1.

Table 4. Relative importance of predictors used in modelling density and structure of *Arnica montana* populations (significant values with α ≤ 0.05 are highlighted in bold).

Tabelle 4. Relative Bedeutung der einzelnen Umweltfaktoren auf die Populationsstruktur von *Arnica montana* (signifikante Werte mit α ≤ 0,05 sind durch Fettdruck hervorgehoben).

	Rosette density per m²	Proportion of vegetative rosettes (%)	Flower head density per m²	# flower heads per flowering rosette
Altitude	**0.99**	**1.00**	0.18	0.27
Slope	0.26	**0.80**	0.14	0.16
Maximum vegetation height	**0.94**	0.10	0.26	0.17
Plant species richness	0.11	0.11	**0.71**	0.16
Vegetation cover	**0.95**	**0.53**	0.42	0.18
Bryophyte cover	0.11	0.22	0.22	0.15
Ca content of the soil	0.10	0.09	0.13	0.16
Mg content of the soil	0.26	0.10	0.45	0.16
Na content of the soil	0.45	0.21	0.17	0.18
Soil organic matter content	0.13	0.33	0.24	**0.54**
pH of the soil	0.11	0.41	**0.50**	0.25
Ellenberg indicator values for nutrients	0.20	0.13	0.14	0.16
Grazing vs. mowing	**0.59**	0.43	0.15	0.15
Abandonment vs. mowing	0.11	**0.55**	0.15	0.19
Nardus grassland vs. hay meadow	0.27	**0.55**	0.33	0.16
Alpine heathland vs. hay meadow	0.09	0.12	0.18	0.16

effect on flower head density (Table 5, Fig. 5). Maximum vegetation height and vegetation cover predicted rosette density in a humped-shape relationship. Soil organic matter content was the only significant predictor with a negative effect on the number of flower heads per flowering rosette. The number of flower heads per m² was influenced by soil pH. Overall, depending on soil pH, the number of inflorescences showed an increase up to 4.5 (optimum value), followed by a decrease at higher values of soil pH. Land use only affected rosette density with less rosettes in grazed vs. mown plots, while the proportion of vegetative rosettes was higher at abandoned sites (Table 5).

5. Discussion

5.1 Habitat types and habitat characteristics of *Arnica montana*

The habitat types identified in the study area were similar to those described in the literature for *A. montana* (DONIŢĂ et al. 2005, GAFTA & MOUNTFORD 2008, FALNIOWSKI et al. 2011). However, most of these studies did not focus on the species itself and provided no information about its population structure (DONIŢĂ et al. 2005, GAFTA & MOUNTFORD 2008). In the only study about *A. montana* in Romania (carried out in the Apuseni Mountains) focussing on the species itself (MICHLER 2007), the species was identified in two habitat types in mountain areas on siliceous soil: 6520 Mountain hay meadows and 6230*

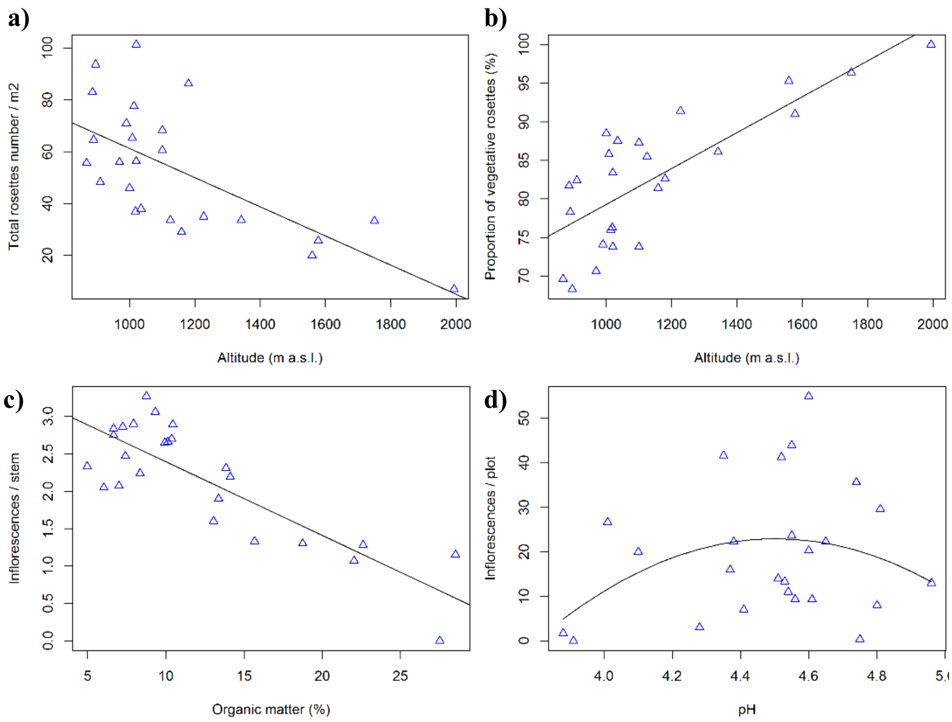

Fig. 5. Relationships between population structure (rosette density, proportion of vegetative rosettes, number of flower heads per flower stem and flower head density) and habitat characteristics (altitude, organic matter content of the soil, pH of the soil) in *Arnica montana*.

Abb. 5. Zusammenhänge zwischen Populationsstruktur (Rosettendichte, Anteil vegetativer Rosetten, Anzahl der Blütenköpfchen pro Blütentrieb und Blütenköpfchendichte) und Lebensraumeigenschaften (Meereshöhe, Gehalt an organischer Substanz sowie pH-Wert des Bodens) bei *Arnica montana*.

Species-rich *Nardus* grasslands. Both habitat types had a floristic composition similar to our stands. Only our study showed the species to grow in Alpine and subalpine heathlands as well.

In our study area *Nardus*-dominated grasslands were not rare and should thus have been accessible for *A. montana*. However, *A. montana* was not frequently found in these grasslands. This can be explained by the fact that, at lower altitudes, these grasslands often represent former *Festuca rubra-Agrostis capillaris* or *Festuca nigrescens* communities subjected to excessive grazing, which negatively affects *A. montana*. This explanation is in accordance with the observation that both communities often colonised eroded terrains and were dominated by *Nardus*. In high altitudes (2000 m a.s.l.) there were also primary *Nardus* grasslands without *A. montana*. In this study the species-rich *Nardus* grasslands (*Violo declinatae-Nardetum* and *Scorzonero-Festucetum nigricantis*) were subordinated to this habitat type as well, despite the recommendation that Species-rich *Nardus* grasslands should not include communities whose species numbers are low due to overgrazing (GALVÁNEK & JANÁK 2008, GAFTA & MOUNTFORD 2008, EUROPEAN COMMISSION 2013). The reason was to include all phytocoenoses with *Nardus* (and *A. montana*) in the studied area, not only those delineated for conservation purposes.

Table 5. Effect of predictors in generalised linear models (GLMs) (predictors selected according to their relative importance). Abbreviations: Std. coef. – standardised coefficient, SE – standard error, *n.s.* – not significant.

Tabelle 5. Bedeutung der Umweltvariablen in den generalisierten linearen Modellen (GLMs) (Auswahl der Prädiktoren nach ihrer relativen Bedeutung). Std. coef. – Standardkoeffizient, SE – Standardfehler, *n.s.* – nicht signifikant.

Parameter	Mean ± SD	Predictor	Std. coef.	SE	*p*
Rosette density per m²	53.1 ± 24.2	Altitude	-0.00015 ↓	0.0002	< 0.001
		Max vegetation height	-0.00079 ∩	0.0002	0.003
		Vegetation cover	-0.00488 ∩	0.0016	0.004
		Grazing vs. mowing	-0.38920	0.1502	0.009
Proportion of vegetative rosettes (%)	82.7 ± 8.6	Altitude	0.00041 ↑	0.0001	< 0.001
		Slope	-0.00004 ↓	0.0028	*n.s.*
		Abandonment vs. mowing	0.20940	0.0632	0.003
		Nardus grassland vs. hay meadow	-0.04505 ↓	0.0620	*n.s.*
Flower head density per m²	19.5 ± 14.9	Soil pH	-3.84700 ∩	1.8890	0.041
		Species richness	-0.00038 ↓	0.0306	*n.s.*
Number of flower heads per flowering rosette	2.15 ± 0.78	Organic matter content of the soil	-0.05097 ↓	0.0243	0.036

The CCA highlighted altitude as the most important factor for the floristic composition of vegetation with *A. montana*. The altitudinal gradient differentiated heathlands dominated by *Vaccinium gaultherioides* and *V. myrtillus* at high elevations and on soils with high organic matter, but low nutrient content from grasslands dominated by *Festuca rubra* or *F. nigrescens*, which were developed on soils with a moderate content in organic matter and a higher nutrient content. Altitude, climate and soil characteristics strongly depend on each other (GANUZA & ALMENDROS 2003, DAI & HUANGA 2006) and were pointed out to be the main factors for the floristic composition in other Carpathian grasslands as well (ŠKODOVÁ et al. 2015).

5.2 Relationships between density and performance of *Arnica montana* and environmental factors

Altitude was an important factor influencing plant density and flower performance of *A. montana*. The decrease in plant density in high altitudes is probably due to abiotic stress. Taking into account an upper altitudinal limit, which is reported to be 2750 m a.s.l. (FALNIOWSKI et al. 2011), *A. montana* cannot be described as an alpine species adapted to very harsh climate conditions. However, because significant genetic differences were highlighted between colline and montane populations of *A. montana* in Western-Central Europe (MAURICE et al. 2016), different ecotypes adapted to different climatic conditions in low and high altitudes seem to be possible in the species. Moreover, the increase of vegetative rosettes in high altitudes may indicate a response to abiotic stress by allocation in *A. montana* (HAUTIER et al. 2009, MAURICE et al. 2012). This shift from sexual reproduction to clonal growth can be interpreted as plastic behaviour, which has also been reported for other plant species along altitudinal gradients, e.g. *Ligularia virgaurea* (XIE et al. 2014), *Sagittaria pygmaea*

(LIU et al. 2009), *Geum reptans* (WEPPLER & STÖCKLIN 2005) and *Poa alpina* (HAUTIER et al. 2009). This strategy is not cost intensive, but reduces colonisation of new habitats due to less seed production (BILLS et al. 2015).

The negative relationship between soil organic matter and proportion of flowering rosettes can also be interpreted as an indirect effect of altitude since soil organic matter increases with elevation. This increase is probably a result of a slowed down decomposition due to low temperatures in high elevations (KIRSCHBAUM 1995, DREWNIK 2006). However, for the lower part of the altitudinal gradient until 1250 m, a positive relationship between altitude and flower ability has been reported from Belgium, Luxembourg, Germany and France (MAURICE et al. 2012).

In our study vegetation cover and vegetation height were unimodally related to rosette density in *A. montana*. Low vegetation cover and low vegetation height are related to high altitude, whereas high and dense vegetation is mainly developed in abandoned grasslands with a high competition for light due to taller plants or litter accumulation (KLIMEŠOVÁ et al. 2008). Especially rosette plants like *A. montana* can hardly react by growth to such shading effects (LETTS et al. 2015). In addition, litter accumulation can prevent seed germination (by forming a mechanical barrier between seedling root and mineral soil) or seedling establishment (by shading) (RUPRECHT & SZABO 2012, LOYDI et al. 2013).

Flower head density followed a hump-shaped response to soil pH with an optimum at pH 4.5. This could reflect underlying effects of other factors such as organic matter accumulation, nutrient availability for plants and Al toxicity, which are significantly influenced by soil pH (PIETRI & BROOKES 2008, LEIFELD et al. 2013). Low soil pH in high altitudes increases organic matter content, but decreases nutrient concentration. In very poor habitats such as heathlands, low P and N concentrations often limit plant growth, even in plants that are adapted to nutrient-poor soils (DE GRAAF et al. 1997). Because *A. montana* needs a certain amount of vegetative biomass for flowering (DUECK & ELDERSON 1992), nutrient shortage in high altitudes could explain less inflorescences on very acidic soils in high altitudes. Available Al in acidic soils (ROUT et al. 2001) may also negatively affect *A. montana* (DE GRAAF et al. 1997) and explain low flower rates. Higher values of soil pH enhance the decomposition rate and can increase the nutrient content of the soil by a factor of four in the pH range of 4.0 to 6.0 (LEIFELD et al. 2008, 2013). In addition, fertilisation of some of the lower altitude grasslands with animal manure may be a significant nutrient input, which can promote grasses at the expense of *A. montana* (DUECK & ELDERSON 1992, PEGTEL 1994). Under these conditions it is difficult for the plant to develop a minimal leaf area necessary for reproduction. A positive relationship between rosette diameter and flowering probability in *A. montana* has been highlighted in several studies (DUECK & ELDERSON 1992, FENNEMA 1992).

Although not among the most important factors in the GLM model, management type can also be regarded an important factor for density in *A. montana* since rosette density is decreased by grazing in contrast to mowing. The influence of management on both species composition of the vegetation and *A. montana* density has been reported by other studies from Romania (PĂCURAR et al. 2007, ROTAR 2010). Management measures (mowing, moderate grazing) were of crucial importance for key species like *A. montana* as they shaped and maintained these mountain grasslands over centuries. By periodic removal of dominant and competitive species like *Dactylis glomerata* (JURKIEWICZ et al. 2010), mowing decreases competition and maintains plant diversity by promoting rosette species such as *A. montana*.

Mowing improves light availability at ground level for a short time and prevents litter accumulation, both of which may facilitate seedling establishment in *A. montana*. Higher rosette density of the species at moderately grazed sites compared to unmanaged sites can reduce dominant grasses and affect the community's vertical structure in favour of rosette plants (KLIMEK et al. 2007). In addition, grazing can improve diaspore dispersal, assuring the connectivity between populations and re-colonisation of former habitats (ROSENTHAL et al. 2012). The lower plant density in unmanaged grasslands can be interpreted as effect of competition by woody plants (e.g. *Betula pendula*, *Picea abies*, *Rosa pendulina*, *Vaccinium vitis-idaea* and *V. myrtillus*). In addition, increased litter accumulation in unmanaged grasslands inhibits seedling establishment by physical obstruction and modifications in light regime (RUPRECHT & SZABO 2012, BONANOMI et al. 2013). Abandonment also promotes dominant native species such as *Pteridium aquilinum* (at low altitudes) or *Veratrum album* (at high altitudes) resulting in high competition.

6. Conservation implications

First of all, successful conservation of *Arnica montana* requires detection of optimal habitats. Our study indicates that Mountain hay meadows and Species-rich *Nardus* grasslands are the species' optimal habitats in Romania, as opposed to Alpine and subalpine heathlands where the species grows in low density and plants flower less. Moreover, the findings of our study emphasise the demand for a proper management of the species' habitats (KATHE 2006, SCHWABE et al. 2019), i.e. extensive grazing or mowing after achene maturation. Fertilisation should only be done with low amounts of cattle manure. Chemical fertilisation, which promotes competitive plants, should be avoided.

Erweiterte deutsche Zusammenfassung

Einleitung – *Arnica montana* ist vielerorts durch Lebensraumzerstörung infolge Intensivierung oder Aufgabe der traditionellen extensiven Landnutzung zurückgegangen und aktuell in vielen Ländern gefährdet. In Rumänien stellt übermäßiges Sammeln für pharmazeutische und kosmetische Zwecke eine weitere Gefährdungsursache dar. Insgesamt ist *A. montana* in Rumänien aber noch relativ häufig; sie wächst hier v. a. in mageren Bergwiesen, Borstgrasrasen oder auch frühen Sukzessionsstadien von Kahlschlägen. Wir untersuchten die Populationsstruktur und Umweltbedingungen von 25 *A. montana*-Populationen in verschiedenen Habitaten der Nord-Ost-Karpaten. Unser Ziel war das Erkennen von Habitatpräferenzen von *A. montana* um daraus Gefährdungsursachen abzuleiten und Schutzstrategien zu entwickeln.

Untersuchungsgebiet – Das Untersuchungsgebiet mit temperat-kontinentalem Klima liegt in Nordost-Rumänien (46°23'-47°65' N und 25°01'-25°91' E) in 700–2100 m Meereshöhe (Abb. 1); die Untersuchungsflächen befinden sich 868–1994 m über dem Meer an Hängen mit unterschiedlicher Neigung und Exposition (Tab. 1–2). Der Jahresniederschlag schwankt zwischen 800 und 1200 mm. Der geologische Untergrund ist vielfältig und umfasst kristallinen Schiefer, Kalk, Vulkangestein und Sandstein aus dem Pliozän sowie Sande und Lehme. Die Bodentypen der meisten Habitate waren Spodosol und Cambisol und etwas seltener Andosol. Die potenzielle natürliche Vegetation der Flächen sind Nadelwälder und Mischwälder (BOHN et al. 2004).

Methoden – Im Jahr 2016 wurde die Populationsstruktur von *A. montana* in 25 Populationen aufgenommen. Jeweils drei 1-m²-Flächen (insgesamt 75 Flächen) mit augenscheinlich für die jeweilige Population typischer Dichte von *A. montana* sowie typischer Vegetation wurden ausgewählt und darauf die Anzahl der Rosetten (Rosettendichte), Anzahl der Blütenköpfchen (Blütenköpfchendichte), Anzahl der blühenden Rosetten und Anzahl der Blütenstände pro blühender Rosette von *A. montana* gezählt. Aus diesen Variablen errechneten wir den Anteil der blühenden und vegetativen Rosetten. Auf denselben Flächen wurden Vegetationsaufnahmen der Gefäßpflanzen durchgeführt sowie Umweltmerkmale wie Hangneigung und Meereshöhe gemessen. Die Landnutzung der Flächen wurde kategorial als Mahd, Weide oder Brache notiert. In jeder Probefläche wurde aus dem A-Horizont eine Bodenprobe entnommen und deren Gehalte an Ca, K, Mg, Na und P sowie der Anteil der organischen Substanz und der pH-Wert gemessen. Zur Einschätzung der Nährstoffversorgung wurden ungewichtete mittlere Ellenberg-N-Zeigerwerte (ELLENBERG et al. 1992) der in den Vegetationsaufnahmen enthaltenen Arten herangezogen. Zur Analyse des Einflusses des Klimas auf die Populationen wurden aus der Datenbank WorldClim (HIJMANS et al. 2005) die Jahresmittel von Temperatur und Niederschlag extrahiert. Die Vegetation wurde mit Hilfe von hierarchischer Schichtenanhäufung klassifiziert und syntaxonomisch eingeordnet. Zusammenhänge zwischen Artenzusammensetzung und Umweltbedingungen wurden mit DCA und CCA analysiert. Beziehungen zwischen Populationsstruktur und Umweltbedingungen wurden mit allgemeinen linearen Modellen (GLMs) mit negativer binominaler Fehlerverteilung untersucht. Unterschiede in der Populationsstruktur von *A. montana* zwischen Habitattypen sowie habitatabhängige Umweltfaktoren wurden mit nicht-parametrischen Kruskal-Wallis-Tests sowie Mann-Whitney-post-hoc-Tests analysiert.

Ergebnisse – In den 25 untersuchten Populationen wuchs *A. montana* in den FFH-Lebensraumtypen *Berg-Heuwiesen*, *artenreiche Borstgrasrasen* und *subalpine und alpine Zwergstrauchheiden* (s. Vegetationstabelle im Anhang E1 sowie Abb. 2–3). Die Anzahl der Rosetten pro m² schwankte hier zwischen 7 und 165 und betrug durchschnittlich 53. Durchschnittlich 83 % der Rosetten waren vegetativ d. h. ohne Blüten. Im Durchschnitt wurden 19,5 Blüteköpfe pro Quadratmeter gezählt und ein durchschnittlicher Blütentrieb trug 2,15 Blütenköpfe. Die Vegetation wurde fünf Assoziationen aus vier Verbänden aus drei Ordnungen/Klassen zugeordnet: a) *Festuco rubrae-Agrostietum capillaris nardetosum strictae* (*Cynosurion* → *Arrhenatheretalia* → *Molinio-Arrhenatheretea*; 60 % der Aufnahmen), b) *Scorzonero roseae-Festucetum nigricantis* und c) *Violo declinatae-Nardetum* (beide *Potentillo-Nardion* → *Nardetalia* → *Calluno-Ulicetea*; jeweils 8 % der Aufnahmen), d) *Cetrario-Vaccinietum gaultherioidis* (*Loiseleurio-Vaccinion* → *Rhododendro-Vaccinietalia* → *Loiseleurio-Vaccinietea*; 8 % der Aufnahmen) und e) *Campanulo abietinae-Vaccinietum myrtilli* (*Rhododendro-Vaccinion* → *Rhododendro-Vaccinietalia* → *Loiseleurio-Vaccinietea*; 16 % der Aufnahmen). Die erste Achse der Vegetation nach einer DCA war am stärksten mit der Meereshöhe korreliert, gefolgt vom P-Gehalt des Bodens, dem Anteil organischer Substanz des Bodens, der Hangneigung und dem Jahresniederschlag (Abb. 4). Allgemeine lineare Modelle zeigen die Bedeutung der einzelnen Umweltfaktoren für die Populationsstruktur von *A. montana* (Tab. 5). Die Meereshöhe war ein wichtiger Prädiktor mit einem negativen Effekt auf die Dichte der Rosetten und einem positiven Effekt auf den Anteil der vegetativen Rosetten (Abb. 5); Pflanzen in hohen Lagen blühten also weniger stark. Auch der Vegetationstyp hatte einen Einfluss auf die Dichte der Rosetten von *A. montana*. Die höchste Rosettendichte wurde in den Berg-Heuwiesen (*Festuco rubrae-Agrostietum nardetosum*) und die niedrigste in den subalpin-alpinen Heiden (*Cetrario-Vaccinietum gaultherioidis* und *Campanulo-Vaccinietum myrtilli*) festgestellt. In den Borstgrasrasen (*Scorzonero-Festucetum nigricantis* und *Violo declinatae-Nardetum*) war die Rosettendichte ebenfalls relativ hoch. Die organische Substanz des Bodens war der einzige Prädiktor für die Anzahl der Blütenköpfchen pro Blütentrieb. Die Anzahl der Blütenköpfchen pro Probefläche nahm mit dem pH-Wert des Bodens zunächst zu und dann wieder ab (Abb. 5). Die Populationsstruktur von *A. montana* unterschied sich auch zwischen den drei Nutzungstypen Mahd, Weide und Brache. Gleichzeitig lag die Rosettendichte in der subalpinen/alpinen Stufe niedriger als in der montanen Stufe.

Diskussion – Die Meereshöhe hatte bei uns den stärksten Effekt auf die Populationsstruktur von *A. montana*. Die mit der Meereshöhe abnehmende Populationsdichte kann mit den zunehmend harschen Bedingungen in höheren Lagen erklärt werden. Darauf deutet auch der mit der Meereshöhe abnehmende Anteil blühender Pflanzen hin. Pflanzen in hohen Lagen investieren oft einen größeren Teil ihrer Ressourcen in vegetatives Wachstum um zu überleben als in die Reproduktion (HAUTIER et al. 2009, MAURICE et al. 2012). Der bestimmende Faktor für die Dichte der Blütenköpfchen war der pH-Wert des Bodens der ein allgemeines Maß für die Bodenfruchtbarkeit bildet. Sowohl Mahd als auch Beweidung hatten einen positiven Einfluss auf die Rosettendichte von *A. montana*, die als Rosettenpflanze grundsätzlich an Beweidung angepasst ist, aber offenbar auch Mahd gut verträgt, wenn die Wiesen mager und licht sind. Die niedrigere Artendichte von *A. montana* in den Brachen interpretieren wir als Folge der Zunahme von anderen konkurrenzstärkeren Arten.

Schlussfolgerung – In unserer Studie erwies sich die Meereshöhe als der wichtigste Faktor für die Populationsstruktur von *A. montana*. Auch die Korrelationen des Gehalts an organischer Substanz des Bodens und der Dichte der Blütenköpfchen von *A. montana* oder zwischen der Dichte der Blütenköpfchen pro Blütentrieb und dem pH-Wert des Bodens stellen wohl indirekte Effekte der Meereshöhe dar.

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Author contribution statement

C.M. and C.T. initiated the study and coordinated the writing of the article. All authors except V.G. and D.D. participated in the field sampling. V.G. and D.D. conducted soil analyses. C.M., C.B. and C.Ș. did the classification and ordination, analysed vegetation-environment relationships, defined habitat types and community types and analysed relationships between population structure and habitat characteristics. All authors critically revised the full text.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Synoptic table with the percentage frequencies of plant species in the communities with *Arnica montana* in the North-Eastern part of the Romanian Eastern Carpathians.

Anhang E1. Synoptische Tabelle mit Prozent-Stetigkeiten der Vegetation mit *Arnica montana* im nordöstlichen Teil der rumänischen Karpaten.

Supplement E2. Model selection for rosette and flower head density and number of flower heads per rosette in *Arnica montana*.

Anhang E2. Auswahl der besten Modelle zur Charakterisierung der Variation in der Populationsdichte und -struktur von *Arnica montana*.

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Supplement E1. Synoptic table with the percentage frequencies of plant species in the communities with *Arnica montana* in the North-Eastern part of the Romanian Eastern Carpathians. Associations are: 1 – *Festuco rubrae-Agrostietum capillaris*, 2 – *Scorzonero roseae-Festucetum nigricantis*, 3 – *Violo declinatae-Nardetum strictae*, 4 – *Campanulo abietinae-Vaccinietum myrtilli*, 5 – *Cetrario-Vaccinietum gaultherioidis*. Different letters indicate significant differences (α = 0.05) according to a Mann-Whitney post-hoc test.

Anhang E1. Synoptische Tabelle mit Prozent-Stetigkeiten der Vegetation mit *Arnica montana* im nordöstlichen Teil der rumänischen Karpaten. Bezüglich der Assoziationen siehe englische Tabellenüberschrift. Mittelwerte mit unterschiedlichen Buchstaben unterscheiden sich signifikant (α = 0,05) nach einem Mann-Whitney Post-hoc-Test.

Association	1	2	3	4	5
No. of relevés	45	6	6	12	6
Species richness per m²	47.9 ± 8.3^{a}	40.8 ± 5.0^{a}	28.3 ± 3.6^{b}	26.5 ± 3.4^{b}	21.8 ± 3.5^{b}
Arnica rosette density per m²	61.3 ± 20.7^{a}	55.8 ± 11.7^{a}	36.8 ± 7.5^{b}	30.2 ± 10.6^{b}	18.2 ± 14.4^{b}
Proportion vegetative Arnica rosettes (%)	80.7 ± 6.8^{a}	78.5 ± 7.4^{abd}	90.8 ± 5.0^{c}	88.6 ± 4.8^{bcd}	98.2 ± 2.0^{ce}
Arnica flower head density per m²	19.0 ± 15.0^{a}	28.3 ± 14.8^{a}	17.3 ± 10.3^{a}	13.2 ± 9.2^{a}	10.2 ± 10.7^{a}
Arnica flower heads per flowering rosette	2.4 ± 0.5^{a}	2.7 ± 0.3^{a}	1.1 ± 0.4^{b}	1.8 ± 0.9^{ab}	1.3 ± 0.6^{b}
Arnica montana	100	100	100	100	100
Festuca rubra	100	67	83	42	.
Agrostis capillaris	96	33	67	50	.
Potentilla erecta	80	67	67	83	17
Cruciata glabra	80	83	17	25	.
Nardus stricta	62	83	100	33	50
Trifolium repens subsp. repens	58	.	17	17	.
Anthoxanthum odoratum	58	17	17	33	17
Thymus pulegioides s. l.	60	83	100	42	.
Campanula serrata	58	33	33	.	.
Briza media	60	33	33	.	.
Stellaria graminea	56	17	33	25	.
Leucanthemum vulgare	53	50	17	33	.
Pilosella officinarum	56	67	17	33	.
Trifolium pratense subsp. pratense	51	33	17	8	.
Centaurea phrygia	44	17	.	8	.
Plantago lanceolata	44	17	.	.	.
Rhinanthus angustifolius	40	33	.	.	.
Hypericum maculatum	40	50	100	17	.
Alchemilla xanthochlora	40	.	50	8	.
Polygala vulgaris subsp. vulgaris	38	67	.	17	.
Achillea millefolium	38	50	.	.	.
Lotus corniculatus	36	33	17	.	.
Ranunculus acris subsp. acris	36	33	17	.	.
Trifolium montanum	33	33	.	.	.
Luzula luzuloides subsp. luzuloides	29	50	33	67	50
Viola tricolor	31	50	.	.	.
Gymnadenia conopsea subsp. conopsea	31	.	33	.	.
Prunella vulgaris	27	.	67	.	.
Veronica chamaedrys subsp. chamaedrys	29	.	.	8	.
Carlina vulgaris	24	33	.	.	.
Pimpinella saxifraga subsp. saxifraga	27	33	.	8	.
Pilosella aurantiaca	27	33	33	17	17
Luzula campestris	22	33	50	.	17
Leontodon autumnalis subsp. autumnalis	24	33	.	8	.
Vaccinium vitis-idaea	20	17	67	83	83
Stachys officinalis	22	50	.	.	.
Vaccinium myrtillus	20	17	100	100	100
Juniperus communis subsp. alpina	.	.	.	25	83
Vaccinium uliginosum subsp. microphyllum	.	.	.	.	100
Deschampsia flexuosa	2	.	17	8	83
Calamagrostis villosa	.	.	.	8	83
Festuca supina	.	.	.	.	83
Veratrum album subsp. album	.	.	67	8	33
Ligusticum mutellina	.	.	.	8	50
Picea abies juv.	16	33	33	58	33
Juncus trifidus	.	.	.	.	33
Hieracium alpinum	.	.	.	.	50
Homogyne alpina	.	.	17	33	50
Pinus mugo	.	.	.	.	33
Carex atrata	.	.	.	.	17
Huperzia selago	.	.	.	17	33
Campanula alpina	.	.	.	.	17
Soldanella hungarica	.	.	.	.	17
Cirsium erisithales	4	50	.	.	.
Pulsatilla alba	.	.	.	.	17
Melampyrum sylvaticum	2	.	.	42	17
Campanula patula subsp. abietina	.	.	.	42	17
Antennaria dioica	16	.	67	17	17
Pseudorchis albida	.	.	.	.	17
Rhododendron myrtifolium	.	.	.	.	17
Campanula polymorpha subsp. polymorpha	.	.	.	.	33
Hypochaeris uniflora	18	50	.	.	17
Ranunculus montanus subsp. pseudomontan	.	.	17	.	.
Crocus vernus	2	.	17	.	.
Polygala major subsp. major	2	.	17	.	.
Festuca nigrescens	.	100	17	.	.
Cerastium fontanum	9	17	33	.	.
Viola declinata	11	17	83	.	.
Botrychium lunaria	4	.	17	.	.
Plantago major subsp. major	7	.	33	.	.
Alchemilla monticola	7	17	33	.	.
Cynosurus cristatus	13	.	.	.	.
Pilosella lactucella subsp. lactucella	9	.	.	.	.
Bromus erectus	7	.	.	.	.
Campanula glomerata	11	.	.	.	.
Phleum alpinum subsp. alpinum	.	.	17	.	.
Holcus lanatus	13	.	.	.	.
Carex pallescens	9	50	33	.	.
Carex montana	2	.	33	.	.
Anacamptys pyramidalis	2	.	17	.	.
Pteridium aquilinum	7	.	.	.	.
Senecio erucifolius subsp. erucifolius	2	.	.	.	.
Lathyrus pratensis	7	.	.	.	.
Gymnadenia odoratissima	4	.	.	.	.
Galium verum	7	.	.	.	.
Melampyrum saxosum	4	.	.	8	.
Platanthera chlorantha	2	.	.	.	.
Vicia sepium	4	.	.	.	.
Knautia arvensis	4	.	.	.	.
Euphorbia amygdaloides	2	.	.	.	.
Gentiana cruciata	4	.	.	.	.
Salix caprea	4	.	.	.	.
Silene nutans subsp. nutans	4	.	.	.	.
Dianthus carthusianorum	4	.	.	.	.
Trifolium aureum	4	.	.	.	.
Veronica montana	7	.	.	.	.
Festuca pratensis	7	.	.	.	.
Genista tinctoria subsp. tinctoria	4	.	.	.	.
Pedicularis verticillata	2	.	.	.	.
Dactylis glomerata	11	.	.	.	.
Alchemilla vulgaris	9	.	.	.	.
Digitalis grandiflora	9	.	.	.	.
Thesium alpinum	9	.	.	.	.
Stellaria holostea	.	.	17	.	.
Scabiosa columbaria subsp. columbaria	.	.	17	.	.
Polygonum bistorta	7	.	.	.	.
Rhinanthus minor	11	.	.	.	.
Rorippa sylvestris subsp. sylvestris	2	.	.	.	.
Acinos alpinus	2	.	.	.	.
Carum carvi	9	.	.	.	.
Parnassia palustris	2	.	.	.	.
Lychnis viscaria subsp. viscaria	11	.	.	.	.
Platanthera bifolia	4	.	.	.	.
Phleum pratense subsp. pratense	2	.	.	.	.
Dactylorhiza maculata subsp. maculata	7	.	.	.	.
Oxalis acetosella	2	.	.	8	.
Gnaphalium sylvaticum	7	.	33	8	.
Sorbus aucuparia juv.	.	.	.	17	.
Ajuga reptans	2	.	.	8	.
Carlina acaulis	16	33	.	8	.
Hypochaeris radicata	20	67	.	8	.
Succisa pratensis	11	.	.	8	.
Cirsium pannonicum	18	17	.	.	.
Dianthus barbatus subsp. compactus	18	50	.	.	.
Trollius europaeus subsp. europaeus	11	50	.	.	.
Dryopteris filix-mas	.	.	.	8	.
Populus tremula juv.	2	.	.	8	.
Campanula patula subsp. patula	.	17	.	.	.
Maianthemum bifolium	2	17	.	17	.
Calamagrostis arundinacea	2	.	.	25	.
Viola reichenbachiana	9	.	.	17	.
Luzula sylvatica	.	.	.	17	.
Achillea distans	16	50	50	42	.
Veronica officinalis	13	17	50	42	17
Gentiana asclepiadea	2	.	.	33	.
Fragaria vesca	7	.	.	17	.
Hieracium virosum	9	.	.	17	.
Solidago virgaurea subsp. alpestris	4	.	.	8	.
Rumex acetosella subsp. acetosella	11	17	.	8	.
Pinus sylvestris	.	.	.	17	.
Deschampsia caespitosa	2	17	50	17	.
Polygonatum verticillatum	.	17	.	17	.
Stellaria media subsp. media	2	.	.	.	.
Trisetum flavescens	16	67	.	.	.
Scorzonera rosea	11	67	.	.	.
Brachypodium pinnatum	2	.	.	.	.
Vincetoxicum hirundinaria subsp. hirundi	2	33	.	.	.
Angelica sylvestris	9	33	.	.	.
Anthyllis vulneraria s. l.	11	33	.	.	.
Lycopodium clavatum	4	.	.	.	.
Filipendula vulgaris	7	.	.	.	.
Linum catharticum	7	.	.	.	.
Potentilla recta	2	.	.	.	.
Daucus carota	2	.	.	.	.
Tanacetum corymbosum	18	33	.	.	.
Tragopogon pratensis subsp. pratensis	7	33	.	.	.
Laserpitium latifolium	2	.	.	.	.
Sanicula europaea	2	17	.	.	.
Astrantia major	4	.	.	.	.
Aquilegia vulgaris	7	50	.	.	.
Phyteum tetramerum	11	17	.	.	.
Trifolium ochroleucon	11	17	.	.	.
Alchemilla graucescens	.	17	.	.	.
Euphrasia officinalis subsp. pratensis	7	17	.	.	.
Arrhenatherum elatius	.	17	.	.	.
Origanum vulgare	2	.	.	.	.
Crepis foetida s. l.	2	.	.	.	.
Silene vulgaris subsp. vulgaris	2	.	.	.	.
Cirsium oleraceum	2	.	.	.	.

Supplement E2. Model selection for rosette and flower head density and number of flower heads per rosette in Arnica montana. AICc – Akaike information criterion corrected for small sample sizes; ΔAICc = difference (Δ) in AIC compared to the best model; weight = Akaike weight (probability that a given model is the best in the whole set). Only models with ΔAICc < 2 are provided. Alt – Altitude, Max height – Maximum vegetation height, Vegcov – Vegetation cover, Bryocov – Bryophyte cover, Slop – Slope, Orgmat – Organic matter of soil, Srichness – Species richness of plots.

Anhang E2. Auswahl der besten Modelle zur Charakterisierung der Variation in der Populationsdichte und -struktur von Arnica montana (AICc – korrigiertes Akaike-Gütekriterium; Δ = AICc-Differenz (Δ) zu dem besten Modell; weight = Akaike-Gewicht (Wahrscheinlichkeit, dass sich eins der Modelle als am besten erweist). Nur Modelle mit ΔAICc < 2 werden präsentiert. Alt – Meereshöhe, Max height – Maximale Höhe der Vegetation, Vegcov – Deckung der Vegetation, Bryocov – Deckung der Bryophyten, Slop – Hangneigung, Orgmat – Gehalt an organischer Substanz des Bodens, Srichness – Artenreichtum der Vegetation.

Model	Alt	Max height	Slop	Mg	Na	Orgmat	pH	Bryo-cov	Vegcov	Srich-ness	Grazed vs. Mown	Unused vs. Mown	Nardus vs. Hay	df	ΔAICc	weight
Alt, Max height, Na, Vegcov	-0.0012	-0.016	–	–	13.150	–	–	–	0.054	–	–	–	–	6	0.00	0.16
Alt, Max height, Na, Slop, Vegcov	-0.0011	-0.017	0.007	–	12.950	–	–	–	0.057	–	–	–	–	7	0.58	0.12
Alt, Max height, Grazed vs. Mown, Vegcov	-0.0012	-0.016	–	–	–	–	–	–	0.045	–	+	–	–	6	0.59	0.12
Alt, Max height, Mg, Grazed vs. Mown, Vegcov	-0.0014	-0.012	–	-0.316	–	–	–	–	0.039	–	+	–	–	7	0.68	0.11
Alt, Nardus vs. Hay, Max height, Grazed vs. Mown, Vegcov	-0.0013	-0.016	–	–	–	–	–	–	0.038	–	+	–	+	7	0.73	0.11
Alt, Max height, Na, Grazed vs. Mown, Vegcov	-0.0012	-0.016	–	–	10.170	–	–	–	0.050	–	+	–	–	7	0.76	0.11
Alt, Max height, Slop, Grazed vs. Mown, Vegcov	-0.0011	-0.017	0.007	–	–	–	–	–	0.048	–	+	–	–	7	1.48	0.08
Alt, Max height, Na, Slop, Grazed vs. Mown, Vegcov	-0.0011	-0.017	0.007	–	10.060	–	–	–	0.053	–	+	–	–	8	1.73	0.07
Alt, Nardus vs. Hay, Max height, Na, Grazed vs. Mown, Vegcov	-0.0013	-0.017	–	–	0.900	–	–	–	0.044	–	+	–	+	8	1.79	0.07
Alt, Nardus vs. Hay, Max height, Mg, Grazed vs. Mown, Vegcov	-0.0014	-0.013	–	-0.270	–	–	–	–	0.035	–	+	–	+	–	1.92	0.06
Alt, Bryocov, Nardus vs. Hay, Orgmat, pH, Slop, Unused vs. Mown, Vegcov	0.0005	–	0.004	–	–	-0.005	-0.202	-0.002	-0.010	–	–	+	+	10	0.00	0.27
Alt, Nardus vs. Hay, Orgmat, pH, Slop, Unused vs. Mown, Vegcov	0.0006	–	0.004	–	–	-0.005	-0.169	–	-0.007	–	–	+	+	9	0.43	0.22
Alt, Nardus vs. Hay, Slop, Grazed vs. Mown	0.0005	–	0.003	–	–	–	–	–	–	–	+	–	+	+	0.69	0.19
Alt, Bryocov, Orgmat, pH, Slop, Unused vs. Mown, Vegcov	0.0005	–	0.004	–	–	-0.005	-0.217	-0.002	-0.012	–	–	+	–	9	0.87	0.18
Alt, Orgmat, pH, Slop, Unused vs. Mown, Vegcov	0.0005	–	0.004	–	–	-0.006	-0.183	–	-0.009	–	–	+	–	8	1.43	0.13
Orgmat	–	–	–	–	–	-0.051	–	–	–	–	–	–	–	3	0.00	0.52
Alt	-0.0011	–	–	–	–	–	–	–	–	–	–	–	–	3	1.35	0.26
Orgmat. pH	–	–	–	–	–	-0.049	0.996	–	–	–	–	–	–	4	1.69	0.22
pH, Srichness, Vegcov	–	–	–	–	–	–	19.290	–	0.182	-0.130	–	–	–	5	0.00	0.51
Mg, pH, Srichness, Vegcov	–	–	–	-0.822	–	–	1.993	–	0.169	-0.110	–	–	–	6	1.41	0.25
Nardus vs. Hay, pH, Srichness, Vegcov	–	–	–	–	–	–	1.791	–	0.161	-0.128	–	–	+	6	1.57	0.23