

Land snails benefit from human alterations in rural landscapes and habitats

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Abstract. Metapopulation functioning in the context of landscape and habitat structure is generally well understood. However, in human-transformed landscapes, human disturbance may affect not only a species of interest but also biotic interactions in which that species is engaged, which has been rarely studied at multiple spatial scales. We tested (1) the associations between local (habitat and micro-habitat) and landscape factors and the occurrence and abundance of the land snail *Cepaea nemoralis* and two of its predators (thrushes and mice); and (2) the hypothesis that human disturbances modify associations between *C. nemoralis* and its predators. We surveyed snail colonies in rural landscapes of Poland. Generalized linear mixed models were used to test the stated hypotheses. At the landscape scale, the occurrence of *C. nemoralis* colonies was positively related to the cover of suitable habitats, fallow/waste land, and road length in the surrounding landscape. Bird predator abundance was positively correlated with the occurrence of snail colonies, mostly at sites with a high human impact, and was negatively correlated with snail abundance at sites with low human disturbance. Snail occurrence and abundance at the micro-habitat scale were positively correlated with variables describing the proximity of shelter and humidity. Avian predation pressure was negatively correlated with forest and settlement cover, whereas rodent predation pressure was positively associated with snail abundance and was negatively correlated with bird abundance. Human disturbance at the habitat and landscape scales benefited *C. nemoralis* through the creation of suitable habitats and scaling down of avian predation pressure. Conditions related to shelter and humidity were linked to the distribution and abundance of snails at the micro-habitat scale.

Key words: birds; human disturbance; landscape structure; micro-habitat; predation pressure; settlements; spatial scale; terrestrial gastropods.

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INTRODUCTION

In fragmented landscapes, local (i.e., relative to habitat patch) and landscape (i.e., associated with structure of area surrounding a habitat patch) factors have been shown to determine species distributions and colonization–extinction dynamics in metapopulation systems (Hanski 1994, Thomas et al. 2001). Area of suitable habitat patch and

patch isolation (i.e., the degree to which landscape structure limits dispersal among habitats) are classic predictors of species distribution and abundance (e.g., Hokit et al. 1999, Hanski and Ovaskainen 2000). However, there is growing evidence that taking into account the role of biotic factors, such as the abundance of predators or parasites, improves the predictive performance of species distribution models (Campomizzi et al.

2008, Morelli and Tryjanowski 2015). Both predation and habitat heterogeneity are related to the landscape composition (Cozzi et al. 2008, Werling and Gratton 2010), and predation pressure may depend on the cover of habitats preferred by predators and sheltered sites used by prey (Whittingham and Evans 2004, Sergio et al. 2007, Nakazawa and Huang 2016). Most landscapes are increasingly being altered by humans (Mendenhall et al. 2014), and factors related to human presence and activity (man-made structures such as roads and buildings) can be both beneficial and detrimental to species distribution and abundance (e.g., Morelli et al. 2014, Myczko et al. 2014, Tryjanowski et al. 2014) and may modify species associations (e.g., prey–predator; Skórka et al. 2016).

Terrestrial gastropods are an excellent, but usually unappreciated, model for studies on relationships between environmental variables at various spatial scales and species distributions and abundances. Due to their limited dispersal ability and high cost of locomotion, land snail species often show a metapopulation structure (Schweiger et al. 2004, Götmark et al. 2008). Moreover, terrestrial gastropods are highly susceptible to local conditions (e.g., humidity) related to the structure of habitats and micro-habitats (e.g., Moreno-Rueda 2014). In addition to environmental factors, predation may strongly affect the occurrence and abundance of land snails. Avian predation on land snail populations is a common, well-known phenomenon (Morris 1954, Cameron 1969). Additionally, rodents (especially mice) have been suggested to be important predators of terrestrial gastropods (Allen 2004), although documented examples are rare (Rosin et al. 2011). The role of humans is also expected to be significant for the occurrence and abundance of land snail species because of the synanthropic character of many of these snails (Wiktor 2004). Human impacts are mostly apparent in the alteration in snail habitats (Groom et al. 2006), creation of novel habitats (Lundholm and Richardson 2010), and direct influence on the behavior and abundance of animals (Ditchkoff et al. 2006). Humans may affect both snails and their predators, and if the relative impact differs between prey (snail) and predators (birds, rodents), then biotic interactions (prey–predator dynamics) may change. However, the interrelationships between biotic

interactions and habitat changes are poorly understood at present.

Although the land snail *Cepaea nemoralis* (L.) is among the best studied animal species, our knowledge of the factors driving its distribution and abundance at landscape and (micro)-habitat scales is incomplete. This snail inhabits a wide range of habitats, from sand dunes to psammophilic vegetation to meadows and woodlands (Cook 1998). However, outside its primary range (e.g., central and southern Poland), this snail shows a highly synanthropic character (Wiktor 2004). Rural landscapes, as a mosaic of agricultural fields, mid-field patches of unmanaged land, human settlements, and the associated infrastructure, may be highly heterogeneous in terms of suitability for *C. nemoralis* and, thus, generate a patchy distribution of this species (Schweiger et al. 2004). Many *C. nemoralis* colonies show traces of avian and/or mammalian predation, with adjacent anvils of thrushes or scattered shell fragments gnawed by mice (Rosin et al. 2011). In Europe, *C. nemoralis* is hunted most heavily by the song thrush (*Turdus philomelos*) and mice (Morris 1954, Allen 2004).

The preference of *C. nemoralis* for habitats associated with humans enables testing of whether human activity modifies predator–prey associations. Some thrush species reside in the vicinity of human settlements (blackbird, *Turdus merula*; fieldfare, *Turdus pilaris*; song thrush), but all of these birds display fear behavior in response to human, although at variable levels (Møller 2010, Mikula et al. 2014). Thus, it is possible that snails benefit from the presence of humans because of lower predation pressure due to the disturbance of thrushes. However, an opposite association may be expected in the case of rodents, which often occur near humans (Baker and Harris 2007).

To the best of our knowledge, no study has yet attempted to integrate various spatial scales and include factors of various characters (i.e., abiotic, biotic, and human related) to explain the occurrence and abundance of a low-mobility species. Moreover, the relationships between a prey species and its predators are poorly understood in the context of their interactions with environmental factors related to humans (Skórka et al. 2016). Thus, the aims of this study were to (1) test the associations between landscape and local (micro) habitat factors and the occurrence and abundance

of *C. nemoralis* in fragmented rural landscapes; (2) test the relationships between landscape and local factors and the abundance of predators and predation pressure on *C. nemoralis*; and (3) test the assumption that landscape and local factors related to humans modify the associations between *C. nemoralis* and its predators.

METHODS

Study areas

Surveys were conducted in three large landscape plots located in rural landscapes near Gdańsk (plot area 251 km²), Poznań (252 km²), and Odolanów (394 km²) in Poland (Fig. 1). Searches for *Cepaea nemoralis* colonies were

performed in randomly selected potential habitats (fallow/waste land, hedges, forest edges). Altogether, 75 colonies were found, and 62 suitable but empty sites were chosen for comparison of their environmental features. *Cepaea* spp. exhibit a low dispersal rate, with the length of a panmictic unit being 40–50 m (Le Mitouard et al. 2010). The distribution of the dispersal of these snails is right-skewed and leptokurtic (Davison 2000), meaning that most individuals cover short distances, and only few disperse over intermediate and long distances (Schweiger et al. 2004). Therefore, we regarded two colonies as separate units if the distance between them was at least 100 m. The colony area subjected to surveys ranged from 100 to 500 m², depending on colony size: Colonies

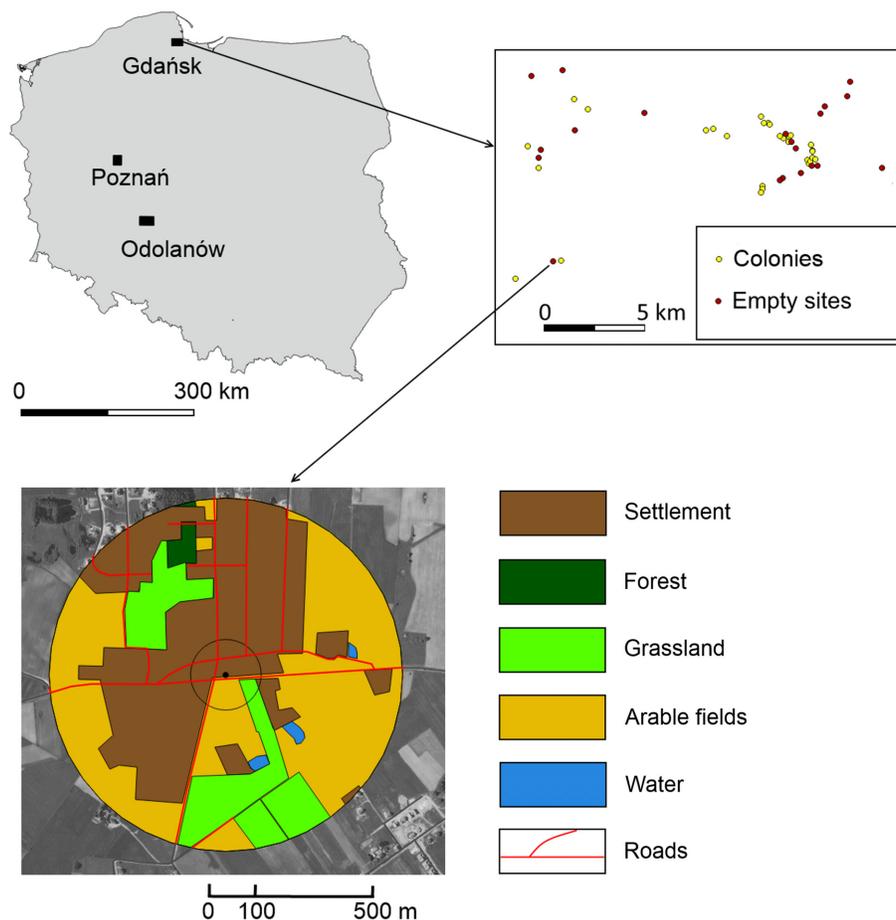


Fig. 1. Map of Poland with the locations of the studied landscapes, the distribution of sampled colonies and random empty sites within one of the landscapes, and an example of the landscape composition within 100 and 500 m radii.

that did not exceed 500 m² were investigated in their entirety, whereas larger colonies (6% of all studied colonies) were surveyed in an area of 500 m² (to maintain the area of one panmictic unit; Lamotte 1951, Le Mitouard et al. 2010). The majority of the identified colonies (86%) were located in fallow/waste land, while only a few were located in forest ecotones (11%) or orchards (3%). The geographic position of each colony and unoccupied site was marked with Global Positioning System (GPS) receiver (Garmin, GPSMAP 62s, Southampton, UK). No other *Cepaea* species were observed in the analyzed plots.

Data collection

Each colony was visited three times: between 1 May and 30 June, between 1 July and 31 August and between 1 September and 31 October 2012, whereas empty patches were visited only once. Surveys were conducted in conditions that were favorable for snail activity between 06:00 and 11:00. In each colony, the snails were counted in 50 × 50 cm squares, spaced 5 m apart along a transect of 20 m (5 squares per transect). Depending on the colony area, the number of transects ranged from 1 to 5, and the distance between adjacent transects was 5 m. The location of the square plots and the number of transects in a colony were not the same during the three visits (i.e., they varied across visits), with the latter depending on colony area. Three main groups of explanatory variables were determined: (1) the structure of the habitat and the surrounding landscape; (2) micro-habitats; and (3) predation.

Variables describing landscape composition and habitat structure and quality.—Three habitat variables were determined for occupied and unoccupied habitat patches:

1. Area of suitable habitat (m²): Patch area is one of the most important predictors of species occurrence and abundance in fragmented landscapes (Hanski and Ovaskainen 2000), and the suitable habitat for *C. nemoralis* in our study area encompasses waste/fallow land (unmanaged or mowed, barely herbaceous and grass strips, sometimes with spontaneously emerging shrubs and trees) and forest edges (Ożgo 2005);
2. The percentage cover of trees and shrubs (%) within an area of 500 m²: determined as

a measure of the percentage of shaded area, as trees and shrubs provide shelter for snails in terms of both the risk of predation and harsh conditions (e.g., extreme temperatures, Jaremovic and Rollo 1978);

3. Human impact in the habitat patch: estimated by noting the presence of rubbish such as plastic bottles, bags, or bar packaging (94.4% of all contaminated habitat patches), bricks, (13.0% of contaminated habitat sites) and garden waste (24.2%) within area of 500 m². All of these items were often mixed together at a single site. Human activity may benefit snails due to involuntary dispersion of snails (Ożgo 2005, Cameron et al. 2009), but a negative effect of the presence of rubbish is also possible (Browne et al. 2013). Moreover, human presence may cause a fear response in birds (Møller 2010) and in turn influence avian predation on snails.

For each colony and randomly chosen empty site, the landscape composition within 100 and 500 m radii was assessed using high-resolution aerial photographs freely available from Geoport (http://geoportal.gov.pl/). We also used vector layers available from the OpenStreetMap project (http://www.openstreetmap.org/). All of these data were verified and corrected by direct mapping in the field. We noted the following variables (Appendix S1: Table S1):

1. Fallow/waste land cover (%): Fallow land and waste land are suitable habitats for *C. nemoralis* (Wiktor 2004) and may therefore facilitate species persistence and dispersal;
2. Forest cover (%): Coniferous forest (prevailing in our research areas) is unsuitable habitat for *C. nemoralis* (Wiktor 2004) and may act as a barrier for dispersal;
3. Grassland cover (%): *C. nemoralis* has been reported to inhabit grasslands (Cook 1998); however, according to our unpublished observations, it is usually absent from this habitat type, at least in western Poland;
4. Arable field cover (%): Agricultural crops are unfavorable habitat types for land snails and act as a barrier to dispersal (Schweiger et al. 2004);

5. Water cover (%): The presence of ponds and other water bodies may increase the probability of the presence of land snails by creating a favorable micro-climate;
6. Human settlement cover (%): Garden plots, orchards, and patches of unmanaged land associated with human settlements favor the presence of *C. nemoralis* (Wiktor 2004); this variable is also a proxy of human impact;
7. Road length (m): Road verges may serve as good habitat and corridors enabling dispersion in fragmented landscapes (Arnaud 2003); however, roads may also negatively influence snails due to animal mortality associated with traffic.

All calculations were performed in Quantum GIS 2.0 (QGIS, Boston, Massachusetts, USA).

During each survey, temperature and humidity were determined using a portable weather station (La Crosse WS2355).

Variables describing micro-habitat structure.—Micro-habitat structure was assessed within the square plots (50 × 50 cm) where the snails were surveyed. In each square, the following variables were determined (Appendix S1: Table S1):

1. Mean height of vegetation (cm): Based on five random measurements of herbaceous plants, the height of plants may positively influence the presence and abundance of snails, as tall herbaceous vegetation may provide shelter against avian predators, extreme temperatures, and dryness (Jaremovic and Rollo 1978);
2. Percentage cover of dead and live vegetation as well as bare ground (%): Both dead and live plants are the basis of the *C. nemoralis* diet (Williamson and Cameron 1976), with live vegetation potentially being more beneficial than dry, dead vegetation because of its higher moisture content; moreover, depending on the background type, the conspicuousness of snails varies, meaning that bare ground is the riskiest background type in terms of predation (Surmacki et al. 2013);
3. Distance to the nearest shrub and tree (m): Shrubs and trees benefit snails as described above;
4. Additionally, each 50 × 50 cm square plot was classified as shaded or open (0/1): At a

micro-habitat scale, shade may be present or not, depending on the time of day, and snails may actively search for shade.

Predators and predation pressure.—As a measure of the density of avian predators, the number of thrushes (song thrush, blackbird, fieldfare, and mistle thrush (*Turdus viscivorus*), which are the main predators of *C. nemoralis*) breeding within a 50 m radius from the center of a colony or empty site was noted (Appendix S1: Table S1). Initially, rodent holes were counted in the square plots as an indicator of rodent abundance (Mitchell and Balogh 2007). However, the number of rodent holes found was quite low (1.8 holes per colony) and did not allow any reasonable statistical analysis; therefore, we used traces of rodent predation instead (see *Statistical analyses*). Shells showing traces of predation by birds or rodents were counted in the square plots as direct evidence of predation and its impact. Only fresh shells were counted (bleached, past-year shells were excluded). Shell damage was attributed to birds based on marks from strikes on the left part of the last whorl, whereas it was attributed to rodents based on teeth marks on the aperture (Rosin et al. 2011). The shells were then collected. These indexes of predation pressure were estimated during each visit in a snail colony.

Statistical analyses

In the first step, we used bootstrapped correlations (1000 bootstraps) to explore the relationships between variables, and some landscape variables were strongly correlated within and between 100 and 500 m radii from a patch (Appendix S1: Table S2). To avoid multi-collinearity, we excluded from further analyses those variables showing a variance inflation factor (VIF) > 2 (Zuur et al. 2010). The cover of forest, grassland, fallow/waste land and human settlements, and the length of roads within a 100 m radius were included in the further analyses of site occupancy. At a micro-habitat scale, dry and live vegetation cover and bare ground cover were also significantly correlated ($-0.67 < r < -0.37$); thus, based on VIF, we used only cover of dry vegetation and bare ground in further analyses.

Landscape and habitat scale processes.—We used generalized linear mixed models (GLMMs) to relate environmental variables to the occurrence and abundance of *C. nemoralis* colonies, their

predators, and the predation pressure on snails at various spatial scales. A GLMM is an extension of a linear mixed model (a linear model that incorporates random effects) that deals with non-normal error distributions or heteroscedasticity of the response variable using link functions. The link function transforms the response variable with the error distribution from the exponential family (e.g., Poisson or negative binomial for count data; Bolker et al. 2009). The data are then fit at this transformed scale, but the expected variance is calculated at the original scale of the predictor variables. The “glmmADMB” package (Fournier et al. 2012, Skaug et al. 2014) implemented in R was used for all of the GLMMs. In all GLMMs, the variables were standardized to allow a direct comparison of beta (slope) estimates. Some variables were log-transformed.

As we hypothesized that the relationships between the occurrence and abundance of snails and their predators may be modified by landscape and local factors related to humans, we included the following interaction terms in the respective models: number of bird predators \times cover of human settlements within 100 m and number of bird predators \times presence of waste.

To test the associations between snail colony occurrence and variables related to landscape and habitat, we used a GLMM with binomial error variance and a logit link function. The dependent variable was the presence/absence of at least one snail in a habitat patch during any visit. The explanatory variables were as follows: habitat patch area, percentage of shading, fallow/waste land cover within a 100 m radius from the colony center or random empty site and, accordingly, the percentage cover of grassland, forest, human settlements and road length, number of bird predators (number of *Turdus* spp. within a 50 m radius; Appendix S1: Table S1), number of bird predators \times presence of waste, and number of bird predators \times cover of human settlements within 100 m. Landscape identity was included as a random effect.

To identify associations between snail abundance in colonies and variables related to landscape and habitat, we used a GLMM with negative binomial error variance and a log link function. The explanatory variables were as follows: visit (categorical variable), habitat patch area, percentage of shading, cover of fallow/

waste land, forest, and human settlements within a 100 m radius from the colony center, number of shells damaged by birds and rodents (as a proxy of predation pressure), number of bird predators (Appendix S1: Table S1), number of bird predators \times presence of waste, and number of bird predators \times cover of human settlements within 100 m. Colony and landscape identities were included as random effects.

To analyze how the features of the habitat patches (occupied and unoccupied by *C. nemoralis*) and the surrounding landscape affect the abundance of bird predators, we used a GLMM with negative binomial error and a log link function. The dependent variable was the number of breeding individuals of *Turdus* spp. noted during a visit in an empty patch (i.e., with *C. nemoralis* absent) and during the first visit at an occupied site (i.e., with *C. nemoralis* present). This procedure was adopted to maintain the comparability of these two types of site. The explanatory variables were as follows: *C. nemoralis* presence/absence, habitat patch area, percentage of shading, fallow/waste land cover within a 100 m radius from the colony center or a random empty site, and, accordingly, the percentage cover of grassland, forest, human settlements, and road length. Landscape identity was included as a random effect.

To analyze how the features of the habitat patches and the surrounding landscape affect the predation pressure from birds (number of snail shells damaged by birds in a colony) and rodents (number of snail shells damaged by rodents in a colony), we used GLMMs with Poisson and negative binomial error variances, respectively, and log link functions. The explanatory variables were as follows: visit, habitat patch area, percentage of shading, fallow/waste land, forest, and human settlement cover within a 100 m radius from the colony center, abundance of bird predators, and number of shells damaged by the other predator (bird or mouse; Appendix S1: Table S1). We also included snail abundance as covariate to account for the obvious relationship between the numbers of snails and damaged shells. Landscape identity and colony identity were included as random effects. Zero inflation was accounted for in a model describing avian predation pressure, due to an excessive number of zeros in the data.

In addition, we performed analysis of predation pressure based on the proportions of

damaged shells. The dependent variables were the proportion of shells damaged by birds (number of shells damaged by birds divided by total number of damaged shells and live snails) and the proportion of shells damaged by rodents (number of shells damaged by mice divided by the total number of damaged shells and live snails). The GLMMs with a Gaussian error distribution and identity link function were used. The explanatory variables were the same as in the models based on shell counts.

Micro-habitat scale.—We analyzed how the features of the small plots (50 × 50 cm) affected the distribution (occurrence and abundance) of snails at a micro-habitat scale. To analyze the factors affecting the occurrence and the number of snails within these plots, we used GLMMs with binomial or negative binomial error variances and logit or log link functions, respectively. The explanatory variables included in the models were as follows: visit, mean vegetation height, percentage cover of dry, dead and live vegetation, and distance to the nearest shrub or tree. The following random categorical effects were included: landscape identity, colony identity, and plot identity. Zero inflation was accounted for in a model describing snail occurrence in these square plots because of an excessive number of zeros in the data.

Model selection.—We used multi-model inference (Burnham and Anderson 2002) to identify the models that best described the data at each spatial scale (landscape and local). For this purpose, Akaike's information criterion (AIC_c) was calculated for each possible model with the aid of the "MuMIn" package (Bartoń 2014). Models showing a $\Delta AIC_c < 2$ (Burnham and Anderson 2002) were assessed as worth considering in the set of competing models, and conditional model averaging (averaged over the models where the parameter appears, Bartoń 2014) was performed within that set. Averaged parameter estimates were presented as a final result of this modeling.

RESULTS

In total, 3841 live *Cepaea nemoralis* individuals were found in three landscape plots, with a mean abundance per colony per visit of 17.2 individuals \pm SD = 22.4 (min = 0, max = 146); additionally, 347 snails that had been killed by rodents

and 173 killed by birds were found (Appendix S2: Fig. S1).

The occurrence of *C. nemoralis* colonies was positively related to the cover of fallow/waste land and road length within a 100 m radius (Table 1; Appendix S1: Table S3). There was a significant interaction between the number of thrushes and the cover of settlements in the best models explaining colony occurrence (Table 1, Fig. 2; Appendix S1: Table S3). The cover of settlements in the surrounding landscape was a positive predictor of *C. nemoralis* occurrence, but only at sites with a high abundance of thrushes (Fig. 2).

The abundance of snails within colonies was positively associated with road length within a 100 m radius, habitat patch size, and the number of shells damaged by birds (Table 1; Appendix S1: Table S3). Forest cover, thrush abundance, and the presence of waste were significant negative predictors of *C. nemoralis* abundance (Table 1; Appendix S1: Table S3). At sites with waste, however, the relationship between the abundance of birds and snails was weak, resulting in a significant interaction between thrush abundance and waste (Table 1, Fig. 3; Appendix S1: Table S3). The number of snails was lower at the second and third visits compared with the first (Table 1; Appendix S1: Table S3).

Snail occurrence and abundance at the micro-habitat scale were negatively correlated with the cover of dry vegetation and the distance to the nearest shrub or tree and positively related to the height of herbaceous vegetation (Table 1; Appendix S1: Table S3). Shadow was a positive predictor of snail numbers within small plots (Table 1; Appendix S1: Table S3). The probability of snail occurrence and snail numbers were lower during the second and third visits compared with the first visit (Table 1; Appendix S1: Table S3).

The number of thrushes breeding within a 50 m radius from the study sites was negatively associated with the cover of human settlements and road length within a 100 m radius (Table 2; Appendix S1: Table S4). Colony presence was a significant positive predictor of thrush abundance (Table 2; Appendix S1: Table S4).

The number of shells damaged by birds was negatively correlated with the cover of forest and settlements within a 100 m radius and positively related to thrush abundance (Table 2; Appendix S1: Table S4). Mouse predation pressure was positively

Table 1. Averaged parameter estimates (and 95% CIs) for the generalized linear mixed models explaining the occurrence and abundance of *Cepaea nemoralis* at landscape–habitat and micro-habitat scales.

Model description	Predictor	Estimate	−95% CI	+95% CI	
Landscape–habitat scale					
Colony occurrence ΔAIC _c null = 154.15	Intercept	−0.216	−1.537	1.105	
	Fallow100	1.012	0.415	1.609	
	Settle100	0.217	−0.299	0.733	
	Road100	0.574	0.040	1.109	
	Patch size	0.539	−0.067	1.146	
	ShadedCov	0.335	−0.133	0.802	
	Waste (present)	0.713	−0.237	1.663	
	ThrushN	0.221	−0.262	0.703	
	ThrushN × Settle100	0.050	0.005	0.096	
	ThrushN × Waste	0.304	−0.228	0.837	
	Snail abundance in colonies ΔAIC _c null = 1584.04	Intercept	2.989	2.593	3.385
Fallow100		−0.081	−0.281	0.120	
Settle100		0.109	−0.119	0.338	
Road100		0.237	0.047	0.428	
Forest100		−0.362	−0.592	−0.131	
Patch size		0.237	0.033	0.440	
ShadedCov		0.179	−0.026	0.384	
Waste (present)		−0.652	−1.125	−0.178	
ThrushN		−0.678	−1.005	−0.351	
ThrushN × Waste		0.363	0.102	0.623	
ThrushN × Settle100		−0.004	−0.009	0.002	
DamBird		0.251	0.122	0.381	
DamRodent		0.104	−0.017	0.226	
Visit 2		−0.674	−0.876	−0.472	
Visit 3	−0.882	−1.099	−0.666		
	Visit 1	0†			
Micro-habitat scale					
Snail occurrence ΔAIC _c null = 3183.62	Intercept	1.858	−2.433	6.149	
	DryPlant	−0.379	−0.628	−0.130	
	BareGround	0.215	−0.018	0.449	
	VegHeight	2.020	1.553	2.487	
	DistShrubTree	−2.325	−2.866	−1.783	
	Shade (present)	0.237	−0.375	0.848	
	Visit 2	−0.996	−1.503	−0.489	
	Visit 3	−1.602	−2.143	−1.061	
		Visit 1	0†		
	Snail abundance ΔAIC _c null = 8163.80	Intercept	−0.005	−1.039	1.029
DryPlant		−0.213	−0.273	−0.153	
BareGround		−0.053	−0.111	0.005	
VegHeight		0.008	0.005	0.010	
DistShrubTree		−0.361	−0.439	−0.283	
Shade (present)		0.247	0.075	0.420	
Visit 2		−0.322	−0.435	−0.210	
Visit 3		−0.564	−0.693	−0.434	
	Visit 1	0†			

Notes: CI, confidence interval; AIC_c, Akaike’s information criterion. For each set of models, ΔAIC_c of the null model is given, and parameters that did not overlap with zero are indicated in bold. The abbreviations for the predictors are given in Appendix S1: Table S1. For a list of the best models, see Appendix S1: Table S3.

† Reference category.

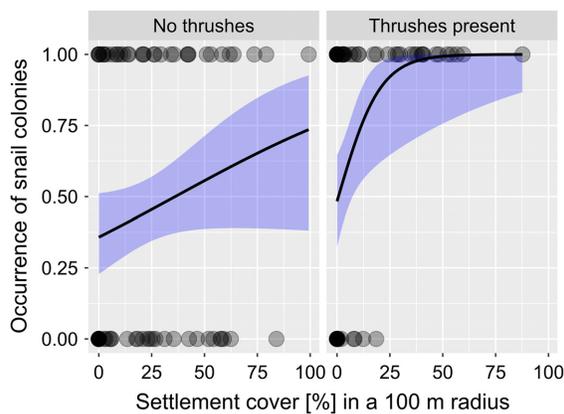


Fig. 2. Probability of *Cepaea nemoralis* colony occurrence in relation to the percentage cover of settlements in a 100 m radius at sites where thrushes (*Turdus* spp.) were absent (left panel) and present (right panel). The shaded area corresponds to the 95% confidence interval.

associated with snail abundance within a colony and was negatively correlated with bird abundance (Table 2; Appendix S1: Table S4). The number of shells damaged by birds and mice was highest during the first visit (Table 2; Appendix S1: Table S4). Models based on proportions showed that the proportion of shells damaged by birds was explained only by the abundance of snails, and the proportion of shells damaged by mice was negatively correlated with bird predatory pressure (Appendix S1: Tables S5, S6).

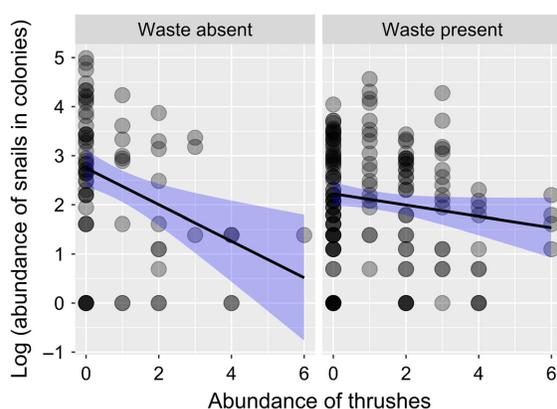


Fig. 3. Relationship between the abundance of *Cepaea nemoralis* and thrushes (*Turdus* spp.) at sites where waste was absent (left panel) and present (right panel). The shaded area represents the 95% confidence interval.

DISCUSSION

Among the many studies on the effects of landscape characteristics on patterns of animal occurrence and abundance, only a few have addressed biotic interactions and their dependency on environmental variability (Heikkinen et al. 2007, Baker et al. 2014, Morelli and Tryjanowski 2015, Skórka et al. 2016). Moreover, the associations between species occurrence and abundance and certain environmental characteristics are considered to be species specific and invariable, due to the assumption that some of these environmental characteristics determine individual fitness (Morris 2011). However, in our complex, multi-scale study, we showed that biotic interactions may change due to human-related alterations in these environmental characteristics. Specifically, it seems that associations between prey (snail) and predators (birds, rodents) depend on the level of human-related change at both landscape and habitat scales. Human-related factors are inevitably important in determining patterns of animal distribution and biotic interactions because urbanization is one of the most prominent processes affecting ecosystems and species worldwide (e.g., Foley et al. 2005, Clergeau et al. 2006).

Occurrence and abundance of the land snails in the landscape and habitat patches

At the landscape scale, the number of suitable habitats and corridors significantly predicted snail occurrence and/or abundance, whereas at the local scale, area of habitat patches, bird predator abundance, and predation pressure were important.

Schweiger et al. (2004) showed that the *Cepaea nemoralis* snails inhabiting agricultural landscapes in Germany exhibit a metapopulation structure, which depends on landscape features and the shape of the dispersal function. We showed that the occurrence of *C. nemoralis* in Polish rural landscapes was positively related to the percentage cover of fallow and waste land within a 100 m radius from a site. Agriculture in Poland underwent large changes in the 1990s, with a substantial area being abandoned, accounting for approximately 14% of the land in Poland at the beginning of the 2000s (Dmochowska 2014). Abandoned parcels of land are still often present in Polish

Table 2. Averaged parameter estimates (and 95% CIs) of the generalized linear mixed models explaining the abundance of thrushes (*Turdus* spp.) within a 50 m radius from sites occupied/unoccupied by *Cepaea nemoralis* and the avian and mouse predation pressure (numbers of shells damaged by thrushes and mice, respectively) exerted on the studied colonies of *C. nemoralis*.

Description	Predictor	Estimate	SE adj	-95% CI	+95% CI
Thrush abundance ΔAIC_c null = 332.31	Intercept	-0.337	0.481	-1.279	0.606
	Fallow100	0.132	0.137	-0.136	0.400
	Settle100	-0.299	0.152	-0.596	-0.002
	RoadLength100	-0.288	0.144	-0.571	-0.006
	Patch size	-0.090	0.048	-0.184	0.003
	Colony presence	0.785	0.255	0.284	1.285
	ShadedCov	0.116	0.105	-0.090	0.322
	Waste (present)	0.293	0.256	-0.210	0.796
Avian predation pressure ΔAIC_c null = 341.47	Intercept	-1.302	0.669	-2.613	0.008
	Settle100	-0.755	0.296	-1.335	-0.175
	Road100	-0.428	0.372	-1.156	0.300
	Forest100	-0.428	0.204	-0.827	-0.029
	Patch size	0.246	0.246	-0.236	0.728
	ShadedCov	0.056	0.231	-0.396	0.508
	Waste (present)	0.985	0.589	-0.170	2.140
	ThrushN	1.798	0.320	1.171	2.424
	SnailN	0.305	0.169	-0.026	0.636
	DamRodent	0.149	0.130	-0.105	0.403
	Visit 2	0.081	0.294	-0.495	0.657
Visit 3	-3.745	0.681	-5.079	-2.410	
Visit 1	0†				
Mouse predation pressure ΔAIC_c null = 601.48	Intercept	-0.914	0.708	-2.301	0.473
	Road100	-0.433	0.227	-0.879	0.012
	Patch size	0.188	0.312	-0.422	0.799
	Waste (present)	0.908	0.514	-0.100	1.915
	ThrushN	-0.368	0.182	-0.725	-0.010
	SnailN	0.276	0.133	0.015	0.536
	DamBird	0.082	0.119	-0.151	0.315
	Visit 2	-1.009	0.236	-1.472	-0.546
	Visit 3	-0.311	0.247	-0.794	0.173
	Visit 1	0†			

Notes: CI, confidence interval; AIC_c , Akaike's information criterion. For each set of models, ΔAIC_c of the null model is given, and parameters that did not overlap with zero are indicated in bold. The abbreviations of the predictors are given in Appendix S1: Table S1. For a list of the best models, see Appendix S1: Table S4.

† Reference category.

farmland, and we believe that this may enhance the functioning of metapopulations of this species, as the amount of suitable habitat in the surrounding landscape positively affects species occurrence in a patch, due to making dispersal and thus gene flow more likely (Hanski and Gaggiotti 2004). Population persistence is usually facilitated by the area of the occupied patch (Hanski 1994, Hanski and Ovaskainen 2000), which was also reflected in our results, as snail abundance was positively correlated with the habitat patch area.

Snail occurrence and abundance were also positively associated with road density, which is

one of the indices of human impact at the landscape scale. The positive response of snails to roads and fallow/waste land may indicate a strong synanthropic character of this species and a human contribution to *C. nemoralis* dispersion (e.g., Ożgo 2005, Cameron et al. 2009). Road verges act as dispersal corridors for many taxa (Trombulak and Frissell 2000, Arnaud 2003) and may therefore positively affect both the occurrence and abundance of individuals within colonies. In contrast, one natural land cover type, forests, was generally found to be avoided by these snails. Forests may constitute a dispersal

barrier and a main habitat for potential bird predators such as thrushes.

We suspect that the waste from garden plots, thrown away by people in rural landscapes (a common behavior in the study area), may be an important mechanism of the colonization of new areas and spreading of this species. However, the presence of waste was found to be negatively correlated with snail abundance. As waste includes unpalatable components such as plastics and inorganic residues, it may negatively influence snails (Browne et al. 2013) and cancel out the effect of waste from gardens.

Importance of micro-habitat variability in the distribution of snails within a habitat patch

The features of a micro-habitat are important for organisms characterized by low mobility, high susceptibility to predation, and the impact of such factors as temperature, light, and humidity (Cameron 1969, 1970a, b, Ożgo and Kubea 2005, Rosin et al. 2011). Most of the studied variables related to micro-habitat were found to be significantly associated with the distribution of individuals within colonies and abundance within micro-habitat plots.

Vegetation height and the proximity of trees or shrubs positively correlated with the occurrence and abundance of snails in plots within a colony. Similar to our results, *Cepaea hortensis* was previously found to be strongly associated with shrubs (Le Mitouard et al. 2010). Trees, shrubs, and tall herbaceous vegetation act as a shelter for snails. Thrushes, which are the main predators of *Cepaea* species, strongly prefer to search for prey on open ground with short vegetation (Skórka and Wójcik 2005), and terrestrial gastropods avoid predation by climbing on plants (Lefcort et al. 2006). Additionally, variable weather conditions may trigger climbing behavior (Jaremovic and Rollo 1978), and an increased presence of shrubs and trees therefore allows unrestricted behavioral responses to these factors. Snails were more abundant in shaded micro-habitat plots, which suggests active avoidance of direct solar radiation and/or predation (Ożgo and Kubea 2005, Rosin et al. 2011).

Snail occurrence and abundance within micro-habitat plots were significantly negatively related to dry plant cover. The diet of *C. nemoralis* consists of both dead and live vegetation

(Williamson and Cameron 1976). Dry dead vegetation may be a substrate that is stressful to snails because of its low humidity and the fact that rodents prefer such vegetation.

Possible moderation of the association between snails, predators, and their pressure by landscape and habitat variables

Some recent theoretical and empirical models have shown that prey–predator relationships may be mediated by their interactions with species-specific habitat preferences (Nakazawa and Huang 2016, Skórka et al. 2016). Our results confirm these assumptions and indicate that some subtle factors like human activity at the local scale as well as human moderations at the landscape scale may alter prey–predator relationships.

Cepaea nemoralis abundance was strongly negatively associated with thrush abundance, which indicates that these birds are indeed an important predator of our study species (Morris 1954, Cameron 1969). However, at sites characterized by a high human impact (with waste present), this relationship was rather weak, suggesting that human activity significantly negatively affects predatory activity of thrushes and/or their abundance. Most papers addressing human-induced changes in predator–prey relationships have considered human impacts at the landscape level, such as associations of human-related habitats and structures (e.g., Fusser et al. 2016, Skórka et al. 2016). Our results highlight the importance of human activity per se as a factor contributing to changes in predator–prey relationships. Moreover, the probability of colony occurrence was positively related to bird abundance, but only at sites with high coverage of human settlements in the surrounding landscape, suggesting that at the landscape scale, thrushes follow *C. nemoralis* but do not drive colonies to extinction at sites characterized by high human impact. This finding was supported by the results of GLMM for avian predation pressure, where the percentage cover of human settlements was a significant negative predictor of the avian pressure. Human presence may disturb birds, leading to, for example, reduced food acquisition and breeding success (Blumstein 2006, Møller 2009, Mikula et al. 2014). Thrush populations inhabiting rural areas show an elevated fear response to humans compared with

those residing in urban areas (Møller 2010); thus, it is possible that the proximity of humans is especially beneficial for snails occurring in rural landscapes. *Cepaea nemoralis* abundance was significantly positively correlated with the presence of traces of avian predation on *C. nemoralis*. This result may indicate direct behavioral and numerical responses of predators to prey abundance (Kareiva 1987).

Similar to snails, the predators also responded to habitat and landscape features, implying that the predatory impact on snails may be altered by these factors. The number of thrushes was positively related to the presence of *C. nemoralis* colonies and negatively related to road density and the cover of human settlements. Thrushes usually breed in woods and parks, and some thrush species (*Turdus philomelos*, *T. viscivorus*) avoid the vicinity of human buildings (Mikula et al. 2014). Roads may negatively influence birds due to disturbance and mortality caused by collisions with cars (Orłowski 2008, Fahrig and Rytwinski 2009). Interestingly, avian predators were found to occur more frequently in areas with snail colonies than in random empty sites after controlling for other confounding factors. This finding may suggest that the presence of snails is an important factor influencing breeding site selection by thrushes. Predation by birds was significantly negatively associated with the cover of human settlements and forest in the surrounding landscape. Human proximity may negatively affect bird behavior and their success of predation, as described above. The negative relationship between forest cover in the surrounding landscape and bird predation pressure may be associated with the lower abundance of snails at sites with a large amount of forest in the vicinity.

The number of shells damaged by mice was also positively related to snail abundance, which indicates a rapid numerical response of these predators to snail populations. Rodents with relatively small home ranges (Rogers and Gorman 1995) may respond to the population size of snails quickly, which may result in a positive prey–predator relationship. As land snails are a rather secondary prey type, mice may moderately exploit snail populations. However, we found more shells that were damaged by rodents than by birds within the investigated colonies. However, this result should be treated carefully

because birds often carry prey away from colonies, and some of the shells predated by birds might therefore have gone undetected. Birds are highly mobile, and their distribution and predatory impact therefore shape population occurrence at larger spatial scales. Moreover, our indexes of predation pressure did not include the eggs and juveniles consumed by mice and birds, as we were not able to detect such incidents. Additionally, models of predation pressure by mice and birds calculated based on the proportion of damaged shells did not confirm the above conclusions. The discrepancy between the two sets of models suggests that predation pressure should be investigated in future studies, including direct behavioral observations and experiments where the impact of other confounding variables is limited.

Temporal trend

In almost all models describing the abundance and occurrence of snails and damaged shells, we detected a significant effect of the visit. Compared with the first visit (May–June), there were significantly lower numbers of snails and shells during the second and third visits (July–August and September–October, respectively). This difference may be associated with increasing dispersion and/or elevated mortality, due to less favorable conditions in summer and autumn, in line with the findings of Aubry et al. (2005), who reported a decreased rate of *Xeropicta derbentina* recaptures in autumn compared with spring. However, we cannot judge whether this is a universal pattern, as our data are based on only one year, with no replication in different years.

CONCLUSIONS

The present study is among the few to model prey–predator associations taking into account interactions with environmental variables at various spatial scales. We highlight the importance of factors associated with humans that may affect various species in different ways and in turn interact with interspecific relationships. The relationship between snail populations and bird predators was found to depend on human impacts, being strongly negative at sites characterized by low human disturbance and neutral at sites with a high human impact.

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