

Spatial prediction of species' distributions from occurrence-only records: combining point pattern analysis, ENFA and regression-kriging

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Abstract

A computational framework to map species' distributions (realized density) using occurrence-only data and environmental predictors is presented and illustrated using a textbook example and two case studies: distribution of root vole (*Microtus oeconomus*) in the Netherlands, and distribution of white-tailed eagle nests (*Haliaeetus albicilla*) in Croatia. The framework combines strengths of point pattern analysis (kernel smoothing), Ecological Niche Factor Analysis (ENFA) and geostatistics (logistic regression-kriging), as implemented in the `spatstat`, `adehabitat` and `gstat` packages of the R environment for statistical computing. A procedure to generate pseudo-absences is proposed. It uses Habitat Suitability Index (HSI, derived through ENFA) and distance from observations as weight maps to allocate pseudo-absence points. This design ensures that the simulated pseudo-absence points fall further away from the occurrence points in both feature and geographical spaces. After the pseudo-absences have been produced, they are combined with occurrence locations and used to build regression-kriging prediction models. The output of prediction are either probability of species' occurrence or density measures. Addition of the pseudo-absence locations has proven effective — the adjusted R-square increased from 0.71 to 0.80 for root vole (562 records), and from 0.69 to 0.83 for white-tailed eagle (135 records) respectively; pseudo-absences improve spreading of the points in feature space and ensure consistent mapping over the whole area of interest. Results of cross validation (leave-one-out method) for these two species showed that the model explains 98% of the total variability for the root vole, and 94% of the total variability for the white-tailed eagle. The framework could be further extended to Generalized multivariate Linear Geostatistical Models and spatial prediction of multiple species. A copy of the R script and detailed instruction on how to run such analysis are available via contact author's website.

Key words: spatial prediction, pseudo-absence, R, `adehabitat`, `gstat`, `spatstat`

1 Introduction

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A Species Distribution Model (SDM) can be defined
as a statistical/analytical algorithm that predicts (ei-
ther actual or potential) distribution of a species, given
field observations and auxiliary maps, as well as ex-
pert knowledge. A special group of Species Distribution
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1 Models (SDMs) focuses on the so-called ‘*occurrence-*
2 *only records*’ — pure records of locations where a
3 species occurred (Elith et al., 2006). The most fre-
4 quently used techniques to generate species’ distribution
5 from occurrence-only records seem to be various kernel
6 smoothing techniques, the Environmental-Niche Factor
7 Analysis (ENFA) approach of Hirzel and Guisan (2002),
8 the Genetic Algorithm for Rule-Set Prediction (GARP)
9 approach of Stockwell and Peters (1999), and the Max-
10 imum entropy method (Maxent) introduced by Phillips
11 et al. (2006). It has never been proven that any of
12 these techniques outperforms its competitors. Zaniwski
13 et al. (2002) evaluated performance of General Additive
14 Models versus ENFA models and concluded that ENFA
15 will likely be better in detecting the potential distri-
16 bution hot-spots, especially if occurrence-only data is
17 used. Tsoar et al. (2007) compared six occurrence-only
18 methods for modeling species distribution (BIOCLIM,
19 HABITAT, Mahalanobis distance method, DOMAIN,
20 ENFA, and GARP), and concluded that GARP is sig-
21 nificantly more accurate than BIOCLIM and ENFA;
22 other techniques performed similarly. Jiménez-Valverde
23 et al. (2008b) argue whether it is sensible to compare
24 SDMs that conceptually aim at different aspects of spa-
25 tial distribution at all — there is especially big differ-
26 ence between models predicting potential and realized
27 distributions (although both are put under SDM).

28 So far, geostatistical techniques have not yet been
29 used to generate (realized) species’ distributions us-
30 ing occurrence-only data, mainly for two reasons: (1)
31 absence locations are missing (‘1’s only), so that it is
32 not possible to analyze the data using e.g. indicator
33 geostatistics; and (2) the sampling is purposive and
34 points are often clustered in both geographical and fea-
35 ture spaces, which typically causes difficulties during
36 the model estimation. Spatial statisticians (e.g. Diggle
37 (2003) and/or Bivand et al. (2008)) generally believe
38 that geostatistical techniques are suited only for mod-
39 eling of features that are inherently continuous (spatial
40 fields); discrete objects (points, lines, polygons) should
41 be analyzed using point pattern analysis and simi-
42 lar techniques. Bridging the gap between conceptually
43 different techniques — point pattern analysis, niche
44 analysis and geostatistics — is an open challenge.

45 Some early examples of using geostatistics with the
46 species occurrence records can be found in the work of
47 Legendre and Fortin (1989) and Gotway and Stroup
48 (1997). Kleinschmidt et al. (2005) uses regression-
49 kriging method, based on the Generalized mixed model,

to predict the malaria incidence rates in South Africa. 50
Miller (2005) uses a similar principle (predict the regres- 51
sion part, analyze and interpolate residuals, and add 52
them back to predictions) to generate vegetation maps. 53
Miller et al. (2007) further provide a review of predictive 54
vegetation models that incorporate geographical aspect 55
into analysis. Geostatistics is considered to be one of 56
the four spatially-implicit group of techniques suited for 57
species distribution modeling – the other three being: 58
autoregressive models, geographically weighted regres- 59
sion and parameter estimation models (Miller et al., 60
2007). Pure interpolation techniques will often out- 61
perform niche based models (Bahn and McGill, 2007), 62
although there is no reason not to combine them. *Hy-* 63
brid spatial/niche-analysis SDMs have been suggested 64
also by Allouche et al. (2008). Pebesma et al. (2005) 65
demonstrates that geostatistics is fit to be used with 66
spatio-temporal species occurrence records. Analysis of 67
spatial auto-correlation and its use in species distribu- 68
tion models is now a major research issue in ecology and 69
biogeography (Guisan et al., 2006; Rangel et al., 2006; 70
Miller et al., 2007). 71

Engler et al. (2004) suggested a hybrid approach to 72
spatial modeling of occurrence-only records — a combi- 73
nation of Generalized Linear Model (GLM) and ENFA. 74
In their approach, ENFA is used to generate the so- 75
called ‘*pseudo-absence*’ data, which are then added to 76
the original presence-only data and used to improve 77
the GLMs. In our opinion, such combination of factor 78
analysis and GLMs is the most promising as it utilizes 79
the best of the two techniques. In this paper, we extend 80
the idea of Engler et al. (2004) by proposing a com- 81
putational framework that further combines density 82
estimation (kernel smoothing), niche-analysis (ENFA), 83
and geostatistics (regression-kriging). We implement 84
this framework in the R statistical computing environ- 85
ment, where various habitat analysis (*adehabitat* pack- 86
age), geostatistical (*gstat* package), and point pattern 87
analysis (*spatstat* package) functions can be successfully 88
combined. We decided to use a series of case studies, 89
starting from a most simple to some real-life studies, 90
to evaluate performance of our framework and then 91
discuss its benefits and limitations. 92

2 Theory: combining kernel density estimation, 93 ENFA and regression-kriging 94

The key inputs to a SDM is the inventory (population) 95
of animals or plants consisting of a total of N individ- 96
uals (a point pattern $\mathbf{X} = \{x_i\}_1^N$; where x_i is a spa- 97

1 tial location of individual animal/plant), covering some
2 area $B_{HR} \subset \mathbb{R}^2$ (where HR stands for home-range and
3 \mathbb{R}^2 is the Euclidean space), and a list of environmental
4 covariates/predictors (q_1, q_2, \dots, q_p) that can be used to
5 explain spatial distribution of a target species. In prin-
6 ciple, there are two distinct groups of statistical tech-
7 niques that can be used to map the realized species' dis-
8 tribution: (a) the point pattern analysis techniques, such
9 as kernel smoothing, which aim at predicting density of
10 a point process; and (b) statistical, GLM-based, tech-
11 niques that aim at predicting the probability distribu-
12 tion of occurrences. Both approaches are now explained
13 in detail in the following sections.

14 2.1 Species' density estimation using kernel smoothing 15 and covariates

16 Spatial density (λ ; if unscaled, also known as “*spatial*
17 *intensity*”) of a point pattern for a given time interval is
18 estimated as:

$$\mathbb{E}[N(\mathbf{X} \cap B)] = \int_B \lambda(x) dx \quad (1)$$

19 In practice, it can be estimated using e.g. a kernel esti-
20 mator (Diggle, 2003; Baddeley, 2008):

$$\lambda(x) = \sum_{i=1}^n \kappa \cdot (\|x - x_i\|) \cdot b(x) \quad (2)$$

21 where $\lambda(x)$ is spatial density at location x , $\kappa(x)$ is the
22 kernel (an arbitrary probability density), x_i is location
23 of an occurrence record, $\|x - x_i\|$ is the distance (norm)
24 between an arbitrary location and observation location,
25 and $b(x)$ is a border correction to account for missing
26 observations that occur when x is close to the border
27 of the region. A common (isotropic) kernel estimator
28 is based on a Gaussian function with mean zero and
29 variance 1:

$$\hat{\lambda}(x) = \frac{1}{H^2} \cdot \sum_{i=1}^n \frac{1}{\sqrt{2\pi}} \cdot e^{-\frac{\|x-x_i\|^2}{2}} \cdot b(x) \quad (3)$$

30 The key parameter for kernel smoothing is the band-
31 width (H) i.e. the smoothing parameter, which can be
32 connected with the choice of variogram in geostatistics.
33 The output of kernel smoothing is typically a map (im-
34 age) consisting of M grid nodes, and showing spatial
35 pattern of species' clustering.

36 Spatial density of a point pattern can also be modeled
37 using a list of spatial covariates q 's (in ecology, we call
38 this environmental predictors), which need to be avail-
39 able over the whole area of interest B . For example, us-
40 ing a Poisson model (Baddeley, 2008):

$$\log \lambda(x) = \log \beta_0 + \log q_1(x) + \dots + \log q_p(x) \quad (4)$$

41 where log transformation is used to account for the
42 skewed distribution of both density values and covari-
43 ates; p is the number of covariates. Models with covari-
44 ates can be fitted to point patterns e.g. in the `spatstat`
45 package (this actually fits the maximum pseudolikeli-
46 hood to a point process; for more details see Baddeley
47 (2008)). Such point pattern–covariates analysis is com-
48 monly run only to determine/test if the covariates are
49 correlated with the feature of interest, to visualize the
50 predicted trend function, and/or to inspect the spatial
51 trends in residuals. Although statistically robust, point
52 pattern–covariates models are typically not considered
53 as a technique to improve prediction of species' distri-
54 bution. Likewise, the model residuals are typically not
55 used for interpolation purposes.

56 2.2 Predicting species' distribution using ENFA and 57 GLM (pseudo-absences)

58 An alternative approach to spatial prediction of species'
59 distribution using occurrence-only records and envi-
60 ronmental covariates is the combination of ENFA and
61 regression modeling. In general terms, predictions are
62 based on fitting a GLM:

$$\mathbb{E}(\mathbf{P}) = \mu = g^{-1}(\mathbf{q} \cdot \beta) \quad (5)$$

63 where $\mathbb{E}(\mathbf{P})$ is the expected probability of species occur-
64 rence ($P \in [0, 1]$), $\mathbf{q} \cdot \beta$ is the linear regression model, and
65 g is the link function. A common link function used for
66 SDM with presence observations is the logit link func-
67 tion:

$$g(\mu) = \mu^+ = \ln \left(\frac{\mu}{1 - \mu} \right) \quad (6)$$

68 so the Eq.(5) becomes logistic regression (Kutner et al.,
69 2004).

1 The problem of running regression analysis with
2 occurrence-only observations is that we work with 1's
3 only, which obviously means that we can not fit any
4 model to such data. To account for this problem, species
5 distribution modelers (see e.g. Engler et al. (2004);
6 Jiménez-Valverde et al. (2008a) and Chefaoui and Lobo
7 (2008)) typically insert the so-called “*pseudo-absences*”
8 — 0's simulated using a plausible model, such as ENFA,
9 to depict areas where a species is not likely to occur.
10 ENFA is a type of factor analysis that uses observed
11 presences of a species to estimate which are the most
12 favorable areas in the feature space, and then uses
13 this information to predict the potential distribution of
14 species for all locations (Hirzel and Guisan, 2002). The
15 difference between ENFA and the Principal Component
16 Analysis is that the ENFA factors have an ecological
17 meaning. ENFA results in a Habitat Suitability Index
18 (HSI ∈ [0 – 100%]) — by depicting the areas of low
19 HSI, we can estimate where the species is very unlikely
20 to occur, and then simulate a new point pattern that
21 can be added to the occurrence locations to produce a
22 ‘*complete*’ occurrences+absences dataset. Once we have
23 both 0's and 1's, we can fit a GLM as shown in Eq.(5)
24 and generate predictions using geostatistical techniques
25 as described in e.g. Gotway and Stroup (1997). Chefaoui
26 and Lobo (2008) recently demonstrated that insertion of
27 pseudo-absences greatly controls the success of species'
28 distribution modeling by GLMs.

29 2.3 Predicting species' spatial density using ENFA and 30 logistic regression-kriging

31 We now describe the technique that is advocated in this
32 article, and that combines the two previously-described
33 approaches. We make several additional steps that make
34 the method somewhat more complicated, but also more
35 suited for occurrence-only observations used in ecology.
36 First, we assume that our input point pattern represents
37 only a sample of the whole population ($\mathbf{X}_S = \{x_i\}_1^n$), so
38 that the density estimation needs to be standardized to
39 avoid biased estimates. Second, we assume that pseudo-
40 absences can be generated using both information about
41 the potential habitat (HSI) and geographical location of
42 the occurrence-only records. Finally, we focus on map-
43 ping the actual count of individuals over the grid nodes
44 (realized distribution), rather than mapping the proba-
45 bility of species' occurrence.

46 Spatial density values estimated by kernel smoothing
47 are primarily controlled by the bandwidth size (Bivand
48 et al., 2008). Obviously, the higher the bandwidth, the

49 lower the values in the whole map; likewise, the higher
50 the sample size (n/N), the higher the overall intensity,
51 which eventually makes it difficult to physically inter-
52 pret mapped values of spatial intensity. To account for
53 this problem, we propose to use relative density ($\lambda_r : B \rightarrow [0, 1]$) expressed as the ratio between the local and
54 maximum density at all locations:
55

$$\lambda_r(x) = \frac{\lambda(x)}{\max\{\lambda(x) | x \in B\}_1^M} \quad (7)$$

56 An advantage of using the relative density is that the
57 values are in the range [0, 1], regardless of the bandwidth
58 and sample size (n/N). Assuming that our sample \mathbf{X}_S is
59 representative and unbiased, it can be shown that $\lambda_r(x)$
60 is an unbiased estimator of the true spatial density (see
61 e.g. Diggle (2003) or Baddeley (2008)). In other words,
62 regardless of the sample size, by using relative intensity
63 we will always be able to produce an unbiased estimator
64 of the spatial pattern of density for the whole population
65 (see further Fig. 1).

66 Furthermore, assuming that we actually know the size
67 of the whole population (N), by using predicted relative
68 density, we can also estimate the actual spatial density
69 (number of individuals per grid node):

$$\lambda(x) = \lambda_r(x) \cdot \frac{N}{\sum_{j=1}^M \lambda_r(x)}; \quad \sum_{j=1}^M \lambda(x) = N \quad (8)$$

70 which can be very handy if we wish to aggregate the
71 species' distribution maps over some polygons of inter-
72 est, e.g. to estimate the actual counts of individuals.

73 Our second concern is the insertion of pseudo-absences.
74 Here, two questions arise: (1) how many pseudo-absences
75 should we insert? and (b) where should we locate them?
76 Intuitively, it makes sense to generate the same num-
77 ber of pseudo-absence locations as occurrences. This is
78 also supported by the statistical theory of model-based
79 designs, also known as “*D-designs*”. For example, as-
80 suming a linear relationship between density and some
81 predictor g , the optimal design that will minimize the
82 prediction variance is to put half of observation at one
83 extreme and other at other extreme. All D-designs are
84 in fact symmetrical, and all advocate higher spreading
85 in feature space (for more details about D-designs, see
86 e.g. Montgomery (2005)), so this principle seems logical.

1 After the insertion of the pseudo-absences, the extended
2 observations dataset is then:

$$\mathbf{X}_f = \left\{ \{x_i\}_1^n, \{x_i^*\}_1^{n^*} \right\}; \quad n = n^* \quad (9)$$

3 where x_i^* are locations of the simulated pseudo-
4 absences. This is not a point pattern any more because
5 now also quantitative values — either relative densities
6 ($\lambda_r(x_i)$) or indicator values — are attached to locations
7 ($\mu(x_i) = 1$ and $\mu(x_i^*) = 0$).

8 The remaining issue is where/how to allocate the
9 pseudo-absences? Assuming that a spreading of species
10 in an area of interest is a function of the potential habi-
11 tat and assuming that the occurrence locations on the
12 HSI axis will commonly be skewed toward high values
13 (see further Fig. 3 left; see also Chefaoui and Lobo
14 (2008)), we can define the probability distribution (τ)
15 to generate the pseudo-absence locations as e.g.:

$$\tau(x^*) = [100\% - \text{HSI}(x)]^2 \quad (10)$$

16 where the square term is used to insure that there are
17 progressively more pseudo-absences at the edge of low
18 HSI. This way also the pseudo-absences will approxi-
19 mately follow Poisson distribution. In this paper we pro-
20 pose to extend this idea by considering location of oc-
21 currence points in geographical space also (see also an
22 interesting discussion on the importance of geographic
23 extent for generation of pseudo-absences by VanDerWal
24 et al. (2009)). The Eq.(10) then modifies to:

$$\tau(x^*) = \left[\frac{d_R(x) + (100\% - \text{HSI}(x))}{2} \right]^2 \quad (11)$$

25 where d_R is the normalized distance in the range
26 $[0, 100\%]$, i.e. the distance from the observation points
27 (\mathbf{X}) divided by the maximum distance. By using Eq.(11)
28 to simulate the pseudo-absence locations, we will pur-
29 positively locate them both geographically further away
30 from the occurrence locations and in the areas of low
31 HSI (unsuitable habitat).

32 After the insertion of pseudo-absences, we can attach to
33 both occurrences-absences locations values of estimated
34 relative density, and then correlate this with environ-
35 mental predictors. This now becomes a standard geosta-
36 tistical point dataset, representative of the area of in-

terest, and with quantitative values attached to point
locations (see further Fig. 2d).

Recall from Eq.(7) that we attach relative intensities to
observation locations. Because these are bounded in the
 $[0, 1]$ range, we can use the logistic regression model to
make predictions. Thus, the relative density at some new
location (x_0) can be estimated using:

$$\widehat{\lambda}_r^+(x_0) = [1 + \exp(-\beta^T \cdot \mathbf{q}_0)]^{-1} \quad (12)$$

where β is a vector of fitted regression coefficients, \mathbf{q}_0
is a vector of predictors (maps) at new location, and
 $\widehat{\lambda}_r^+(x_0)$ is the predicted logit-transformed value of the
relative density. Assuming that the sampled intensities
are continuous values in the range $\lambda_r \in (0, 1)$, the model
in Eq.(12) is in fact a linear model, which allows us to ex-
tended it to a more general linear geostatistical model
such as regression-kriging (also known as “*universal kriging*”
or “*kriging with external drift*”). This means that
the regression modeling is supplemented with the mod-
eling of variograms for regression residuals, which can
then be interpolated and added back to the regression
estimate (Hengl, 2007):

$$\widehat{\lambda}_r^+(x_0) = \mathbf{q}_0^T \cdot \widehat{\beta}_{\text{GLS}} + \delta_0^T \cdot (\lambda_r^+ - \mathbf{q} \cdot \widehat{\beta}_{\text{GLS}}) \quad (13)$$

where δ is the vector of fitted weights to interpolate the
residuals using ordinary kriging. In simple terms, logistic
regression-kriging consists of five steps:

- (1) convert the relative intensities to logits using
Eq.(6); if the input values are equal to 0/1, replace
with the second smallest/highest value;
- (2) fit a linear regression model using Eq.(12);
- (3) fit a variogram for the residuals (logits);
- (4) produce predictions by first predicting the regression-
part, then interpolate the residuals using ordinary
kriging; finally add the two predicted trend-part
and residuals together (Eq.13)
- (5) back-transform interpolated logits to the original
(0, 1) scale by:

$$\widehat{\lambda}_r(x_0) = \frac{e^{\widehat{\lambda}_r^+(x_0)}}{1 + e^{\widehat{\lambda}_r^+(x_0)}} \quad (14)$$

After we have mapped relative density over area of in-
terest, we can also estimate the actual counts using the
Eq.(8).

1 2.4 Species' Distribution Modeling using a textbook ex-
 2 ample

3 At this stage the above introduced theory might seem
 4 rather difficult to follow (especially because it links to
 5 different statistical theories such as ENFA, geostatistics,
 6 D-designs and point pattern analysis), hence we will also
 7 try to illustrate this theory using a real data set and
 8 prove our assumptions using a simple example. For read-
 9 ers requiring more detail, the complete R script used in
 10 this exercise with plots of outputs and interpretation of
 11 steps is available from the contact authors' homepage¹.

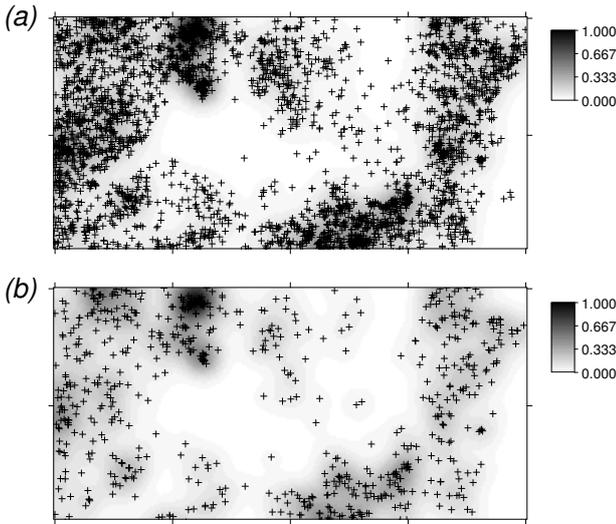


Fig. 1. Relative density estimated for the original `bei` data set (a), and its 20% sub-sample (b). In both cases the same bandwidth was used: $H=23$ m.

12 We use the `bei` dataset, distributed together with the
 13 `spatstat` package, and used in textbooks on point pattern
 14 analysis by Baddeley (2008) and many other authors.
 15 This data set consists of a point map showing locations
 16 of trees of the species *Beilschmiedia pendula* Lauraceae
 17 (in this case we deal with the whole population) and
 18 Digital Elevation Model (5 m resolution) as an auxiliary
 19 map, which can be used to improve mapping of the tree
 20 species. What makes this dataset especially suitable for
 21 such testing is the fact that the complete population of
 22 the trees has been visited/mapped for the area of interest
 23 (N is known, and so is B_{HR}). We will now implement all
 24 steps described in section 2.3 to predict spatial density
 25 of trees over the area of interest ($M=20301$ grid nodes).
 26 We will use a sample of 20% of the original population,
 27 and then validate the accuracy of our technique versus
 28 the whole population.

¹ <http://spatial-analyst.net>

29 We start by estimating a suitable bandwidth size for
 30 kernel density estimation (Eq.3). For this, we use the
 31 method of Berman and Diggle (1989) (as described in
 32 Bivand et al. (2008, p.166–167)) that looks for the small-
 33 est Mean Square Error (MSE) of a kernel estimator.
 34 This only shows that we should not use bandwidths sizes
 35 smaller than 4 m (which is below resolution of our GIS);
 36 higher values seem plausible. We also consider the least
 37 squares cross validation method to select the bandwidth
 38 size using the method of Worton (1995), and as imple-
 39 mented in the `adehabitat` package. This does not con-
 40 verge, hence we need to set the bandwidth size using
 41 some *ad hoc* method (this is unfortunately a very com-
 42 mon problem with many real point patterns). As a rule
 43 of thumb, we can start by estimating the smallest suit-
 44 able range as the average size of block ($\sqrt{area(B)/N}$),
 45 and then set the bandwidth size at two times this value.
 46 There are 3605 trees (N) in the area of size 507,525 m²,
 47 which means that we could use a bandwidth of 24 m (H).

48 We next derive a relative kernel density map (Eq.7),
 49 which is shown in Fig. 1a. If we randomly subset the
 50 original occurrence locations and then re-calculate the
 51 relative densities, we can notice that the spatial pattern
 52 of the two maps does not differ significantly, neither do
 53 their histograms. This supports our assumption that the
 54 relative density map (Eq. 7) can be indeed reproduced
 55 also from a representative sample ($n=721$).

56 We proceed with preparing the environmental predic-
 57 tors and testing their correlation with the density val-
 58 ues. We can extend the original single auxiliary map
 59 (DEM) by adding some hydrological parameters: slope,
 60 topographic wetness index and altitude above channel
 61 network (all derived in SAGA GIS). The result of fitting
 62 a non-stationary point process with a log-linear density
 63 using the `ppm` method of `spatstat` shows that density
 64 is negatively correlated with wetness index, and posi-
 65 tively correlated with all other predictors. A comparison
 66 between the Akaike Information Criterion (AIC) for a
 67 model without predictors and with predictors shows that
 68 there is a slight gain in using the covariates to predict the
 69 spatial density. Visually (Fig. 2a), we can see that the
 70 predicted trend seriously misses some hot-spots/clusters
 71 of points. This shows that using point pattern analysis
 72 techniques only to map (realized) species' distribution
 73 with covariates will be of limited use.

74 We proceed with ENFA. It shows that this species gen-
 75 erally avoids the areas of low wetness index, i.e. it prefers
 76 ridges/dry positions (Fig. 2b; see also supplementary
 77 materials). This spatial correlation is now more distinct

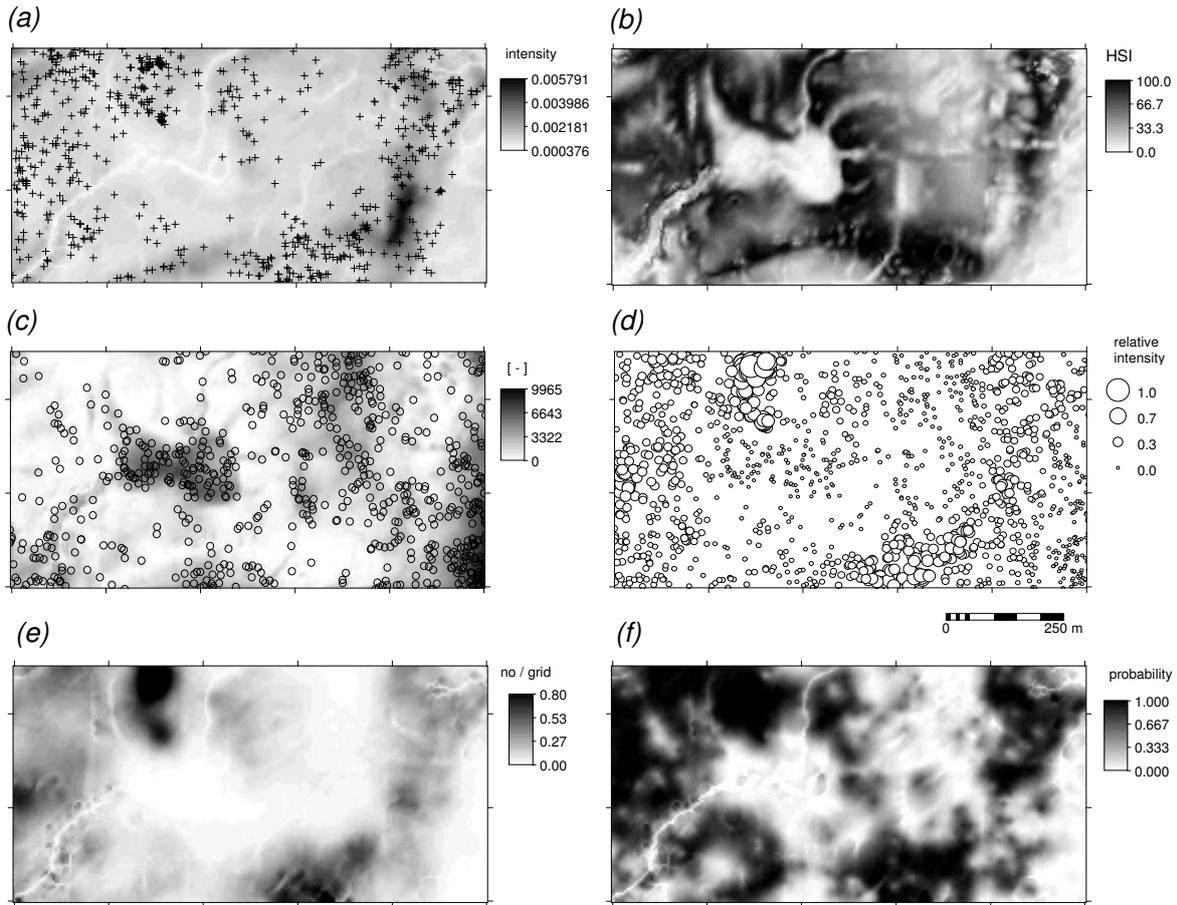


Fig. 2. Spatial prediction of the species distribution using the `bei` data set (20% sub-sample): (a) fitted trend model (`ppm`) using elevation, slope, topographic wetness index and altitude above channel network as environmental covariates; (b) Habitat Suitability Index derived using the same covariates; (c) the weight map and the randomly generated pseudo-absences using the Eq.(11); (d) input point map of relative intensities (includes the simulated pseudo-absences); (e) the final predictions of the overall density produced using regression-kriging (showing number of individuals per grid cell as estimated using Eq.8); and (f) predictions using a binomial GLM.

1 (compare with the trend model in Fig. 2a). This demon-
 2 strates the power of ENFA, which is in this case more
 3 suited for analysis of the occurrence-only locations than
 4 the regression analysis i.e the point pattern analysis.

5 By combining HSI and buffer map around the occur-
 6 rence locations (Eq. 11), we are able to simulate the
 7 same amount of pseudo-absence locations (Fig. 2c).
 8 Note that the correlation between the HSI and density
 9 is now clearer, and the spreading of the points around
 10 the HSI feature space is symmetric (Fig. 3, right). Con-
 11 sequently, the model fitting is more successful: the ad-
 12 justed R-square fitted using the four environmental pre-
 13 dictors jumped from 0.07 to 0.28. This demonstrates the
 14 benefits of inserting the pseudo-absence locations. If we
 15 would randomly insert the pseudo-absences, the model

would not improve (or would become even noisier).

17 We proceed with analyzing the point data set indi-
 18 cated in Fig. 2d using standard geostatistical tools. We
 19 can fit a variogram for the residuals, and then run the
 20 regression-kriging, as implemented in the `gstat` pack-
 21 age. For a comparison, we also fit a variogram for the
 22 occurrence-absence data but using the residuals of the
 23 GLM modelling with binomial link function, i.e. 0/1
 24 values (Fig. 4). As with any indicator variable, the var-
 25 iogram of the binomial GLM will show higher nugget
 26 and less distinct auto-correlation than the variogram
 27 for the density values. This is also because the residuals
 28 of the density values will still reflect kernel smoothing,
 29 especially if the predictors explain only a small part of
 30 variation in the density values.

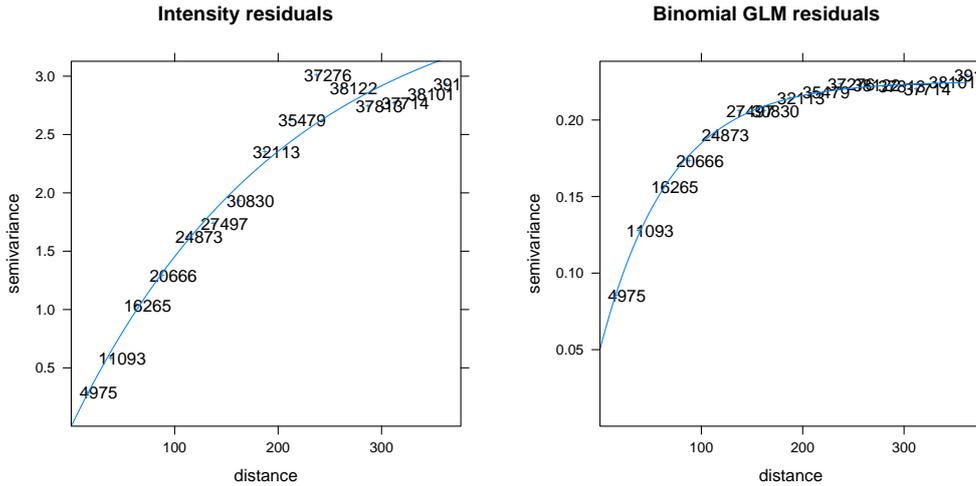


Fig. 4. Variogram models for residuals fitted in `gstat` using occurrence-absence locations: (left) density values (logits), and (right) probability values.

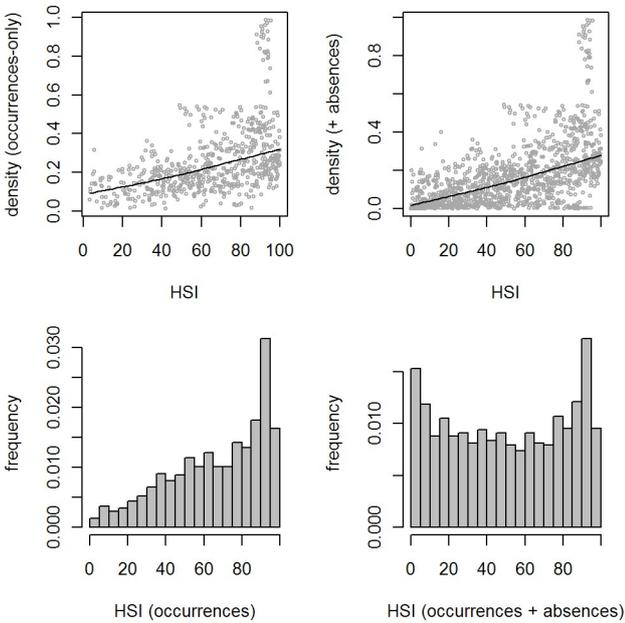


Fig. 3. Correlation plot HSI vs relative density with occurrence-only locations (left) and after the insertion of the pseudo-absence locations (right). Note that the pseudo-absences ensure equal spreading around the feature space (below).

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It is completely independent from point pattern analysis), its output is limited in content because it also misses to represent the hot-spots/quantities of individuals. GLM-kriging in fact only shows the areas where a species' is likely to occur, without any estimation of how dense will the population be. Another advantage of using the occurrences+absences with attached density values is that we are able not only to generate predictions, but also to generate geostatistical simulations, map the model uncertainty, and run all other common geostatistical analysis steps.

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In the last step of this exercises we want to validate the model performance using cross-validation and the original complete population. The ten-fold cross validation (as implemented in `gstat`) for the intensities interpolated regression-kriging shows that the model is highly precise — it explains over 99% of the variance in the training samples. Further comparison between the map shown in Fig. 2e and Fig. 1a shows that, with a 20% of samples and four environmental predictors, we are able to explain 96% of the pattern in the original density map ($R^2=0.96$). Fig. 5 indeed confirms that this estimator is unbiased.

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One last point: although it seems from this exercise that we are recycling auxiliary maps and some analysis techniques (we use auxiliary maps both to generate the pseudo-absences and make predictions), we in fact use the HSI map to generate the pseudo-absences, and the original predictors to run predictions, which not necessarily need to reflect the same features. Relative densities, do not have to be directly correlated with the HSI,

1 The resulting map of density predicted using regression-kriging (Fig. 2e) is indeed a hybrid map that reflects kernel smoothing (hot spots) and environmental patterns, thus it is a map richer in contents than the pure density map estimated using kernel smoothing only (Figs. 1), or the Habitat Suitability Index (Fig. 2b). Note also that, although the GLM-kriging with bimodal link function (Fig. 2f) is statistically a more straight forward procedure

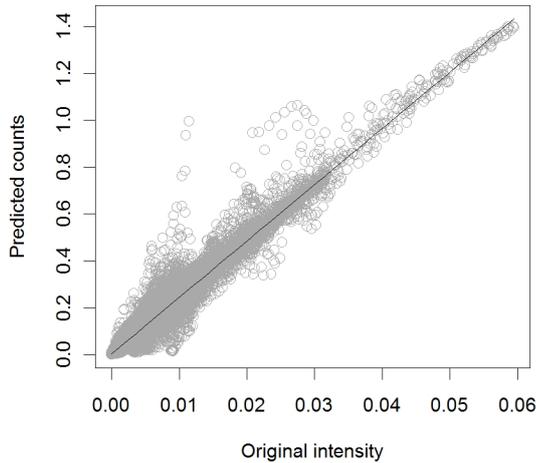


Fig. 5. Evaluation of the mapping accuracy for the map shown in Fig. 2e versus the original mapped density using 100% of samples (Fig. 1a).

1 although a significant correlation will typically be anticipated. Likewise, we use kernel smoother to estimate the intensities, but we then fit a variogram, which is obviously controlled by the amount of smoothing, i.e. value of the bandwidth, hence the variogram will often show artificially smooth shape, as shown in Fig. 4. The only way to avoid this problem is to estimate the bandwidth using some objective technique (which we failed to achieve in this example), or to scale the variogram fitted for the indicator variable (Fig. 4; right) to the density values scale.

12 3 Methods and materials

13 The computational framework used in this article follows the example described in the previous section (2.3), except it implies a larger number of predictors and several additional processing steps. A general workflow, as implemented in the R environment for statistical computing, is presented in Fig. 6. In order to fully understand all processing steps in detail, the interested readers can look at the R script provided via the contact authors' website.

22 The framework comprises six major steps. First, the occurrence locations are used to derive the density of a species for a given area based on the kernel smoother. Kernel density can be estimated in R using several methods; here we use the `density.ppp` method, as implemented in the `spatstat` package (Baddeley and Turner,

2005). In R, the smoothing parameter (bandwidth) can be estimated objectively; when it does not converges to a local minimum we use an *ad hoc* bandwidth selected as two times the average length of the block occupied by an individual ($2 \cdot \sqrt{\text{area}(B)/N}$). The output kernel density image can be coerced to the widely accepted spatial R format (`SpatialGridDataFrame`) of the `maptools/sp` package (Bivand et al., 2008); coercion to this format is important for further geostatistical analysis and export to GIS.

The second step is ENFA, which we run using the occurrence-only records. For ENFA, we use the `ade-habitat` package, which is a collection of tools for the analysis of habitat selection by animals (Hirzel and Guisan, 2002; Calenge, 2006). Third, the resulting Habitat Suitability Index map (HSI, see further Fig. 8b and Fig. 11b) are used to generate the pseudo-absence locations. To achieve this, we use the `rpoint` method of the `spatstat` package. This method generates a random point pattern with the density of sampling proportional to the values of the weights map derived using Eq.(11).

In the fourth step, where possible, the simulated absence locations are reprojected to the Latitude/Longitude WGS84 system, exported to Google Earth (`writeOGR` method in `rgdal` package) and validated by an expert e.g. by doing photo-interpretation of high resolution satellite imagery.

Once we produce an equal number of occurrence and simulated absence locations, they can be packed together and used to build regression models using the ecological predictors. The residuals of the regression model are then analyzed for auto-correlation by fitting a variogram (`fit.variogram` method in `gstat`).

In the last, sixth step, after both the regression model and the variogram parameters have been determined, final predictions are generated using the generic `predict.gstat` method (Eq.13) as implemented in the `gstat` package (Pebesma, 2004; Bivand et al., 2008). More details on how to run regression-kriging and interpret its outputs can be found in Hengl (2007).

For a comparison, we also map the distribution of a species based on the occurrences+absences by fitting a binomial GLM. This is possible using the `glm` method in R, by setting a binomial link function (`binomial(link=logit)`). By using library `mgcv`, one can also fit Generalized Additive Models (GAM), using the same type of link function (`family=binomial`);

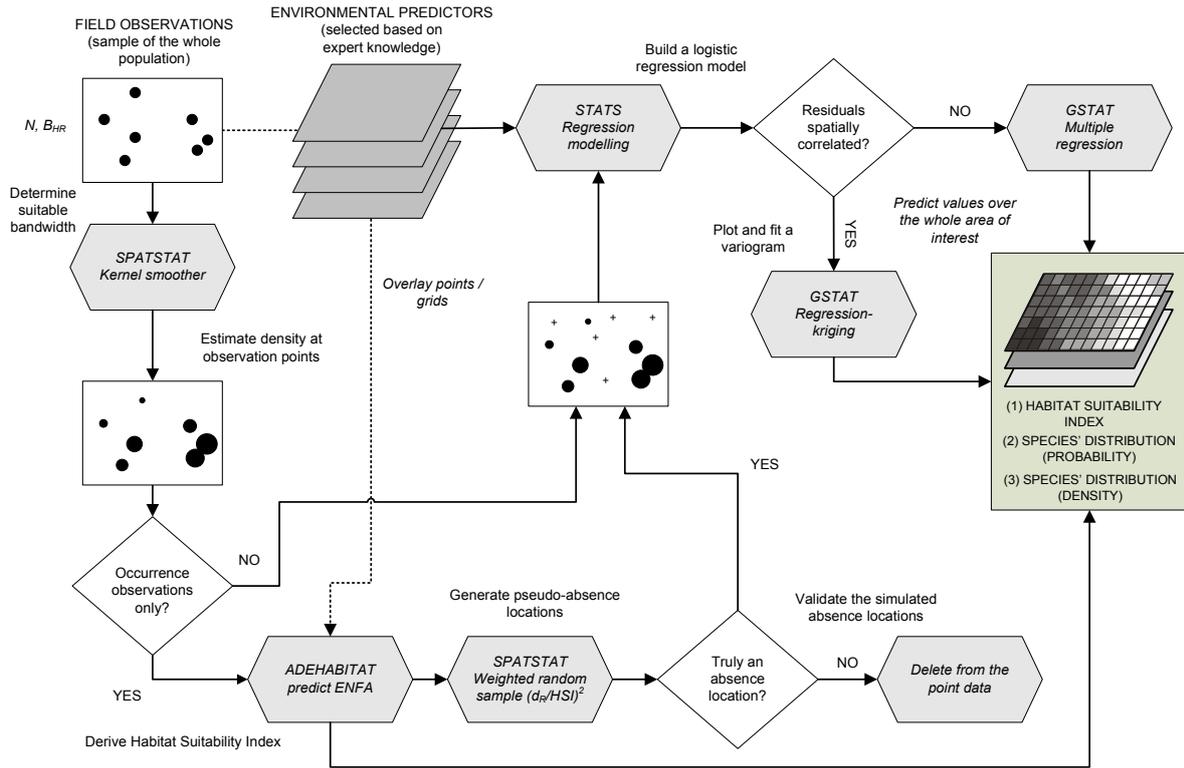


Fig. 6. Data processing steps and related R packages used in this paper.

1 in this paper we focus on fitting linear models only.
 2 The output of running binomial GLM are probabilities,
 3 ranging from 0 to 1 (see further Fig. 8c and Fig. 11c).

4 The final results of running regression-kriging can
 5 be evaluated using the leave-one-out cross validation
 6 method, as implemented in the `krige.cv` method of
 7 `gstat` package (Pebesma, 2004). The algorithm works
 8 as follows: it visits a data point, predicts the value at
 9 that location by leaving out the observed value, and
 10 proceeds with the next data point. This way each indi-
 11 vidual point is assessed versus the whole data set. The
 12 results of cross-validation are used to pinpoint the most
 13 problematic locations, e.g. exceeding the three stan-
 14 dard deviations of the normalized prediction error, and
 15 to derive the summary estimate of the map accuracy
 16 (Bivand et al., 2008, p.222–226).

17 We have tested this framework using occurrence-only
 18 records for two different species: distribution of root vole
 19 (*Microtus oeconomus*) in the Netherlands, and distribu-
 20 tion of nests of white-tailed eagle (*Haliaeetus albicilla*)
 21 in Croatia. In both cases, we have jointly run analysis

and then made the interpretation of the results and dis-
 22 cussed strength and limitations of this framework. 23

4 Case studies 24

4.1 Root vole (*Microtus oeconomus*) in the Netherlands 25

The root vole (*Microtus oeconomus*) is a widespread, ho-
 26 larctic mouse species that inhabits the northern regions
 27 of Europe, Asia and Alaska. In Europe six subspecies
 28 are described (Mitchell-Jones et al., 2002). One of these
 29 subspecies, *Microtus oeconomus arenicola* is endemic to
 30 the Netherlands and listed as a species of conservation
 31 concern in the Habitats Directive of the European Union
 32 (van Apeldoorn, 2002). Its presence in the Netherlands
 33 is seen as a relict from the Ice Age and the Dutch pop-
 34 ulation has no contact anymore with other European
 35 populations of the root vole. It is a good swimmer and
 36 well adapted to wetlands with varying water tables and
 37 has a high reproductive power. Therefore, root voles can
 38 swiftly recolonize wetlands after flooding. 39

It is thought that the Dutch root vole suffers heavily 40

1 from competition with two other *Microtus*-species: the
 2 common vole (*Microtus arvalis*) and the field vole (*Mi-*
 3 *crotonus agrestis*) (van Apeldoorn et al., 1992; van Apel-
 4 doorn, 2002). On the isle of Texel, for example, the root
 5 vole was until recently the only occurring mouse species,
 6 which enable it to occupy a wider variety of habitats.
 7 Root vole populations are known to co-exist with popu-
 8 lations of the other two *Microtus*-species on various loca-
 9 tions in the country. Since these competitive species are
 10 not good swimmers, islands and large wetlands are the
 11 core areas of root voles, while smaller habitat patches
 12 in the vicinity of wetland throughout the country are
 13 places where the three species co-occur.

14 Following this knowledge about the biology of root vole,
 15 we selected two groups of environmental predictors to
 16 explain the distribution of root vole in the Netherlands:
 17 (1) habitat variables (wetland areas): **marsh** — marsh-
 18 land areas (0/1), **island** — island areas (0/1), **flooded**
 19 — flooded regions (0/1), **freat1** — duration of primary
 20 drainage in days (obtained from the [http://rijks-](http://rijks-waterstaat.nl)
 21 [waterstaat.nl](http://rijks-waterstaat.nl)), and **fgr** — map of the Physical Ge-
 22 ographic Regions (denoting the same characteristics in
 23 physiography); and (2) biological factors: **nofvole** —
 24 indicator variable showing the areas in the north-west
 25 of the country where field voles are absent, **nofvole25**
 26 — 25 km wide band where root and field voles co-occur
 27 (all variables at 1 km resolution). Since the species are
 28 not mutually exclusive in most of the country on a land-
 29 scape and/or local scale, other variables were sought
 30 fore that relate to the great ability of the root vole
 31 to recolonize adjacent areas from core areas. Hence, in
 32 addition to the maps showing locations of marshlands
 33 (**marsh**) and islands (**island**), we also used their density
 34 for 1 and 2 km search radiuses: (**island1km**, **island2km**,
 35 **marsh1km**, **marsh2km**), and **flooded2km**.

36 The occurrence records (562) of root vole were ob-
 37 tained from the Dutch organization for mammals (VZZ)
 38 (<http://www.vzz.nl/soorten/noordsewoelmuis/>).
 39 The records and environmental maps refer to the 2004–
 40 2007 period.

41 The occurrence records and derived kernel density is
 42 shown in Fig. 8a. The habitat suitability analysis shows
 43 that the potential spreading of the species is much larger
 44 than the actual locations show. The HSI map shown
 45 in Fig. 8b mainly follows the pattern of the primary
 46 drainage duration (**freat1**) and flooding intensity (**fgr**).
 47 The target variable (kernel density) is heavily skewed
 48 toward small values, so we used a log-transform for fur-
 49 ther modeling. The biplot graph of the principal com-

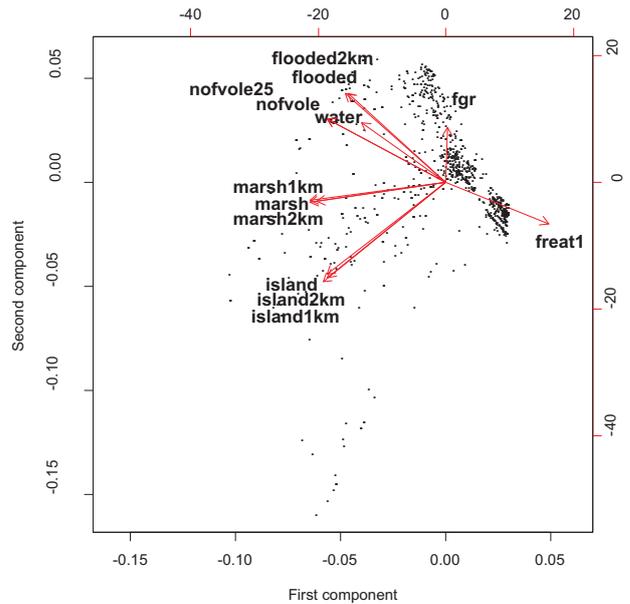


Fig. 7. Biplot showing the multicollinearity of the environ-
 mental predictors used to map distribution of root vole in the
 Netherlands: **marsh** — marshland areas (0/1), **island** — is-
 land areas (0/1), **flooded** — flooded regions (0/1), **freat1** —
 duration of primary drainage in days, **island1km**, **island2km**,
marsh1km, **marsh2km**, and **flooded2km** — density of marsh-
 lands and flooded areas for 1 and 2 km search radiuses.

ponent analysis output (Fig. 7), calculated using the
 sampling locations, shows four clusters of variables (a)
flooded, **nofvole** and **fgr** (b) **marsh**, (c) **islands** and
 (d) **freat1**. Further Principal Component transformation of the original grid maps shows that PC1 explains
 30% of total variance, PC2 20%, PC3 18%, PC4 10% and
 PC5 still 8% of the variation. The stepwise regression
 of PC-transformed variables reduces the number of vari-
 ables as compared with the original variables from 8 to 9.
 The most significant predictors are now PC1 (**islands**)
 and PC3 (**flooded** and **marsh**). The PCA based-model
 is not statistically different from the model fitted using
 the original variables. The *gstat* fitted an exponential
 variogram model with a zero nugget, sill parameter of
 0.00625 and a range parameter of 3.7 km to remaining
 residuals.

Regression analysis showed that, if occurrence-only
 data is used, the tailored predictors explain 71.0% of
 the variation. After including the simulated absence-
 observations the explained variation increases to 80.2%.
 The most significant predictors of root vole density
 are **marsh2km**, **flooded2km**, **freat1**, **islands2km**,
nofvolebuf25 and **water**.

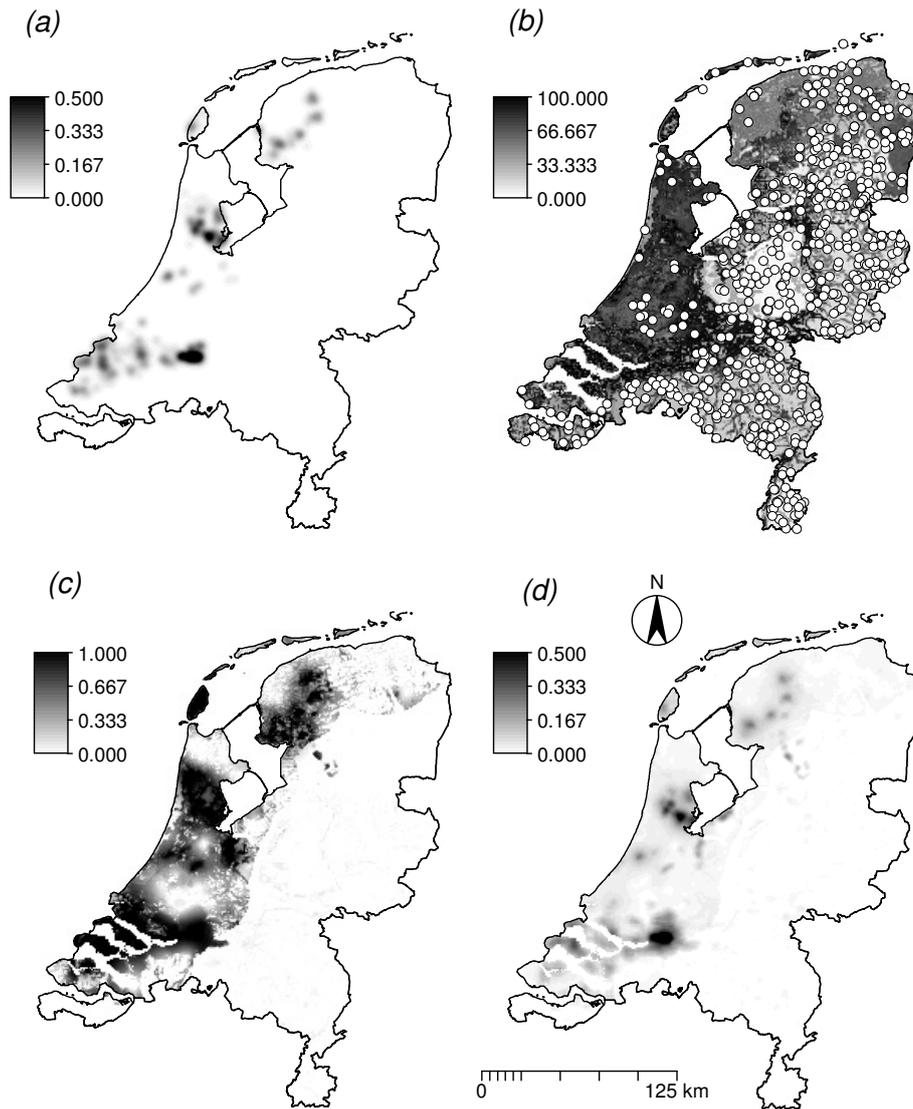


Fig. 8. Spatial prediction of root vole in the Netherlands: (a) the kernel density map (stretched to min–max range); (b) the Habitat Suitability Index and simulated pseudo-occurrence locations; (c) probabilities predicted using the Binomial GLM-based regression-kriging; and (d) the final predictions of densities produced using regression-kriging.

1 The final result of regression-kriging of 0/1 values and
 2 observation densities for root vole is shown in Figs. 8c
 3 and d. The root mean square prediction error at the
 4 leave-one-out validation points for model in Fig. 8d
 5 is 23% of the original variance; the regression-kriging
 6 model explains 98% of the original variance, which is
 7 quite high.

8 **4.2 Nests locations of white-tailed eagle (*Haliaeetus al-***
 9 ***bicilla*) in Croatia**

10 In the second case study we focus on modeling the dis-
 11 tribution of white-tailed eagle (*Haliaeetus albicilla*) in

12 Croatia. At the beginning of the 1990s, about 80 pairs
 13 were recorded in Croatia (Tucker et al., 1994); a decade
 14 after, Croatia had 80–90 pairs. Some most recent records
 15 by Radović and Mikuska (2009) indicate a continuity of
 16 increase in population number in the period 2003–2006.
 17 This makes Croatia a country with the second largest
 18 population of *Haliaeetus albicilla* among the neighbor-
 19 ing central European countries (Schneider-Jacoby et al.,
 20 2003; BirdLife International, 2004).

21 *Haliaeetus albicilla* breeds in various habitats but com-
 22 monly needs sea coasts, lake shores, broad rivers, is-
 23 land and wetlands with high productivity. It breeds in

1 different climates ranging from continental to oceanic.
 2 In Norway and Iceland nests are rarely placed above
 3 300 m above sea level (Cramp, 2000). Same territories
 4 and eyries being occupied over many decades. Normally,
 5 only one or two alternate nests are built in a breeding ter-
 6 ritory (Helander and Stjernberg, 2002), which makes the
 7 nests most interesting for population distribution assess-
 8 ments. Breeding areas of *Haliaeetus albicilla* in Croatia
 9 are primarily alluvial wetlands along rivers Sava, Kupa,
 10 Drava and Mura (Pannonian plain), in Central and East-
 11 ern part of the country (Radović and Mikuska, 2009).

12 Following the habitat characteristics of *Haliaeetus albi-*
 13 *cilla*, we have prepared a total of 13 environmental pre-
 14 dictors (all at 200 m resolution): **dem** — a Digital El-
 15 evation Map showing height of land surface; **canh** —
 16 derived as the difference between the topo-map DEM
 17 and the SRTM DEM, so that it reflects the height of
 18 canopy; **drailroad** — distance to rail roads; **droads** —
 19 distance to roads; **durban** — distance to urban areas;
 20 **dwater** — distance to water bodies; **pcevi1-4** — PCs
 21 from 12 MODIS Enhanced Vegetation Index (EVI)
 22 images obtained for the year 2005; **slope** — slope map
 23 derived using the DEM; **solar** — incoming solar insola-
 24 tion derived using the DEM; and **wetlands** — boolean
 25 map showing location of the wetlands. The proximity
 26 maps (**drailroad**, **droads**, **durban** and **dwater**) were
 27 derived from the vector features from the 1:100k topo-
 28 maps. **dem** and derivatives (**canh**, **slope** and **solar**)
 29 and EVI components are standard exhaustive predic-
 30 tors used for geostatistical mapping of environmental
 31 variables. The wetland habitats distribution map was
 32 obtained from the Croatian State Institute for Nature
 33 Protection (<http://www.cro-nen.hr/map/>). This is a
 34 boolean map (1/0) showing locations of the wetland ar-
 35 eas, covered by both forests and swamps.

36 The nest positions used in this paper were recorded in the
 37 period 2003–2006. Altogether, 155 nest locations were
 38 recorded, out of which 125 locations showed clear signs of
 39 breeding (Radović and Mikuska, 2009). An additional 10
 40 presumably active territories were detected but without
 41 knowing the exact position of the nests. Because of some
 42 problems during the fieldwork (minefields, flooded areas
 43 and extreme sensitivity of birds to our presence) the
 44 exact coordinates were taken for a total of 135 nests. We
 45 assume that this number represents about 80% of the
 46 total nests ($N=169$, $B_{HR}=330$ km²), but this is hard
 47 to validate. Grlica (2007) most recently discovered some
 48 new breeding territories along Drava river coasts, but
 49 without recording the exact position of the nests.

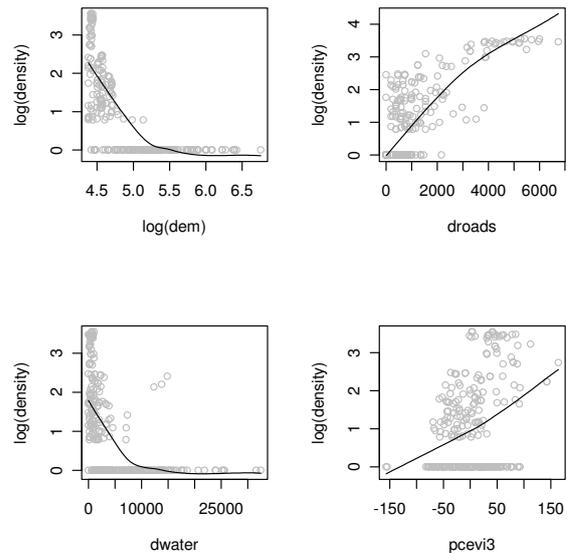


Fig. 9. Correlation plots between the log of nest densities and ecological predictors: **dem** — digital elevation model in meters; **droads** — distance to roads in meters; **dwater** — distance to water in meters; **pcevi** — the third component of the MODIS Enhanced Vegetation Index for year 2005.

The nest density estimated using a Gaussian kernel smoother with bandwidth set at 75% of the distance to the nearest neighbors (3.4 km) is shown in Fig. 11a. The areas with nest density close to zero are masked and 135 absence points generated using random sampling are shown in Fig. 11b. From these, 11 were found to fall in areas where potentially the species might occur, and were masked out from further analysis. We start by correlating the nest density estimated at observation points with the ecological predictors. If occurrence-only data are used, the ecological predictors explain 69% of variation of the target variable. Merging of the occurrence and absence observations gives 259 points in total, and the regression model explains 83% of variation. The most significant ecological predictors are **droads**, **wetlands**, **dem**, **pcevi3** and **dwater** (Fig. 9). Adding simulated absence locations was relatively inexpensive as it took only one day to validate simulated 135 locations.

The ecological predictors are highly inter-correlated and with skewed distributions. The biplot graph (Fig. 10) calculated at sampling locations shows that there are four clusters of predictors: (a) **dem** is correlated with **dwater** and **slope**; (b) **droads**, **durban**, **pcevi3**, **canh** and with **wetlands**; (c) **solar** and **pcevi4**; and (d)

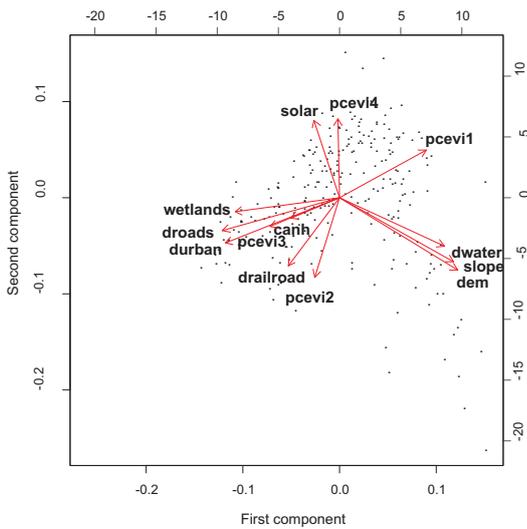


Fig. 10. Biplot showing the multicollinearity of the environmental predictors used to map distribution of white-tailed eagle: **dem** — digital elevation model; **canh** — height of canopy; **drailroads** — distance to rail roads; **droads** — distance to roads; **durban** — distance to urban areas; **dwater** — distance to water bodies; **pcevi1--4** — four PCs from 12 EVI images for year 2005; **slope** — slope map; **solar** — incoming solar insolation; and **wetlands** — boolean map showing location of wetlands.

1 **pcevi**.

2 The Principal Component transformation of the original
 3 predictors produces somewhat different picture. In this
 4 case, PC1 explains 80.1% of total variance and reflects
 5 mainly **pcevi01**, PC2 explains 7.9% of variance and re-
 6 flects the position of **wetlands** and **dem**, PC3 explains
 7 4.5% of variance, PC4 2.0% and PC5% 1.4% etc.

8 The step-wise regression shows that the most significant
 9 predictors of the nest density are PC2 (reflecting posi-
 10 tion of the wetlands and elevation) and PC1 (reflecting
 11 distance to roads and urban areas). Step-wise regression
 12 has much less problems in selecting the significant pre-
 13 dictors if they are spatially independent. The number
 14 of significant predictors after the principal component
 15 transformation was reduced from 9 to 6; the adjusted
 16 R-square stays unchanged.

17 Further analysis of the residuals shows that they are
 18 spatially auto-correlated. We fitted an exponential var-
 19 iogram with 0 nugget, 0.263 sill parameter and range
 20 parameter of 5.2 km. The variogram for binomial GLM

residuals is noisier than the variogram derived for den- 21
 sities. As expected, continuous variables (densities) are 22
 easier to model using geostatistics than the binary vari- 23
 ables. This is true for both success of fitting a regression 24
 model and a for a success of fitting a variogram of resid- 25
 uals. 26

The accuracy of the map shown in Fig. 11a evaluated 27
 using the leave-one-out cross validation method shows 28
 that the map is fairly accurate: the root mean square 29
 prediction error at the validation points is only 16% of 30
 the original variance, or in other words, the regression- 31
 kriging model explains 94% of the original variance. 32

5 Discussion and conclusions 33

The results of the case studies described in this paper 34
 demonstrate that more informative and more accurate 35
 maps of the actual species' distribution can be generated 36
 by combining kernel smoothing, ENFA and regression- 37
 kriging. In order to improve estimation of regression 38
 model and final interpolation results, we advocate sim- 39
 ulation of pseudo-absence data using inverted HSI and 40
 distance maps (Eq.11). This has shown to improve the 41
 regression models — the adjusted R-square increased 42
 from 0.69 to 0.83 for white-tailed eagle and from 0.71 to 43
 0.80 for root vole — while improving the spreading of 44
 the points in feature space (see Fig. 12). This confirms 45
 the results of Chefaoui and Lobo (2008). 46

We believe that the method proposed in this article, as 47
 described in section 2.3, has several advantages over the 48
 known species' distribution modeling methods: 49

- The pseudo-absence locations are generated using a 50
 model-based design that spreads the points based on 51
 the geographical distance from the occurrence loca- 52
 tions and the potential habitat. Compare with the 53
 purely heuristic approaches to generate the pseudo- 54
 absence by Chefaoui and Lobo (2008) or Jiménez- 55
 Valverde et al. (2008a). 56
- Both spatial auto-correlation structure and the trend 57
 component of the spatial variation are used to make 58
 spatial prediction of species' distribution. This leads 59
 to the Best Linear Unbiased Prediction of the pres- 60
 ence/density values. Compare, for example, with the 61
 heuristic approach by Bahn and McGill (2007). 62
- Final output map shows distribution of a real phys- 63
 ical parameter (number of individuals per grid cell) 64
 and can be directly validated using measures such as 65
 RMSE and similar. Compare with the often abstract 66

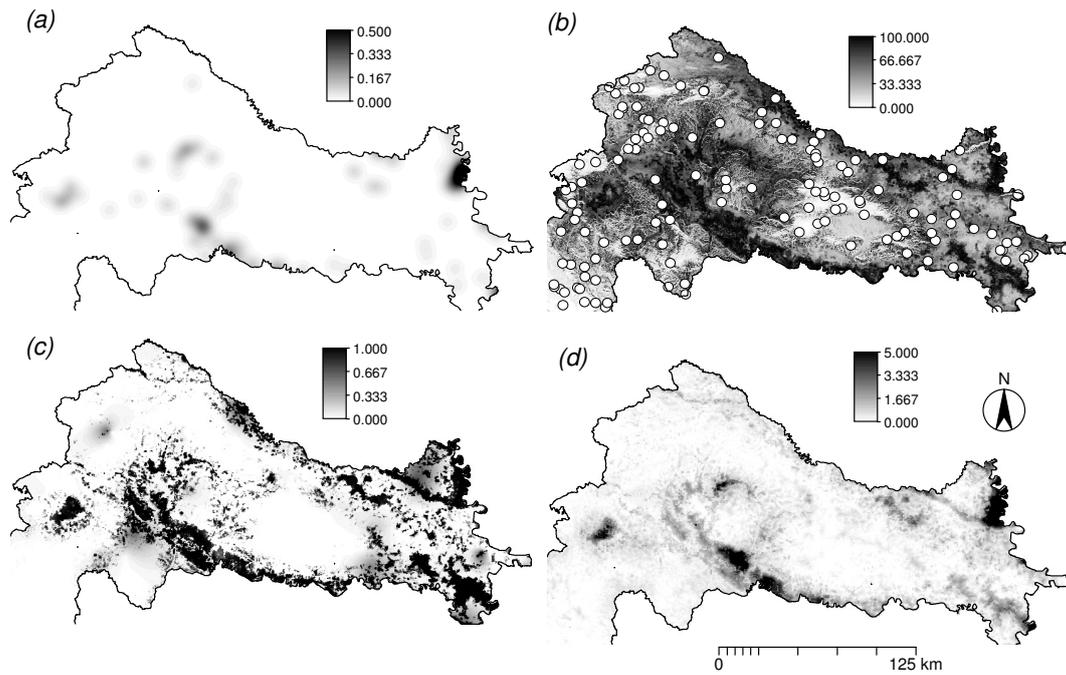


Fig. 11. Spatial prediction of white-tailed eagle in Croatia: (a) the kernel density map (stretched to min–max range); (b) the Habitat Suitability Index and simulated pseudo-occurrence locations; (c) probabilities predicted using the Binomial GLM-based regression-kriging; and (d) densities predicted using regression-kriging.

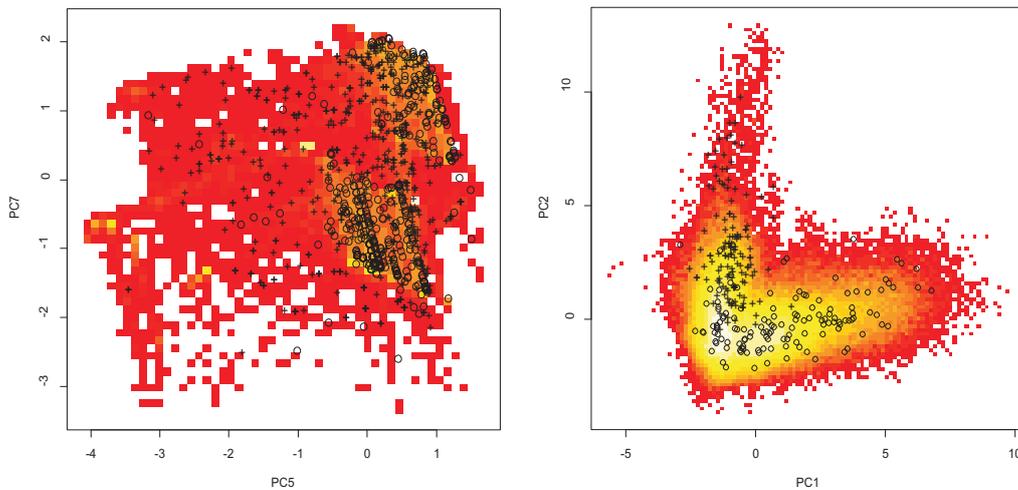


Fig. 12. Position of the occurrence (+) and the pseudo-absence (o) locations when displayed in feature space (as defined using the most significant predictors): for root vole (left) and white-tailed eagle (right). Compare with Figs. 8a and 11b. The plot was produced using the `hist2D` function of the R package `gplots`.

1 evaluation measures (e.g Kappa, MaxKappa, AUC,
 2 adjusted D^2 , AVI, CVI, Boyce index etc.) used in pre-
 3 dictive habitat mapping (Hirzel et al., 2006).
 4 • The whole mapping process can be automated in R,
 5 which is attractive for projects where the maps need
 6 to be constantly up-dated. The only interventions ex-

7 pected from a user is to provide an estimate of the to-
 8 tal population of the species (N), the size of the area
 9 occupied (the home range area $area(B_{HR})$), and a list
 10 of environmental predictors.

11 Although we primarily advocate regression-kriging of

1 relative densities, we are convinced that a species' distri-
2 bution analyst should aim at producing all three types
3 of maps: (1) the ENFA-based HSI map showing the po-
4 tential habitat (Fig. 2b); (2) the species' distribution
5 (probability) map (Fig. 2f); and (3) the species' distri-
6 bution (density) map (Fig. 2e). ENFA can help under-
7 stand the relationship between species and environmen-
8 tal conditions and generate pseudo-absence locations.
9 The probability-based species' distribution map can be
10 used to delineate home range areas (probability > 0.5),
11 and the actual species' distribution map (density) quan-
12 tifies the spreading of the species and can be used to esti-
13 mate the number of individuals per area. Certainly, both
14 binomial GLM using indicators and logistic regression-
15 kriging using intensities are valid geostatistical tech-
16 niques to handle this type of data.

17 In addition, visual validation of the simulated absence
18 locations using Google Earth™ is fast, convenient and
19 leads to more useful geostatistical models. The simulated
20 absence points that are hard to validate visually (in the
21 case of mapping the white-tailed eagle, any area close
22 to wetlands and within natural forests), can be either
23 omitted from the analysis or visited on the field. For
24 example, in the case of mapping the white-tailed eagle
25 in Croatia, only 11 simulated absence points (out of 135)
26 were evaluated as unreliable and hence omitted from
27 further analysis.

28 The proposed technique to generate pseudo-absences
29 could be much improved. First, one could also build mod-
30 els that slowly increase the size of pseudo-absences until
31 the prediction accuracy stabilizes. In this approach, we
32 simply use a single number (number of pseudo-absences
33 = number of presences), which is somewhat naïve ap-
34 proach. More absences can be generated for species that
35 have narrow distributions/niche. Second, we ignore the
36 fact that our pseudo-absences might be bias, so that our
37 fitted model becomes over-optimistic. In the case of nar-
38 rowly distributed species in a wide region, the selection
39 of absences by our approach will generate absences far
40 from the environmental conditions of presences, and pos-
41 sibly artificially increase the coefficient of variation. Both
42 Chefaoui and Lobo (2008) and VanDerWal et al. (2009)
43 clearly demonstrate that the way the pseudo-absence are
44 generated has a significant impact on the resulting maps.
45 More research is certainly needed to analyze impacts of
46 techniques used to derive pseudo-absence, and the im-
47 pacts they make on the success of prediction models.

48 Although the cross-validation statistics shows that we
49 have produced a fairly accurate maps, in the case of map-

ping the distribution of root vole, it appears that the
output map mainly reflects geometry of the points (note
that even the buffer-based predictors we selected, also
reflect geometry rather than environmental features). To
prove this, we have excluded occurrence records from
the most densely populated area (*Biesbosch*), only to
see if the model would be able to predict the same pat-
tern (extrapolation). The result of this exercise showed
that our model is not successful in predicting the area
that has been masked out, which finally means that the
predictions by regression-kriging will be highly sensitive
to how representative is the sample data set considering
the whole population of this species.

Why does regression modeling performs poorer if only
presence data is used? Obviously, the sampling designs
are typically extremely biased considering the spreading
of points in the feature space (Sutherland, 2006), which
makes it very hard to estimate the true relationship be-
tween the distribution of a species and the ecological fac-
tors. It would be as if we would like to fit a model to esti-
mate people's weight using their height, and then sample
only extremely tall people. We illustrate this problem in
Fig. 3 and 12, where you can compare spreading of the
sampling points with occurrence only and with occur-
rence and simulated absence data. This shows that the
occurrence only samples for specialized species are heav-
ily clustered in the feature space (this is more distinct
for the white-tailed eagle than for root vole). After addi-
tion of the absence locations, the feature space is much
better represented, so that the output prediction maps
become more reliable.

The geostatistical technique used in this paper could
be expanded to accommodate even more complex data:
spatio-temporal observations, multiscale predictors,
clustered observations, trajectory-type of data, observa-
tions of multiple species and similar. In this article, we
rely on the state-of-the-art geostatistical mapping tech-
niques as implemented in the R package `gstat`. To run a
GLM and then explore the residuals e.g. via variograms,
is a routine practice, but it does not always tell the
whole story. In the case of multiple regression, covari-
ance matrix is used to account for spreading (clustering)
of the points in the space. In our example (Fig. 11c),
we fit a GLM that completely ignores location of the
points, which is obviously not statistically optimal. In
comparison, fitting a Generalized Linear Geostatistical
Model (GLGM) can be more conclusive since we can
model the spatial/regression terms more objectively
(Diggle and Ribeiro Jr, 2007). This was, for example,

1 the original motivation for the `geoRglm` and `spBayes`
2 packages (Ribeiro Jr et al., 2003). However, GLGMs are
3 not yet operational for geostatistical mapping purposes
4 and R code will need to be adapted.

5 Automated retrieval and generation of distribution maps
6 from biodiversity databases is possible but tricky. The
7 biggest problem for such applications will be the qual-
8 ity of the occurrence records — especially their spatial
9 reference that is extremely variable (from few meters to
10 tens of kilometers), but also the sampling bias, and the
11 matic quality of the records (incorrect taxonomic clas-
12 sification, incompleteness). Although Jimenez-Valverde
13 and Lobo (2006) in general do not see the sampling bias
14 as a big problem for the success of spatial prediction,
15 in the case of regression-kriging the output maps will
16 be heavily controlled by the sampling bias. Hence if you
17 are considering implementing this framework, have in
18 mind that your input data (point sample) should be a
19 good spatial representation of the whole population (it
20 is not so much about the size, but about how well are
21 all presence locations represented geographically). An-
22 other issue is the computational burden of the frame-
23 work we propose in Fig. 6 that can easily grow beyond
24 the capacities of standard PCs. In fact, we could imagine
25 that multiple species (all species in the GBIF database?)
26 could be handled at the same time through a co-kriging
27 framework, which would result in large quantity of mod-
28 els and combinations of models that would need to be
29 fitted. The benefits of running the models jointly versus
30 isolated modeling are obvious — this is rather a techni-
31 cal than conceptual problem. At this moment, we simply
32 can not foresee when would such type of analysis become
33 a reality.

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