



## Distribution and habitat requirements of red wood ants in Switzerland: Implications for conservation



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### ABSTRACT

Mound-building red wood ants (*Formica rufa* group) fulfill keystone roles in forest ecosystems, and several species are on the red list of the International Union for Conservation of Nature. Nonetheless, detailed information on their distribution and habitat requirements is lacking, yet needed to evaluate population changes and develop conservation strategies.

To assess their status in Switzerland, we studied red wood ant mounds in a nationwide, systematic survey of forests (Swiss National Forest Inventory). We identified key predictors of mound occurrence and mound size related to forest structure, forest composition, climate, and topography.

Red wood ants were found to be relatively rare across Switzerland (1.4 mounds per ha of forest), especially at lower elevations (0.16 mounds per ha). *Formica lugubris* and *F. paralugubris* were common only in mountainous areas. Few *F. rufa* and *F. polyctena* mounds were found countrywide, the latter mostly at lower elevations. *Formica aquilonia* was restricted to the Engadine region of the Alps. Wood ants mainly depended on slope aspect, climate, forest structure, and conifer abundance, but did not depend on forest fragment size, distance to forest edges, or woody vegetation diversity.

Our baseline data will enable population changes of red wood ants to be quantified, to reassess their conservation and protection status. For now, based on their observed rarity, conservation measures for red wood ants seem advisable in Switzerland. Our data suggest that red wood ants are not restricted to large, continuous, or diverse forests. Conservation strategies could thus focus on optimizing the structure of coniferous forests.

### 1. Introduction

Mound-building red wood ants (*Formica rufa* group) are legally protected in several European countries (Sorvari, 2016). In addition, five of the six European red wood ant species are globally listed as “lower risk/near threatened” by the International Union for Conservation of Nature (IUCN, 2016). The protection of red wood ant species, which in some countries has a long history (e.g., Gfeller, 1975), relates to the long-standing recognition of their importance as keystone species, ecosystem engineers, and biocontrol agents against forest pests (Domisch et al., 2016; Frouz et al., 2016; Gößwald, 1990; Robinson et al., 2016).

The impact of red wood ants extends over several trophic levels and ecosystem processes (Domisch et al., 2016; Frouz et al., 2016; Johansson and Gibb, 2016; Robinson et al., 2016). These ants engage in a mutualism with aphids and other phloem-feeding insects, which provide the ants with nutritious honeydew in return for protection (Domisch et al., 2016; Morales, 2000; Stadler and Dixon, 2005). Wood ants also prey on invertebrates (Domisch et al., 2009; Gößwald, 1989; Punttila et al., 2004; Robinson et al., 2016) often suppressing insect pests of forest trees (Gößwald, 1990; Karhu and Neuvonen, 1998; Maňák et al., 2013; Punttila et al., 2004). As predators, wood ants compete with other invertebrate predators (Hawes et al., 2013;

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Reznikova and Dorosheva, 2004), including other ants (Gibb, 2011; Savolainen and Vepsäläinen, 1988), and insectivorous birds (Aho et al., 1999). On the other hand, wood ants are a food source for birds and mammals (Rolstad et al., 2000; Swenson et al., 1999). Their mounds harbor a suite of myrmecophilous species (Paivinen et al., 2002; Parmentier et al., 2015) and are hotspots of nutrient accumulation and CO<sub>2</sub> production (Finér et al., 2013; Frouz and Jílková, 2008; Risch et al., 2005), while the ants deplete nutrients from the surroundings and increase the pH of the mound and the soil surrounding the mound (Jílková et al., 2011; Jílková et al., 2012). Wood ants disperse plant seeds (Gorb and Gorb, 1995; Pfeiffer et al., 2010) and can cause vegetation changes with wide-ranging effects on the soil food web (Wardle et al., 2011).

Given this wealth of information about red wood ants' ecological importance and the resulting conservation interest, knowledge of their distribution and abundance is surprisingly limited (Risch et al., 2016). Even though five European red wood ant species are on the IUCN red list, they were added twenty years ago, and the general criteria for inclusion on the red list have since been updated (IUCN, 2016). The conservation status of most other species in the subgenus *Formica sensu stricto* has not yet been assessed (Sorvari, 2016). There is thus a clear need to evaluate the current situation of the different red wood ant species and, if necessary, to develop conservation strategies accordingly. However, both these objectives are currently difficult to achieve for two reasons.

First, our knowledge of red wood ant distribution is fragmented, stemming mostly from studies conducted in areas where ants were known to occur or from various small-scale surveys often based on opportunistic rather than systematic sampling (e.g., Freitag and Cherix, 2009; Freitag et al., 2016a, but see Glaser, 2008; Punttila and Kilpeläinen, 2009). Such studies report declines (Cherix et al., 2012; Dekoninck et al., 2010; Mäki-Petäys and Breen, 2007; Mäki-Petäys et al., 2005), but also increases (Freitag, 2008) in some local red wood ant populations. Therefore, good baseline information is unavailable to quantify population changes over time, which form a main component of the currently used IUCN criteria (IUCN, 2012).

Second, the development of effective conservation measures for red wood ant species is hampered by a limited understanding of their natural habitat requirements (Robinson and Stockan, 2016). Most studies of red wood ants' habitat associations have been conducted at very local scales, limited to a few habitat characteristics, or based on presence only rather than presence/absence data (Risch et al., 2016).

Nevertheless, some general patterns can be gleaned from these earlier studies. Red wood ants seem to prefer slopes with aspects between south and west, avoiding north-facing slopes (Risch et al., 2016). In Central Europe, *F. polyctena*, *F. rufa*, and *F. pratensis* occur mainly below 1500 m, whereas *F. aquilonia*, *F. lugubris*, and *F. paralugubris* mostly live at higher elevations (Risch et al., 2016). Depending on colony strategy, certain red wood ant species are thought to perform best in the interior of large forest fragments and others at the edges of smaller, more isolated fragments (Punttila, 1996; Risch et al., 2016; Sundström et al., 2005). Mound size, a general proxy for the size and health of the colony (Freitag et al., 2016b), tends to be greater under more closed canopies (Chen and Robinson, 2014; Kilpeläinen et al., 2008), as only large nests can thermoregulate independently of sun exposure (Coenen-Staß et al., 1980; Rosengren et al., 1987). However, this limited information is not sufficient to determine which habitat properties are most important for wood ants, and thus need to be prioritized in conservation efforts.

As part of the National Forest Inventory (NFI) of Switzerland, we surveyed (presence/absence) and measured mounds of red wood ant species in a systematic grid of forest plots across the entire country. The survey started in 2009, and each year a different set of plots was surveyed. A large set of environmental variables related to forest composition and structure, climate, and topography was determined for these plots. These data provide a unique opportunity to study both the

distribution of red wood ant species and the relative importance of many habitat characteristics for red wood ants at a large spatial scale. In this study, we: i) provide a systematic assessment of the distribution of red wood ant species across Switzerland, which can serve as a baseline for future population changes; ii) identify the most important predictors of occurrence and size of red wood ant mounds from a large set of environmental variables; iii) evaluate how the resulting information about distribution and habitat preferences can be used to derive conservation strategies for red wood ants.

## 2. Material and methods

### 2.1. Study area and study species

The study area was the entire country of Switzerland (41,248 km<sup>2</sup>; 45°49'–47°48' N, 5°57'–10°30' E). The Jura Mountains cover 12% of the country and run along the northwestern border. The Alps (Prealps, Alps, and Southern Alps) cover the southeastern 65% of the country. The Swiss Plateau, covering 23% of the country, is located between the Jura and the Alps. Within Switzerland, our study was restricted to forested areas. Forests cover about one third of the country and increase in area from lower to intermediate elevations, but are lacking from the highest regions, which are above the tree line (Abegg et al., 2014).

Our study focused on the subgenus *Formica sensu stricto*, and more specifically on the red wood ants, i.e., the *F. rufa* group, which is a subgroup of this subgenus. Currently, 13 Palearctic and 19 Nearctic species are considered members of the *Formica sensu stricto* subgenus, although its taxonomy is far from stable (Stockan et al., 2016). Of these 32 species, eight have been recorded in Switzerland: *F. aquilonia* Yarrow, 1955, *F. lugubris* Zetterstedt, 1838, *F. paralugubris* Seifert, 1996, *F. rufa* Linnaeus, 1761, *F. polyctena* Förster, 1850, *F. uralensis* Ruzsky, 1895, *F. truncorum* Fabricius, 1804, and *F. pratensis* Retzius, 1783 (Kutter, 1977; Seifert, 1996). Of these eight species, *F. uralensis* and *F. truncorum* do not belong to the *F. rufa* group according to Goropashnaya et al. (2004). *F. uralensis* would even form its own subgenus, distinct from *Formica s. str.*, according to Goropashnaya et al. (2012). Thus, in this view, the red wood ants are represented by six species in Switzerland.

### 2.2. Ant mound survey

As part of the ongoing fourth National Forest Inventory (NFI), the occurrence of wood ant mounds was recorded between 2009 and 2014 in 4271 plots across the entire country (Fig. A1), in forested areas according to the NFI definition of forest (Brassel and Lischke, 2001; Keller, 2011). The NFI plots are located on the intersections of a systematic 1.4 km × 1.4 km grid mapped onto the country, and cover the entire range of forest types present in Switzerland. In each plot, ant mounds were recorded in a circle of 12.62 m radius (500 m<sup>2</sup> surface area) around the plot center. Of these plots, 267 randomly selected ones were reassessed for ant mounds during a control survey. In three of them where no ant mounds were found during the first survey, one red wood ant mound was found during this second survey (1.1% of reassessed plots). In one plot where only one red wood ant mound was found during the first survey, two additional mounds belonging to the same species were detected during the second survey (0.37% of reassessed plots). We consider this detection probability satisfactory, even though it was not 100%. Of each mound, a first diameter was measured along the line connecting plot center with mound center. A second diameter was measured through the mound center (highest point), perpendicular to the first diameter. At each of the four intersections of the diameters with the edge of the mound, mound height was measured from the ground to the highest point of the mound (mound center). The mean of these four measurements was used as the height of the mound. Around 12 ants were collected from each mound, stored in 95% ethanol, and morphologically identified based on Seifert (2007),

**Table 1**

Overview of the different predictor variables used in the model selection procedure. Variables are grouped into measures of forest composition, forest structure, climate, and topography. Time of ant mound recording (date and time of day) was included as a variable in all models to test for temporal dependencies in the data, but was not selected by LASSO for any of the dependent variables. Variable names in italics denote groups of conceptually linked variables, as explained under 'Description'.

Variable	Description
<b>Forest composition</b>	Methodological details for all forest composition variables can be found in Keller (2011) and Brassel and Lischke (2001).
<i>Percentage crown cover per tree taxon</i>	11 variables. Percentage of the crown cover occupied by a certain taxon of tree, calculated separately for all conifers, spruce ( <i>Picea</i> spp.), fir ( <i>Abies</i> spp.), pine ( <i>Pinus</i> spp. excluding <i>P. cembra</i> and <i>P. mugo prostrata</i> ), larch ( <i>Larix</i> spp.), Swiss stone pine ( <i>Pinus cembra</i> ), beech ( <i>Fagus sylvatica</i> ), maple ( <i>Acer</i> spp.), ash ( <i>Fraxinus</i> spp.), oak ( <i>Quercus</i> spp.), sweet chestnut ( <i>Castanea sativa</i> ). Other coniferous trees and other deciduous trees were used as reference levels.
Tree diversity	Number of tree species in the upper crown layer.
Woody plant diversity	Number of woody plant species with a height > 40 cm.
Conifer dominance	Binary variable. Plot dominated by coniferous trees (i.e., conifers make up the largest proportion of the basal area): yes or no.
<i>Dominant tree taxon</i>	11 binary dummy variables. Dominant tree taxon on the plot (i.e., tree taxon with the largest proportion of the basal area): spruce ( <i>Picea</i> spp.), fir ( <i>Abies</i> spp.), pine ( <i>Pinus</i> spp. excluding <i>P. cembra</i> and <i>P. mugo prostrata</i> ), larch ( <i>Larix</i> spp.), Swiss stone pine ( <i>Pinus cembra</i> ), beech ( <i>Fagus sylvatica</i> ), maple ( <i>Acer</i> spp.), ash ( <i>Fraxinus</i> spp.), oak ( <i>Quercus</i> spp.), sweet chestnut ( <i>Castanea sativa</i> ), or other coniferous trees. Other deciduous trees was used as reference level.
<i>Live stem number per tree taxon</i>	11 variables. Number of living stems per ha for each of the same tree taxa as percentage crown cover.
<i>Dead stem number per tree taxon</i>	11 variables. Number of dead stems per ha for each of the same tree taxa as percentage crown cover.
<i>Live timber volume per tree taxon</i>	11 variables. Live timber volume for each of the same tree taxa as percentage crown cover (m <sup>3</sup> ha <sup>-1</sup> ).
<i>Dead timber volume per tree taxon</i>	11 variables. Dead timber volume for each of the same tree taxa as percentage crown cover (m <sup>3</sup> ha <sup>-1</sup> ).
<i>Berry bushes</i>	5 binary dummy variables. Degree of cover (%) of berry bushes ( <i>Rubus</i> and <i>Vaccinium</i> spp.). 6 classes: < 1, 1–9, 10–25, 26–50, 51–75, 76–100, using < 1 as reference level.
<i>NFI biotope value</i>	2 binary dummy variables. Biotope value, an index integrating woody plant species diversity, several aspects of structural diversity, and closeness to the natural forest state, with levels low, intermediate, and high, using low as reference level.
<b>Forest structure</b>	Methodological details for all forest structure variables, except the first seven, can be found in Keller (2011) and Brassel and Lischke (2001).
Forest patch size	Surface area of the forest patch in which the sampling plot was located (m <sup>2</sup> ). See text for details.
Forest core area	Binary variable. Location of plot inside or outside the core area of the forest patch. See text for details.
Distance to forest edge	Distance from the plot center to the nearest forest edge (m). See text for details.
Mean vegetation height	Mean vegetation height derived from a digital vegetation height model with resolution 1 m, using a circular buffer with a radius of 12.5 m around the plot center (m).
Standard deviation of vegetation height	Standard deviation of vegetation height, based on the same values as the mean vegetation height (m).
Degree forest cover	Degree of forest cover (%) calculated from a digital forest layer (forest/non-forest) with resolution 1 m, using a circular buffer with radius of 12.5 m around the plot center.
NDVI	Mean Normalized Difference Vegetation Index derived from Disaster Monitoring Constellation satellite images (resolution = 22 m, period: Jul–Aug 2012).
<i>Stand layer</i>	3 variables: degree of cover (%) of understory, midstory, and overstory.
<i>Shade</i>	2 variables: shade (%) measured at 40 cm and 130 cm from the soil surface.
Diameter at breast height	Mean tree diameter at breast height (cm).
Dominant diameter	Mean diameter of the 100 thickest trees per ha (cm).
Lying deadwood	Volume of lying dead wood (m <sup>3</sup> ha <sup>-1</sup> ).
Top height	Mean height of the 100 thickest trees per ha (m).
Total live stem number	Total number of live stems per ha.
Total dead stem number	Total number of dead stems per ha.
Total live timber volume	Total live timber volume (m <sup>3</sup> ha <sup>-1</sup> ).
Total dead timber volume	Total dead timber volume (m <sup>3</sup> ha <sup>-1</sup> ).
<i>NFI structural diversity</i>	2 binary dummy variables. Structural diversity index, with levels low, intermediate, and high, using low as reference level.
Forest edge	Binary variable. Presence/absence of a forest edge in the plot.
Root plates	Binary variable. Presence/absence of root plates.
Stumps	Binary variable. Presence/absence of stumps.
Heaps of branches	Binary variable. Presence/absence of heaps of branches.
Snags	Binary variable. Presence/absence of snags.
Traces of fire	Binary variable. Presence/absence of traces of fire.
Traces of grazing	Binary variable. Presence/absence of traces of domestic grazers.
Water bodies	Binary variable. Presence/absence of water bodies (lakes, ponds, rivers, creeks, puddles).
<i>Basic forest type</i>	4 binary dummy variables. Basic forest type with levels: high forest, coppice forest, coppice with standards, selva (sweet chestnut or walnut), or plantation (poplar or willow), using high forest as reference level.
<i>Crown closure</i>	7 binary dummy variables. Crown closure type with levels: crowded, normal, loose, open, scattered, grouped crowded, grouped normal, and stepped/heterogeneous, using normal as reference level.
<i>Vertical stand structure</i>	3 binary dummy variables. Vertical stand structure type with levels: single-layered, multi-layered, all-aged/all-sized, and clustered, using single-layered as reference level.
<i>Regeneration</i>	6 binary dummy variables. Degree of cover (%) of the regeneration (trees higher than 0.1 m with diameter at breast height < 12 cm). 7 classes: < 1, 1–4, 5–9, 10–25, 26–50, 51–75, 76–100, using < 1 as reference level.
<i>Shrub layer</i>	5 binary dummy variables. Degree of cover (%) of the shrub layer (all woody species between 0.5 and 3.0 m height). 6 classes: < 1, 1–9, 10–25, 26–50, 51–75, 76–100, using < 1 as reference level.
<i>Ground vegetation</i>	5 binary dummy variables. Degree of cover (%) of ground vegetation. 6 classes: < 1, 1–9, 10–25, 26–50, 51–75, 76–100, using < 1 as reference level.
<b>Climate</b>	Details for all climate variables, except cloudiness and potential radiation, can be found in Zimmermann and Kienast (1999) and are averages for the period 1961–1990.
Cloudiness	Mean July cloudiness for period 1981–1990, based on 85 measuring stations (1/1000 [per mille]).
Potential radiation	Potential radiation of the vegetation period (1 April–31 October), calculated in GIS, based on a digital terrain model with 25 m resolution using methods described in Fu and Rich (2002) (Wh/m <sup>2</sup> ).
Climate continentality (Gams angle)	A continentality index derived from precipitation and temperature, which is not sensitive to variation in topography, only to regional differences in precipitation and temperature at given elevations (1/10 °C).

(continued on next page)

Table 1 (continued)

Variable	Description
Precipitation	3 variables: annual precipitation sum and precipitation sum for January and July (1/10 mm).
Radiation	2 variables: radiation for March and July ( $10 * 2 \text{ kJ/m}^2$ ).
Temperature	Average annual temperature (1/100 °C).
<b>Topography</b>	All topographic variables were calculated from a digital terrain model with 25 m resolution (Swisstopo, 2016).
Cell balance	Inflow/outflow per cell within the direct neighborhood (index).
Position index	A topographic position index calculated using a program of Zimmermann (2000), with radii from 3 to 80 pixels and an increment of 10 pixels (index). Measure of the exposure of a site in relation to the surrounding terrain.
Curvature	Curvature in all directions (index).
Plan curvature	Plan curvature (index).
Profile curvature	Profile curvature (index).
Elevation	Elevation based on a digital elevation model with 25 m resolution (m).
Eastness	Sine of aspect in radians, measured clockwise from the direction of the north (index).
Northness	Cosine of aspect in radians, measured clockwise from the direction of the north (index).
Slope	Slope (degrees).
Wetness index	Topographic wetness index, calculated after an algorithm of Tarboton (1997) (index).

followed by analysis of mitochondrial DNA (Gen COI) to distinguish between *F. lugubris* and *F. paralugubris*, according to the protocol of Bernasconi et al. (2010). For a few ant samples the genetic analysis did not yield results, presumably because the available DNA was too degraded. All samples were deposited in the Museum of Zoology in Lausanne.

### 2.3. Predictor variables

Our predictor variable set included variables related to forest composition, forest structure, climate, and topography. Forest composition variables (Table 1) were all derived from field data collected from NFI plots from 2009 to 2013 as described by Brassel and Lischke (2001) and Keller (2011). More specifically, these variables included percentage canopy cover, number of living and dead trees, and living and dead timber volume of the main tree taxa (species or groups of species, see Table 1), dominance (i.e., which of the main tree taxa made up the highest proportion of the basal area), as well as different measures of woody plant species richness. Because we expected conifers in general to be important to red wood ants (Risch et al., 2016), we also determined the different measures of abundance for all coniferous species combined.

Forest structure characteristics included variables based on 2009–2013 NFI field measurements (details in Brassel and Lischke, 2001; Keller, 2011) and based on remote sensing data (Table 1). Mean Normalized Difference Vegetation Index (NDVI) was derived from Disaster Monitoring Constellation satellite images, with a resolution of 22 m, taken during July and August of 2012. We calculated the distance from the plot center to the nearest forest edge from a digital forest layer for Switzerland. This forest layer was derived from a 1-m resolution digital vegetation height model (Ginzler and Hobi, 2015) based on aerial stereo photographs, by using the criteria of the NFI forest definition (minimum tree height of 3 m, minimum crown coverage of 20% in a 51 m × 51 m moving window, and minimum width of 25 m) to distinguish between forest and non-forest (Waser et al., 2015). We also used this forest layer to calculate the surface area of individual forest patches in which sampling plots were located. We also included a binary variable indicating whether a plot center was located in- or outside the core area of a forest patch, i.e., the area of a forest patch excluding a 20-m wide outer margin. In addition, we used the 1-m resolution vegetation height model to calculate the mean and standard deviation of the vegetation height as well as the degree of forest cover for a circular buffer of 25 m diameter around the plot center.

Climate variables (Table 1), except potential radiation, were obtained from models based on interpolations of measurements taken by the Federal Office of Meteorology and Climatology MeteoSwiss during the period 1961–1990, using a digital elevation model with a resolution

of 25 m (details in Zimmermann and Kienast, 1999). Potential radiation during the ants' activity period (1 April–31 October) was calculated using the hemispherical viewshed algorithm, implemented in ARCGIS Desktop (v. 10; ESRI Inc., Redlands, CA, US), based on a digital terrain model with 25 m resolution, as described in Fu and Rich (2002).

All topographic variables (Table 1) were calculated based on the 25-m resolution digital elevation model (Swisstopo, 2016). The topographic wetness index, an indicator of relative soil moisture conditions, was based on an algorithm by Tarboton (1997). The topographic position index, with positive values indicating ridges and tops, and negative values indicating sinks, gullies, valleys, or toe slopes, was calculated as described in Zimmermann (2000).

### 2.4. Data analyses

The occurrence of red wood ant mounds per plot was determined, with presence implying one or more mounds of any of the red wood ant species. We similarly determined the occurrence per plot for each red wood ant species. The size of each recorded ant mound was calculated using the formula for the volume of half an ellipsoid (Gößwald, 1990; Risch et al., 2005), with the mean of the four height measurements used as height. We present averages of mound volume, height (mean of four measurements), and diameter (mean of two diameters) for the *F. rufa* group as a whole as well as for each individual red wood ant species. We used a generalized linear mixed model to test whether mound volume differed between *F. lugubris* and *F. paralugubris*, including plot as a random factor and using a Gamma distribution (lme4 package, R 3.3.1). Significance of the species difference was tested with a likelihood ratio test. Other red wood ant species were too rare to statistically compare their mound volumes.

We estimated mound density (number  $\text{ha}^{-1}$ ) for each red wood ant species separately as well as for the entire *F. rufa* group, as such density estimates are independent of plot size and thus comparable across studies. Density estimates were based on the total number of mounds recorded and the total surface area assessed. If a 500  $\text{m}^2$  plot was partly inaccessible, the plot area was reduced accordingly. Mounds that could not be assigned to a single species with certainty were assigned to the possible species based on the countrywide proportions of the mounds that certainly belonged to these species. Ignoring these unidentified mounds would give plots without mounds too much weight, negatively biasing the mound density estimates. Because there seemed to be differences in the prevalence of red wood ant mounds between mountainous areas and the plateau (see Results section; Freitag and Cherix, 2009), we also calculated mound densities for plots above and below 900 m. Since within Switzerland, *F. aquilonia* is so far only known to occur in the Engadine region, we also calculated mound density for this species based only on plots located in the Engadine region (including

the lower and upper Engadine, Bregaglia, Poschiavo, Müstair, and Samnaun valleys).

From our large set of predictor variables, we performed a dual selection procedure to identify the most important predictors of the occurrence (presence/absence) and volume of the mounds of the *F. rufa* group as a whole and of the two species *F. lugubris* and *F. paralugubris*. Other red wood ant species were too rare for meaningful analysis. For each of the mound volume analyses, volumes were averaged per plot if more than one mound was present. Very high correlations (Pearson  $r > 0.95$ ) were found among average annual, January, June, July, and August temperatures and degree days, as well as between July water budget and July precipitation. From these variables, we therefore only retained average annual temperature and July precipitation in the predictor set. To improve normality of model residuals, mound size variables were all log-transformed. In a first variable selection step, we used the least absolute shrinkage and selection operator (LASSO) method (Tibshirani, 1996) for variable selection. This is a penalized maximum likelihood method, which includes a constraint on the sum of the absolute values of the regression coefficients, shrinking many of the coefficients to zero (Hastie et al., 2009). We used LASSO (glmnet package, R 3.3.1) to fit a penalized binomial logistic regression model for the mound occurrence data, and a penalized Gaussian linear regression model for the mound size data. We used cross-validation to select the optimal penalty parameter  $\lambda$ . For the binomial models, we used area under the receiver operating characteristic (ROC) curve and for the Gaussian models mean squared error as criterion for the cross-validation. For each dependent variable, we performed a 10-fold cross validation 100 times for each of a sequence of  $\lambda$  values. We then selected the  $\lambda$  that minimized the mean cross-validated error in the Gaussian case, or maximized the mean area under the ROC curve in the binomial case, averaged over these 100 runs. For each dependent variable, we retained all predictor variables with a non-zero coefficient from the model with the optimal  $\lambda$ .

These predictor variables selected by LASSO were used to fit generalized linear models (GLMs) for each dependent variable: binomial logistic regressions for the mound occurrence data and Gaussian linear regressions for the mound size data (stats package, R 3.3.1). Predictor variables were standardized to zero mean and unit standard deviation to enable direct comparison of their coefficients as measures of relative importance. Because our objective was to obtain parsimonious models, we conducted a second variable selection step to further optimize the GLMs by performing a stepwise selection procedure based on the Akaike Information Criterion (AIC) to come to a final model (stats package, R 3.3.1). Residuals of the final GLMs were checked for spatial autocorrelation by fitting a spline correlogram (nfc package, R 3.3.1) with 95% pointwise bootstrap confidence intervals over varying lag distances of up to 100 km (Zuur et al., 2009), and for normality in the case of Gaussian models using Shapiro-Wilk's test (stats package, R 3.3.1). No significant spatial autocorrelation was detected in any of the models' residuals. Mounds belonging to red wood ants that could not be assigned to a species with certainty were omitted from the species-level analyses of mound occurrence and mound volume, but were included in the analyses for the *F. rufa* group as a whole. Mounds of ants other than red wood ants or of which no ants could be identified were omitted from all analyses of mound occurrence and volume.

### 3. Results

#### 3.1. Distribution and size of red wood ant mounds

Mounds of five species of red wood ant (*F. rufa* group) were detected in our survey: *F. aquilonia*, *F. lugubris*, *F. paralugubris*, *F. polyctena*, and *F. rufa* (Table 2). We found red wood ant mounds in 203, or 5%, of the 4271 visited plots. Plots with red wood ant mounds showed an uneven distribution across the country with most of the plots located in the mountainous areas of the Jura and the Alps, and very few in the lower-

lying Swiss Plateau (Fig. 1a). Red wood ant mound density was 14 times higher above than below the 900 m contour (Table 2).

Of the five encountered species, two were relatively abundant. *Formica lugubris* mounds occurred throughout the Jura and Alps, with a high concentration in the eastern part of the Swiss Alps (Fig. 1b), but much lower mound densities in the lower-lying Swiss Plateau (Fig. 1b, Table 2). *Formica paralugubris* mounds showed a somewhat similar distribution, but were lacking from the northern regions of the Jura. *Formica paralugubris* was less abundant than *F. lugubris* in the eastern Swiss Alps (Fig. 1c) and was absent at lower elevations (Table 2). Mounds of the other three species were encountered much less frequently. *Formica aquilonia* showed a very restricted distribution, occurring only in the southeastern Engadine region of the Swiss Alps, at elevations higher than 900 m (Fig. 1d, Table 2). Mounds of *F. rufa* were recorded at scattered locations throughout the country (Fig. 1e) with similar densities in the lower and higher zones (Table 2). *Formica polyctena* mounds were found in a few locations in the Jura, Swiss Plateau, and the northern Alps (Fig. 1f), predominantly at lower elevations (Table 2). Mounds of *F. polyctena* were the largest, though *F. paralugubris* mounds were not much smaller (Table 2). *Formica rufa* mounds were intermediate in volume and diameter, but had the highest average height (Table 2). *Formica lugubris* mounds were substantially smaller, but *F. aquilonia* mounds were the smallest (Table 2). *Formica paralugubris* mounds had a significantly higher volume than *F. lugubris* mounds ( $\chi^2_1 = 12.50$ ,  $P = 0.0004$ ).

#### 3.2. Red wood ant mound occurrence and mound size in relation to forest composition, forest structure, climate, and topography

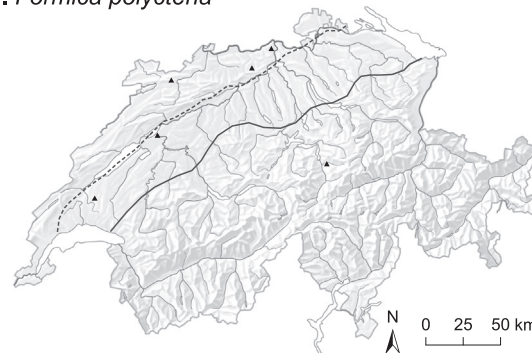
Our analysis indicated that red wood ant mounds were more likely to occur in locations on east-facing slopes in areas with a more continental climate and high summer solar radiation, in forests of low mean height, high structural diversity, and with high levels (75–100%) of ground vegetation cover (Table 3). Ant mounds were also more likely to be found under loose or grouped tree crowns than under a homogeneously closed canopy, and in forests with a high proportion of the crown cover composed of conifers or a high number of live conifer stems. Relationships between wood ant mound occurrence and shrub and berry bush cover were more idiosyncratic, with lower chances of mound occurrence under certain levels of shrub and berry bush cover compared to either lower or higher cover levels.

There were some similarities as well as differences between the main habitat characteristics affecting *F. lugubris* and *F. paralugubris* mound occurrence (Table 3). *Formica lugubris* mounds were more likely to occur on east-facing slopes in locations with a continental climate and high summer solar radiation levels. In addition, *F. lugubris* mounds were more likely to occur in forests dominated by spruce, and in forests with tree clusters of different height, or several indistinct layers of trees of different sizes and ages, rather than a single-layered vertical structure (Table 3). Mounds of *F. paralugubris* were more likely to be found at higher elevations in forests with grouped tree crowns and high numbers of live coniferous trees. The probability of *F. paralugubris* mound occurrence was lower when berry bush cover was between 10 and 25% (Table 3). Chances of *F. paralugubris* mound occurrence increased in forests with a low degree of cover and a high proportion of the crown cover made up of conifers. Occurrence of *F. paralugubris* mounds was also more probable in forests dominated by conifers from the “other coniferous trees” category (Table 1). Most of these forests were dominated by *P. mugo prostrata*. Thus, in general, *F. lugubris* occurrence was more dependent on climate, aspect, vertical forest stand structure, and the presence of spruce, whereas *F. paralugubris* occurrence was more related to elevation, canopy closure, and the presence of conifers. However, both *F. lugubris* and *F. paralugubris* were more likely to build mounds in locations with very high levels of ground vegetation cover (Table 3). Our analyses suggest that *F. lugubris* mounds occurred mostly at higher elevations because these have a more continental climate and

**Table 2**

Number, density ( $\text{ha}^{-1}$ ), volume ( $\text{m}^3$ ), diameter (m), and height (m) of mounds across all 4271 plots, and mound density for plots above (2613 plots) and below (1658 plots) 900 m elevation, for the individual red wood ant species and for the entire *F. rufa* group. For *F. aquilonia*, mound density was also estimated based only on plots located in the Engadine region (204 plots, of which 2 below 900 m). Diameter: the mean of two perpendicular diameters measured through the center of the ant mound. Height: the mean of four heights measured at each intersection of the two diameters and the mound circumference. Volume: calculated as half an ellipsoid using the mean height and two diameters. Values for volume, diameter, and height: mean with standard deviation in parentheses. Mound number: number of mounds certainly belonging to a particular species or to the *F. rufa* group. Densities: based on extrapolations for mounds with uncertain species identity (see main text for details). Eng.: Engadine region.

	Number of mounds	Density ( $\# \text{ ha}^{-1}$ ) (all plots)	Density ( $\# \text{ ha}^{-1}$ ) (< 900 m)	Density ( $\# \text{ ha}^{-1}$ ) (> 900 m)	Volume ( $\text{m}^3$ )	Diameter (m)	Height (m)
<i>F. rufa</i> group	258	1.37	0.16	2.15	0.41 (0.87)	1.07 (0.55)	0.39 (0.21)
<i>F. lugubris</i>	141	0.78	0.02	1.27	0.30 (0.38)	1.02 (0.46)	0.37 (0.19)
<i>F. paralugubris</i>	82	0.46	0.00	0.75	0.58 (1.32)	1.15 (0.64)	0.42 (0.24)
<i>F. rufa</i>	11	0.06	0.06	0.07	0.46 (1.03)	0.92 (0.65)	0.44 (0.28)
<i>F. polycтена</i>	6	0.03	0.08	0.01	0.60 (0.55)	1.26 (0.81)	0.42 (0.23)
<i>F. aquilonia</i>	7	0.04	0.00	0.06	0.22 (0.19)	1.01 (0.34)	0.33 (0.11)
<i>F. aquilonia</i> (Eng.)	7	0.70	0.00	0.71	0.22 (0.19)	1.01 (0.34)	0.33 (0.11)

**a. *Formica rufa* group****b. *Formica lugubris*****c. *Formica paralugubris*****d. *Formica aquilonia*****e. *Formica rufa*****f. *Formica polycтена***

**Fig. 1.** Distribution of mounds of red wood ants (*Formica rufa* group) in Switzerland, based on a systematic survey of forest plots. Each triangle denotes a plot in which one or more mounds were recorded. a) All *F. rufa* group species. b) *F. lugubris*. c) *F. paralugubris*. d) *F. aquilonia*. e) *F. rufa*. f) *F. polycтена*. Solid line: border between Swiss Plateau and Alps. Dashed line: border between Jura Mountains and Swiss Plateau.

higher levels of summer radiation, whereas the positive relationship between *F. paralugubris* and elevation was due to other, unmeasured factors correlated with elevation.

For the entire *F. rufa* group as well as for *F. lugubris*, only the degree of forest cover was selected as predictor of mound size, with larger mounds when the degree of forest cover was higher (Table 3). Our

**Table 3**

Predictor variables selected by LASSO followed by AIC selection for occurrence and size of mounds of the *F. rufa* group, *F. lugubris*, and *F. paralogubris*. Predictor variables were standardized, so that their coefficients are indicative of relative effect size. Test statistics are z-statistics for predictors of mound occurrence and t-statistics for predictors of mound size. No predictors of *F. paralogubris* mound size were retained. COMP: Forest composition. STRU: Forest structure. CLIM: Climate. TOPO: Topography.

	Category	Estimate	Std. Err.	z or t	P
<b>Red wood ant mound occurrence</b>					
Percentage crown cover: all conifers	COMP	0.619	0.212	2.916	0.004
Climate continentality (Gams angle)	CLIM	0.568	0.116	4.886	< 0.0001
Eastness	TOPO	0.392	0.098	3.994	< 0.0001
July radiation	CLIM	0.391	0.122	3.212	0.001
Mean vegetation height	STRU	-0.306	0.139	-2.203	0.028
NFI structural diversity: high	STRU	0.282	0.107	2.624	0.009
Shrub layer: 1–9% cover	STRU	-0.281	0.122	-2.292	0.022
Crown closure: loose	STRU	0.269	0.092	2.918	0.004
Live stem number: all conifers	COMP	0.266	0.097	2.735	0.006
Ground vegetation: 76–100% cover	STRU	0.255	0.094	2.711	0.007
Berry bushes: 10–25% cover	COMP	-0.250	0.108	-2.310	0.021
Degree of cover (%) of midstory	STRU	0.184	0.109	1.688	0.091
Crown closure: grouped normal	STRU	0.168	0.060	2.825	0.005
Root plates	STRU	-0.167	0.096	-1.730	0.084
Berry bushes: 1–9% cover	COMP	0.148	0.090	1.643	0.100
Vertical stand structure: clustered	STRU	0.077	0.045	1.708	0.088
<b><i>Formica lugubris</i> mound occurrence</b>					
Climate continentality (Gams angle)	CLIM	0.853	0.151	5.653	< 0.0001
July radiation	CLIM	0.811	0.172	4.730	< 0.0001
Eastness	TOPO	0.500	0.136	3.663	0.0002
Dominant tree taxon: spruce	COMP	0.376	0.143	2.626	0.009
Vertical stand structure: all-aged/all-sized	STRU	0.305	0.098	3.117	0.002
Ground vegetation: 76–100% cover	STRU	0.238	0.117	2.028	0.043
Vertical stand structure: clustered	STRU	0.119	0.055	2.169	0.030
<b><i>Formica paralogubris</i> mound occurrence</b>					
Berry bushes: 10–25% cover	COMP	-0.790	0.324	-2.440	0.015
Elevation	TOPO	0.764	0.222	3.443	0.0006
Percentage crown cover: all conifers	COMP	0.710	0.366	1.940	0.052
Ground vegetation: 76–100% cover	STRU	0.292	0.143	2.039	0.041
Live stem number: all conifers	COMP	0.275	0.135	2.036	0.042
Degree forest cover	STRU	-0.246	0.126	-1.945	0.052
Crown closure: grouped normal	STRU	0.181	0.081	2.247	0.025
Dominant tree taxon: other coniferous trees	COMP	0.130	0.069	1.890	0.059
<b>Red wood ant mound size</b>					
Degree forest cover	STRU	0.164	0.048	3.404	0.0009
<b><i>Formica lugubris</i> mound size</b>					
Degree forest cover	STRU	0.239	0.058	4.135	0.0001
<b><i>Formica paralogubris</i> mound size</b>					
No variables retained as predictor					

variable selection procedure did not retain any of the tested variables as predictor of *F. paralogubris* mound volume, which on average was almost double the volume of *F. lugubris* mounds.

In addition to predictors retained by our analyses, those not retained can also yield important insights. None of our indicators of forest biodiversity, such as tree or woody species diversity, were retained as predictors of mound occurrence or mound size of the *F. rufa* group, *F. lugubris*, or *F. paralogubris*. Furthermore, forest patch size and presence of, or distance to, forest edges were not retained as predictors in any of our final models.

## 4. Discussion

### 4.1. State of red wood ants in Switzerland

Five of the six red wood ant species known from Switzerland were observed in our survey. *Formica pratensis* was not detected, likely because this species prefers open habitat (Freitag et al., 2008; Seifert, 2007) and our survey was restricted to forested areas. No *F. uralensis* or *F. truncorum* mounds were observed in this systematic survey. *Formica uralensis* is considered extinct in Switzerland, as it has only been recorded in a single location (Kutter, 1977), a marsh that no longer exists. Even though *F. truncorum* is relatively rare (Freitag and Cherix, 2009),

it may also have been overlooked in our survey, as it does not build real mounds.

In a recent literature review, Risch et al. (2016) found that red wood ant mounds can reach densities of up to 20 mounds per ha in Eurasian forests, but densities rarely exceed 5 mounds per ha. However, most reported densities come from studies conducted at small spatial scales, many of whom focused on locations where wood ants were already known to occur (see Table 4.1 in Risch et al., 2016). There are only a few systematic surveys of red wood ants across the full range of forest types of a large area, which can thus be meaningfully compared to our results. The Finnish National Forest Inventory recorded ants in a systematic grid across the entire country and found an average mound density for the *F. rufa* group of 2.39 mounds per ha (Punttila and Kilpeläinen, 2009), as compared to 1.37 in our study. Another systematic study was performed in the Austrian state of Tyrol (Glaser, 2008), where 2.94 mounds of red wood ants per ha were observed. Thus, in Switzerland red wood ant mounds are rather rare in comparison. The lower overall mound density in Switzerland was mostly due to mounds of *F. aquilonia* being much rarer than in either Finland (1.60 ha<sup>-1</sup>) or Tyrol (2.41 ha<sup>-1</sup>), where it was the most abundant species. In Switzerland, *F. aquilonia* only occurred in the mountainous Engadine region, but even if we only considered plots within this region, its mound density (0.70 ha<sup>-1</sup>) was still much lower than in

Finland or Tyrol. Without *F. aquilonia* mounds, the mound density for the combined other red wood ant species drops to 0.79 and 0.53 mounds per ha in Finland and Tyrol respectively, but still reaches 1.34 mounds per ha in Switzerland. *Formica rufa* and *F. polyctena* seemed comparably rare in each of these three study regions. However, the density of *F. lugubris* mounds was much higher in our survey than in Finland (0.41 ha<sup>-1</sup>) and Tyrol (0.26 ha<sup>-1</sup>), and the mound density of *F. paralugubris*, which did not occur in Finland, was much higher than in Tyrol (0.17 ha<sup>-1</sup>). Our survey revealed a notable difference in red wood ant distribution between low- and high-elevation plots, with the two most common species, *F. lugubris* and *F. paralugubris*, as well as *F. aquilonia* almost entirely restricted to higher elevations, and all species rare or absent in the lower-lying areas. If we only included plots above 900 m, overall mound density rose to 2.15 mounds per ha. This is, however, still lower than the values reported from Tyrol, which is mostly mountainous, or from Finland.

Mound volumes in our survey were not atypical, but some studies report much larger average volumes for *F. aquilonia* (Punttila and Kilpeläinen, 2009), *F. polyctena* (Ceusters, 1979; Eichhorn, 1964; Punttila and Kilpeläinen, 2009), and *F. rufa* (Sudd et al., 1977), suggesting that conditions in Switzerland may not be favorable for mounds of these three rare species to reach their potential maximum size, even though our sample size for these species may be too small for robust conclusions. It should be noted that we only measured the aboveground part of the mound, which may be smaller when the soil is deep and the belowground part can be larger. The average volume of *F. paralugubris* mounds in our study was almost double the volume of *F. lugubris* mounds. In Switzerland, *F. paralugubris* has multiple queens per nest (polygyny), and multiple nests per colony (polydomy), whereas *F. lugubris* colonies can be mono- or polygynous and mono- or polydomous (Pamilo et al., 2016; Seifert, 2007). The higher efficiency of the polydomous colonies of *F. paralugubris* may explain why their mounds attained larger sizes on average than those of *F. lugubris* (Punttila, 1996).

As this is the first systematic survey of red wood ants across Switzerland, we cannot yet establish whether red wood ant populations are declining, stable, or increasing. However, as the Swiss National Forest Inventory will continue monitoring wood ants on the same plots, our current data will serve as a baseline to quantify population changes, enabling a reassessment of the conservation status and protection needs of red wood ants. Nevertheless, our current results suggest that red wood ants are rather rare in Switzerland, especially at lower elevations. Only *F. lugubris* and *F. paralugubris* attained fairly high densities in the mountainous regions, yet *F. paralugubris* has a restricted distribution across Eurasia, occurring only in the region of the Jura Mountains and western Alps (Stockan et al., 2016). Furthermore, the conservation needs of wood ants are easily underestimated (Sorvari, 2016). Wood ants are ecologically dominant and defend their food resources, limiting the number of colonies a habitat can support (Savolainen and Vepsäläinen, 1988). Even though workers are numerous, only queens produce offspring, resulting in small effective population sizes, and thus an increased risk of population extinction (Chapman and Bourke, 2001; Mäki-Petäys and Breen, 2007). These risks can be further compounded by low levels of genetic diversity, inbreeding, and poor dispersal ability (Mäki-Petäys and Breen, 2007; Pamilo et al., 2016). Thus, adhering to the precautionary principle, until population changes can be meaningfully evaluated, conservation measures for red wood ants seem justified in Switzerland. In the following section, we discuss which habitat characteristics were most important for red wood ants and can thus be prioritized in conservation efforts. However, *F. rufa*, *F. polyctena*, and *F. aquilonia* were too rare in our survey to meaningfully relate to environmental variables. Therefore, it would be prudent to protect all forests in which these three species occur until sufficient data are available to develop targeted conservation strategies.

#### 4.2. Red wood ant habitat requirements

Mounds of all red wood ant species combined as well as *F. lugubris* mounds were most likely to occur on east-facing slopes. In a survey conducted in the Swiss canton of the Grisons, a similar tendency of *F. lugubris* mounds to occur on east-facing slopes was observed (Freitag et al., 2016a). An eastern orientation may enable the mound to be warmed by the morning sun during the coldest hours of the day, yet also to avoid too intense radiation around noon, which may be advantageous at the high elevations at which *F. lugubris* mostly occurs. This would be in line with our result that high summer solar radiation positively affected *F. lugubris* mound occurrence. There seems to be a trade-off whereby *F. lugubris* generally depends on sunny locations, where large enough mounds can also develop in forests with more cover, whereas *F. paralugubris* generally builds larger mounds in more open forests, enabling it to colonize less sunny locations as well. Thus, even though they are sister species, *F. lugubris* and *F. paralugubris* have somewhat different ecological strategies, which may in part have emerged as a result of competition between both species.

Both *F. lugubris* and *F. paralugubris* are considered mountain species in central Europe (Cherix et al., 2007; Freitag and Cherix, 2009), which was confirmed by our survey. Our analyses revealed that *F. lugubris* mound occurrence was higher at higher elevations because of their more continental climate and higher levels of summer radiation. For *F. paralugubris* mound occurrence, elevation itself was retained as predictor, indicating that other factors correlated with elevation were important. For example, human disturbances such as urbanization, recreation pressure, and road density are known to be negatively correlated with elevation in Switzerland and are thought to negatively affect wood ants (Dekoninck et al., 2010; Sorvari, 2016). However, the ecological niche of *F. paralugubris* may also be restricted to high elevations because of natural factors we did not measure, or driven by competition from lowland species, which once may have been more abundant.

Unlike *F. paralugubris*, *F. lugubris* seemed to rely on forests with a rich vertical structure, which may harbor more abundant and more diverse prey and honeydew-producing insects (Halaj et al., 2000; Ishii et al., 2004). This suggests that, though both ant species forage in tree canopies, *F. lugubris* may depend on a more diverse range of food items than *F. paralugubris*. It is noteworthy that very high degrees of ground vegetation cover positively related with mound occurrence of both *F. lugubris* and *F. paralugubris* and of the entire *F. rufa* group. We hypothesize that ground vegetation cover protects ants from predators such as woodpeckers (Rolstad et al., 2000) and/or provides ants with insect prey, seeds, or other food resources (Gorb and Gorb, 1995; Wardle et al., 2011). Alternatively, a higher ground vegetation cover may be indicative of lower disturbance, which could benefit wood ants (Sorvari, 2016). Our findings that mound occurrence of the *F. rufa* group, *F. lugubris*, and *F. paralugubris* increased when the proportion, abundance, or dominance of conifers was higher is not surprising, as conifers harbor large colonies of honeydew-producing aphids and scales such as *Cinara* and *Physokermes* species (Domisch et al., 2016). Moreover, wood ants often incorporate conifer resin into their mounds, which suppresses the growth of microorganisms (Christe et al., 2003). Furthermore, wood ants commonly use conifer needles to build their mounds (Risch et al., 2016), although it is not clear whether this is a consequence of the higher availability of needles in coniferous forest, or whether wood ants actively select conifer needles, for example because conifer needles contain certain defense compounds and decompose more slowly than deciduous leaves (Cornelissen et al., 1999).

Our survey revealed that red wood ant occurrence was related to several aspects of forest structure and the presence of conifers, rather than on large or continuous forest fragments, the presence of or distance to forest edges, or a high tree and shrub diversity. This has an important conservation implication, as it suggests that even small or fragmented forests with relatively low woody vegetation diversity can be suitable habitat for red wood ant species, if other habitat



requirements are met. However, the potential short-term suitability of small forest fragments comes with the caveat that they are more likely to be disturbed or disappear in the future, and therefore do not provide the long-term security of large and well-connected forests. Based on our results, we propose that conservation of red wood ant species should focus on improving the structure of coniferous forests. Specifically, conservation or creation of forests with a rich variety of structures, a rather open canopy, and a high percentage of ground vegetation cover could benefit red wood ants and the ecosystem functions they provide.

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