Hierarchical Bayesian species distribution models with the **hSDM** R Package

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Ghislain Vieilledent[⋆,1] Cory Merow[2] Jérôme Guélat[3]
Andrew M. Latimer[4] Marc Kéry[3]
Alan E. Gelfand[5] Adam M. Wilson[6] Frédéric Mortier[1]
and John A. Silander Jr.[2]

[⋆] **Corresponding author:** \E-mail: ghislain.vieilledent@cirad.fr \Phone: +33.(0)4.67.59.37.51 \Fax: +33.(0)4.67.59.39.09
[1] **Cirad** – UMR AMAP, F–34398 Montpellier, France
[2] **University of Connecticut** – Department of Ecology and Evolutionary Biology, Storrs, CT 06269, USA
[3] **Swiss Ornithological Institute** – 6204 Sempach, Switzerland
[4] **University of California** – Department of Plant Sciences, Davis, CA 95616, USA
[5] **Duke University** – Department of Statistical Science, Durham, NC 27708, USA
[6] **Yale University** – Department of Ecology and Evolutionary Biology, New Haven, CT 06520, USA

Florebo quocumque ferar

“I will flower everywhere I am planted”

Abstract

Species distribution models (SDM) are useful tools to explain or predict species range from various environmental factors. SDM are thus widely used in conservation biology. Based on the observations of the species in the field (occurence or abundance data), SDM face two major problems which lead to bias in models' results: imperfect detection and spatial correlation of the observations.

At the present time, there is a lack of statistical tools to analyse large occurence or abundance data-sets (typically with tens of hundreds observation points) taking into account both imperfect detection and spatial correlation.

Here, we present the **hSDM** R package wich aims at providing user-friendly statistical functions to fill this gap. Functions were developped through a hierarchical Bayesian approach. They call a Metropolis-within-Gibbs algorithm coded in C to estimate model's parameters. Using compiled C code for the Gibbs sampler reduce drastically the computation time.

By making these new statistical tools available to the scientific community, we hope to democratize the use of more complex, but more realistic, statistical models for increasing knowledge in ecology and conserving biodiversity.

Keywords: R, C code, site-occupancy models, CAR process, spatial autocorrelation, biodiversity, SDM, niche modelling, detection probability, counts data, presence-absence, false absence, uncertainty, hierachical Bayesian models, Metropolis, MCMC, Gibbs sampler

CHAPTER 1

Introduction

1.1 Species distribution models

Biogeography is the study of the distribution of species over space and time and biogeographers try to understand the factors determining a species distribution (Smith, 1868; Wallace, 1876). A species distribution is often represented with a map (Wallace, 1876). This knowledge on the ecology of the species can be used for several applications such as conservation biology (Thuiller, 2014).

Species distribution modelling (alternatively known as "environmental niche modelling", "ecological niche modelling", "predictive habitat distribution modelling", and "climate envelope modelling") refers to the process of using computer algorithms to predict the distribution of species in geographic space on the basis of a mathematical representation of their known distribution in environmental space (i.e. the realized ecological niche). The environment is in most cases represented by climate data (such as temperature, and precipitation), but other variables such as soil type and land cover can also be used. Species distribution models (SDM) allow estimating the probability of presence or abundance of a species on a large geographical range using a limited number of species observations (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). Species observations can be occurence data (presence-absence data or presence only data) or abundance data (also known as count data).

1.2 Imperfect detection and spatial correlation of the observations

When considering presence-absence or abundance data for species distribution modelling, strong assumptions are usually made (Araujo & Guisan, 2006; Guisan & Thuiller, 2005; Sinclair *et al.*, 2010). Among these assumptions, two can lead to biased estimates of species distribution. The first one deals with imperfect detection and the second one with spatial correlation of the observations.

Regarding imperfect detection, occurrence of a species is typically not observed perfectly. Species traits, survey-specific conditions and site-specific characteristics may influence species detection probability which is often < 1 (Chen *et al.*, 2013). Thus, observations might include false absences. For example, the habitat can be suitable and the species is present but individuals have not been seen during the census. Or the habitat can be suitable but the species has not dispersed yet to the site (typical example for plant species, see Latimer *et al.* (2006)) or was not present on the site at the moment of the observation (typical example for animal species such as birds, see Kéry *et al.* (2005)). Treating observed occurrence and species distributions as the true occurrence and distribution, failing to make amendments for imperfect detection, may lead to problems in species distribution studies, habitat models and biodiversity management (Kéry & Schmidt, 2008; Lahoz-Monfort *et al.*, 2014; Latimer *et al.*, 2006).

Regarding spatial correlation, most species present geographical patchiness (positive spatial autocorrelation). This pattern is often driven by multiple causes that may be associated to exogenous environmental factors such as climate or soil (which might be partly taken into account in species distribution models), but also to endogeneous biotic processes, called contagious processes, such as dispersal, migration, conspecific attraction or mortality which are rarely considered (Dormann *et al.*, 2007; Legendre, 1993; Lichstein *et al.*, 2002; Sokal & Oden, 1978). Due to the contagious biotic processes, the presence or abundance of a species at one site is influenced by the presence or abundance of the species at surrounding sites. A species might be present at a site where the environment is less suitable because of the presence of the species at neighbouring sites where the environment is higly suitable. Thus, ignoring spatial correlation may lead to biased conclusions about ecological relationships (Lichstein *et al.*, 2002) and even invert the slope of relationships from non-spatial analysis in some particular cases (Kühn *et al.*, 2006). In addition to its ecological significance, spatial autocorrelation is problematic for classical species distribution models which assume independently distributed errors (Dormann *et al.*, 2007; Legendre, 1993; Lichstein *et al.*, 2002).

1.3 Methods and software to account for imperfect detection and spatial correlation

New classes of models, called site-occupancy models (MacKenzie *et al.*, 2002) or zero inflated binomial (ZIB) models (Latimer *et al.*, 2006) for presence-absence data and N-mixture models (Royle, 2004) or zero inflated Poisson (ZIP) models for abundance data (Flores *et al.*, 2009), were developed to solve the problems created by imperfect detection. These models combine two processes, an ecological process which describes habitat suitability and an observation process which takes into account imperfect detection. Because they mix probability distributions to represent the suitability and observation processes, these models have also been called mixture models. Mixture models use information from repeated observations at several sites to estimate detectability. Detectability may vary with site characteristics (e.g., habitat variables) or survey characteristics (e.g., weather conditions), whereas suitability relates only to site characteristics.

One additional point regarding site-occupancy models is that they form a unifying framework for a very large array of capture-recapture models to estimate population size in animal ecology (Nichols, 1992): using parameter-expanded data augmentation (Royle *et al.*, 2007), most models for population size, survival, recruitment and similar demographic quantities (presented in detail in standard references such as Williams *et al.* (2002), Royle & Dorazio (2008) and Kéry & Schaub (2012)) can be cast into the framework of an occupancy model and this makes their fitting much easier.

Several studies have demonstrated the advantages of site-occupancy and N-mixture models over classical models which do not consider imperfect detection. These studies have focused on the distribution of various plant or animal species in marine and terrestrial ecosystems (see Chen *et al.* (2013); Latimer *et al.* (2006) for plants, Dorazio *et al.* (2006); Kéry *et al.* (2005); Rota *et al.* (2011); Royle (2004) for birds, Kéry *et al.* (2010) for insects, Bailey *et al.* (2004); Chelgren *et al.* (2011); MacKenzie *et al.* (2002) for amphibians, Monk (2014) for fishes, and Gray (2012); Poley *et al.* (2014) for mammals).

Several softwares can be used to fit site-occupancy and N-mixture models (Table 1.2). Some are based on the maximum likelihood approach (such as the widely used free Windows programs **MARK** and **PRESENCE** and the R package **unmarked**) while other are based on the hierarchical Bayesian approach (such as **WinBUGS** and **OpenBUGS** programs).

Softwares	Socc	Nmix	Sp	Approach	OS	Reference	URL
PRESENCE	1	1	0	ML	MS-W	MacKenzie (2006)	PRESENCE
MARK	1	1	0	ML	MS-W	White & Burnham (1999)	MARK
E-SURGE	1	0	0	ML	MS-W	Choquet *et al.* (2009)	E-SURGE
unmarked	1	1	0	ML	cross-platform	Fiske & Chandler (2011)	unmarked
stocc	1	0	1	Bayesian	cross-platform	Johnson *et al.* (2013)	stocc
JAGS	1	1	0	Bayesian	cross-platform		JAGS
Stan	1	1	0	Bayesian	cross-platform	Stan Development Team (2014)	Stan
WinBUGS	1	1	1	Bayesian	MS-W	Lunn *et al.* (2009)	WinBUGS
OpenBUGS	1	1	1	Bayesian	cross-platform	Lunn *et al.* (2009)	OpenBUGS
hSDM	1	1	1	Bayesian	cross-platform		hSDM

Table 1.2: **Softwares available for modeling species distribution including imperfect detection.**

A variety of methods have been developed to correct for the effects of spatial autocorrelation in species distribution models based on occurence or abundance data (Cressie & Cassie, 1993; Dormann *et al.*, 2007; Keitt *et al.*, 2002; Miller *et al.*, 2007). In their review article, Dormann *et al.* (2007) described six different statistical approaches to account for spatial autocorrelation: autocovariate regression; spatial eigenvector mapping; generalised least squares; autoregressive models and generalised estimating equations.

Several studies have demonstrated the advantages of these mehods focusing on a variety of plant or animal species (see Gelfand *et al.* (2005); Kühn *et al.* (2006); Latimer *et al.* (2006) for plants, Lichstein *et al.* (2002) for birds, and Johnson *et al.* (2013); Poley *et al.* (2014) for mammals).

Among the methods available to account for spatial autocorrelation, conditional autoregressive (CAR) models, which incorporate spatial autocorrelation through a neighbourhood structure, are commonly implemented in statistical softwares (Dormann *et al.*, 2007). The most commonly used softwares to implement CAR models are **OpenBUGS** and **WinBUGS** softwares (Lunn *et al.*, 2009) which have in-built functions (`car.normal` and `car.proper`) to describe the CAR process. CAR models can also be implemented in **BayesX** (Brezger *et al.*, 2005) and in the following R packages: **R-INLA** (Rue *et al.*, 2009), **CARBayes** (Lee, 2013), **stocc** (for binary data only), **spatcounts** (for count data only), **CARramps** (for Gaussian data only), and **spdep** (for Gaussian data only) (Table 1.4).

Softwares	Type of data	Approach	OS	Reference	URL
OpenBUGS	all	Bayesian	cross-platform	Lunn *et al.* (2009)	OpenBUGS
WinBUGS	all	Bayesian	MS-W	Lunn *et al.* (2009)	WinBUGS
BayesX	all	Bayesian	cross-platform	Brezger *et al.* (2005)	BayesX
R-INLA	all	Bayesian	cross-platform	Rue *et al.* (2009)	R-INLA
CARBayes	all	Bayesian	cross-platform	Lee (2013)	CARBayes
stocc	all	Bayesian	cross-platform	Johnson *et al.* (2013)	stocc
spatcounts	count	Bayesian	cross-platform		spatcounts
CARramps	Gaussian	Bayesian	cross-platform		CARramps
spdep	Gaussian	ML	cross-platform		spdep
hSDM	binomial and count	Bayesian	cross-platform		hSDM

Table 1.4: **Softwares available for modeling species distribution including spatial autocorrelation.**

1.4 Objectives of the hSDM R package

Among the available statistical programs, only **OpenBUGS** can be used on any operating system to fit both site-occupancy or N-mixture models including also a spatial autocorrelation process (Table 1.2 and Table 1.4). One problem is that **OpenBUGS**, for such models, cannot handle large data-sets (typically, data-sets with tens of thousands sites). Moreover, for smaller data-sets, models can be fitted but computation time can be long due to the fact that the **OpenBUGS** code is interpreted and not compiled. For this reason, we decided to develop the **hSDM** (for hierarchical Bayesian species distribution models) R package. The **stocc** R package (Johnson *et al.*, 2013; Poley *et al.*, 2014), which can handle binary data only, has been developed for the same reasons. The **hSDM** package allows the user to fit mixture models which take into account imperfect detection (site-occupancy, N-mixture, ZIB and ZIP models) and account for spatial autocorrelation. Spatial autocorrelation is represented through an intrinsic CAR process (Besag *et al.*, 1991). Functions in the **hSDM** R package use an adaptive Metropolis algorithm (Metropolis *et al.*, 1953; Robert & Casella, 2004) in a Gibbs sampler (Casella & George, 1992; Gelfand & Smith, 1990) to obtain the posterior distribution of model's parameters. The Gibbs sampler is written in C code and compiled to optimize computation efficiency. Thus, the **hSDM** package can be used for very large data-sets while reducing drastically the computation time.

In this vignette, we present examples to illustrate the use of the **hSDM** package in the R statistical environment (R Development Core Team, 2014). Examples use virtual or real data-sets. Results obtained with functions in the **hSDM** package are compared with the results obtained with other softwares and models.

CHAPTER 2

Occurence data

2.1 Binomial model

2.1.1 Mathematical formulation

Let's consider a random variable y_i representing the total number of presences of a species after several visits v_i at a particular site i. Random variable y_i can take values from 0 to v_i and can be assumed to follow a Binomial distribution having parameters v_i and θ_i (Eq. 2.1). Parameter θ_i can be interpreted as the probability of presence of the species at site i . Using a logit link function, θ_i can be expressed as a linear model combining explicative variables X_i and parameters β (Eq. 2.1).

$$\begin{aligned} y_i &\sim \mathcal{B}inomial(v_i, \theta_i) \\ \text{logit}(\theta_i) &= X_i\beta \end{aligned} \tag{2.1}$$

Using this statistical model, we aim at representing a "suitability process". Given environmental variables X_i, how much is habitat at site i suitable for the species under consideration? Parameters β indicate how much each environmental variable contributes to the suitability process. Like every other function in the **hSDM** R package, function `hSDM.binomial()` estimates the parameters β of such a model in a Bayesian framework. Parameter inference is done using a Gibbs sampler including a Metropolis algorithm. The Gibbs sampler is coded in the C language to optimize computation efficiency.

2.1.2 Data generation

To explore the characteristics of the `hSDM.binomial()` function, we generate a virtual data-set on the basis of the Binomial model described above (Eq. 2.1). In the most general case, sites are visited once ($v_i = 1$). Thus, the random variable y_i follows a Bernoulli distribution of parameter θ_i and habitat characteristics X_i are fixed for site i. We generate a virtual data-set in this particular case. For data generation, we import virtual altitudinal data in R. Altitude is used as an explicative variable to determine habitat suitability, i.e. the probability of presence of a virtual species. Altitudinal data are loaded at the same time as the **hSDM** R package (data frame `altitude` in the working directory).

These data are transformed into a raster object using the function `rasterFromXYZ()` from the **raster** package. The raster has 2500 cells (50 columns and 50 rows) and the altitude ranges roughly between 100 and 600 m (Fig. 2.1). For linear models, explicative variables are usually centered and scaled to facilitate inference and interpretation of model parameters.

```r
# Load altitudinal data and create raster
library(raster)
library(hSDM)
data(altitude,package="hSDM")
alt.orig <- rasterFromXYZ(altitude)
extent(alt.orig) <- c(0,50,0,50)
plot(alt.orig)
# Center and scale altitudinal data
alt <- scale(alt.orig,center=TRUE,scale=TRUE)
plot(alt)
```

A linear model including altitude (variable denoted A) is used to compute the probability of presence of the species (Eq. 2.2).

$$\begin{gathered} y_i \sim \mathcal{B}ernoulli(\theta_i) \\ \text{logit}(\theta_i) = \beta_0 + \beta_1 A_i \end{gathered} \tag{2.2}$$

We fix the parameters to $\beta_0 = -1$ and $\beta_1 = 1$. The species has a higher probability of presence at higher altitudes (Fig. 2.2).

```r
# Target parameters
beta.target <- matrix(c(-1,1),ncol=1)
# Matrix of covariates (including the intercept)
ncells <- ncell(alt)
X <- cbind(rep(1,ncells),values(alt))
# Probability of presence as a linear function of altitude
logit.theta <- X %*% beta.target
```

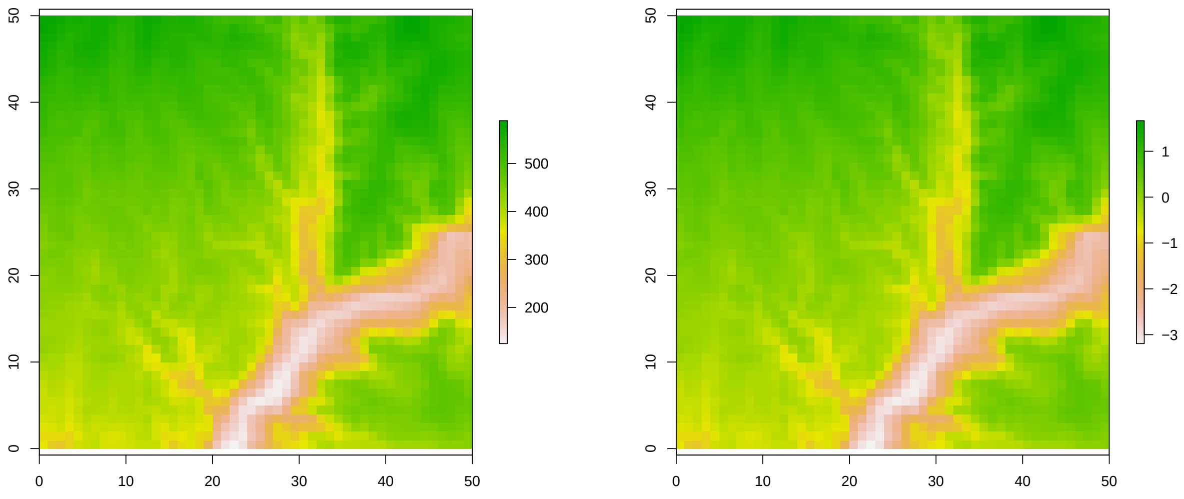


Figure 2.1: **Altitudinal data**. Original values (in m) on the left. Centered and scaled values on the right.

```r
theta <- inv.logit(logit.theta)
# Coordinates of raster cells
coords <- coordinates(alt)
# Transform the probability of presence into a raster
theta <- rasterFromXYZ(cbind(coords,theta))
# Color palette for probability plots
colRP <- colorRampPalette(c("white","yellow","orange",
                            "red","brown","black"))
# Plot the probability of presence
brks <- seq(0,1,length.out=100)
arg <- list(at=seq(0,1,length.out=5), labels=c("0","0.25","0.5","0.75","1"))
nb <- length(brks)-1
plot(theta,main="Initial probabilities",col=colRP(nb),
     breaks=brks,axis.args=arg,zlim=c(0,1))
```

We can assume a number n of sites in the landscape where we have been able to observe or not the presence of the species. We can simulate the presence or absence of the species at these n sites given our model (Fig. 2.3).

```r
# Number of observation sites
nsite <- 200
# Set seed for repeatability
seed <- 1234
# Sample the observations in the landscape
```

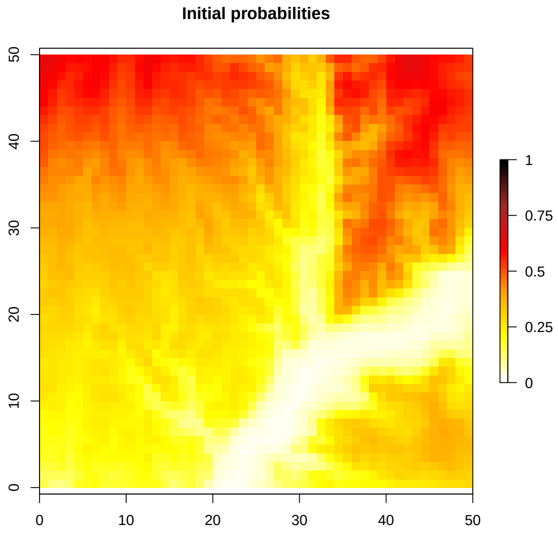


Figure 2.2: **Probability of presence**.

```
set.seed(seed)
x.coord <- runif(nsite,0,50)
set.seed(2*seed)
y.coord <- runif(nsite,0,50)
library(sp)
sites.sp <- SpatialPoints(coords=cbind(x.coord,y.coord))
# Extract altitude data for sites
alt.sites <- extract(alt,sites.sp)
# Compute theta for these observations
X.sites <- cbind(rep(1,nsite),alt.sites)
logit.theta.site <- X.sites %*% beta.target
theta.site <- inv.logit(logit.theta.site)
# Simulate observations
visits <- rep(1,nsite) # One visit per site for the moment
set.seed(seed)
Y <- rbinom(nsite,visits,theta.site)
# Group explicative and response variables in a data-frame
data.obs.df <- data.frame(Y,visits,alt=X.sites[,2])
# Transform observations in a spatial object
data.obs <- SpatialPointsDataFrame(coords=coordinates(sites.sp),
                                   data=data.obs.df)
# Plot observations
plot(alt.orig)
points(data.obs[data.obs$Y==1,],pch=16)
points(data.obs[data.obs$Y==0,],pch=1)
```

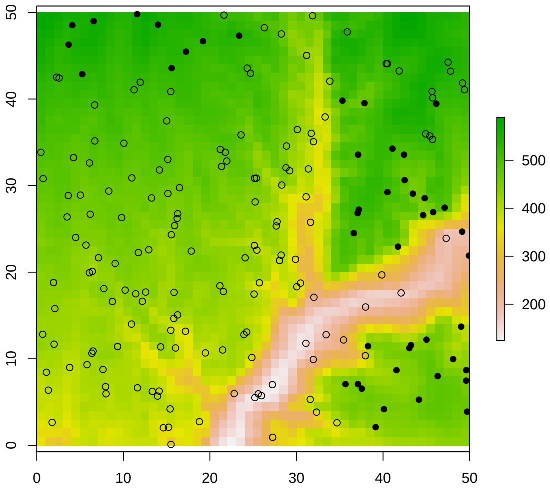


Figure 2.3: **Observation points**. Presences (full circles) and absences (empty circles) are localized on the altitude map (in m).

2.1.3 Parameter inference using the `hSDM.binomial()` function

The `hSDM.binomial()` function performs a Binomial logistic regression in a Bayesian framework. Before using this function we need to prepare a bit the data for predictions. We want to have predictions on the whole landscape, not only at observation points. To directly obtain these predictions, we can create a data frame including altitudinal data on the whole landscape. This data frame will be used for the `suitability.pred` argument. The data frame for predictions must include the same column names as those used in the formula for the `suitability` argument (i.e. "alt" our example).

```
data.pred <- data.frame(alt=values(alt))
```

We can now call the `hSDM.binomial()` function. Setting parameter `save.p` to 1, we can save in memory the MCMC values for predictions. These values can be used to compute several statistics for each predictions (mean, median, 95% quantiles). For example, mean and 95% quantiles are useful to estimate the uncertainty around the mean predictions.

```
mod.hSDM.binomial <- hSDM.binomial(presences=data.obs$Y,
                                   trials=data.obs$visits,
                                   suitability=~alt,
                                   data=data.obs,
                                   suitability.pred=data.pred,
                                   burnin=1000, mcmc=1000, thin=1,
                                   beta.start=0,
                                   mubeta=0, Vbeta=1.0E6,
                                   seed=1234, verbose=1, save.p=1)
```

2.1.4 Analysis of the results

The `hSDM.binomial()` function returns an MCMC (Markov chain Monte Carlo) for each parameter of the model and also for the model deviance. To obtain parameter estimates, MCMC values can be summarized through a call to the `summary()` function from the **coda** package. We can check that the values of the target parameters, $\beta_0 = -1$ and $\beta_1 = 1$, are within the 95% confidence interval of the parameter estimates.

```
summary(mod.hSDM.binomial$mcmc)

##
## Iterations = 1001:2000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                      Mean     SD Naive SE Time-series SE
## beta.(Intercept)  -1.4127 0.2255 0.007131        0.02234
## beta.alt           0.9844 0.2961 0.009363        0.03277
## Deviance         202.1663 2.2848 0.072252        0.16607
##
## 2. Quantiles for each variable:
##
##                      2.5%      25%      50%     75%    97.5%
## beta.(Intercept)  -1.8432  -1.5566  -1.4128  -1.265  -0.9583
## beta.alt           0.4509   0.7832   0.9692   1.175   1.6814
## Deviance         199.8948 200.4900 201.3279 203.193 207.6644
```

Parameters estimates can be compared to results obtained with the `glm()` function.

```
#== glm results for comparison
mod.glm <- glm(cbind(Y,visits-Y)~alt,family="binomial",data=data.obs)
summary(mod.glm)
```

```
##
## Call:
## glm(formula = cbind(Y, visits - Y) ~ alt, family = "binomial",
##     data = data.obs)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -1.1290  -0.7509  -0.6041  -0.1749   2.7277
##
## Coefficients:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -1.3822     0.1966  -7.032 2.03e-12 ***
## alt           0.9518     0.2764   3.444 0.000573 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##     Null deviance: 215.71  on 199  degrees of freedom
## Residual deviance: 199.79  on 198  degrees of freedom
## AIC: 203.79
##
## Number of Fisher Scoring iterations: 5
```

MCMC can also be graphically summarized with a call to the `plot.mcmc()` function, also in the **coda** package. MCMC are plotted with a trace of the sampled output and a density estimate for each variable in the chain (Fig. 2.4). This plot can be used to visually check that the chains have converged.

```
plot(mod.hSDM.binomial$mcmc)
```

The `hSDM.binomial()` function also returns two other objects. The first one, `theta.latent`, is the predictive posterior mean of the latent variable θ (the probability of presence) for each observation.

```
str(mod.hSDM.binomial$theta.latent)

##  num [1:200] 0.2191 0.0992 0.1038 0.1878 0.221 ...

summary(mod.hSDM.binomial$theta.latent)

##    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
##  0.0171  0.1540  0.2179  0.2297  0.2974  0.4970
```

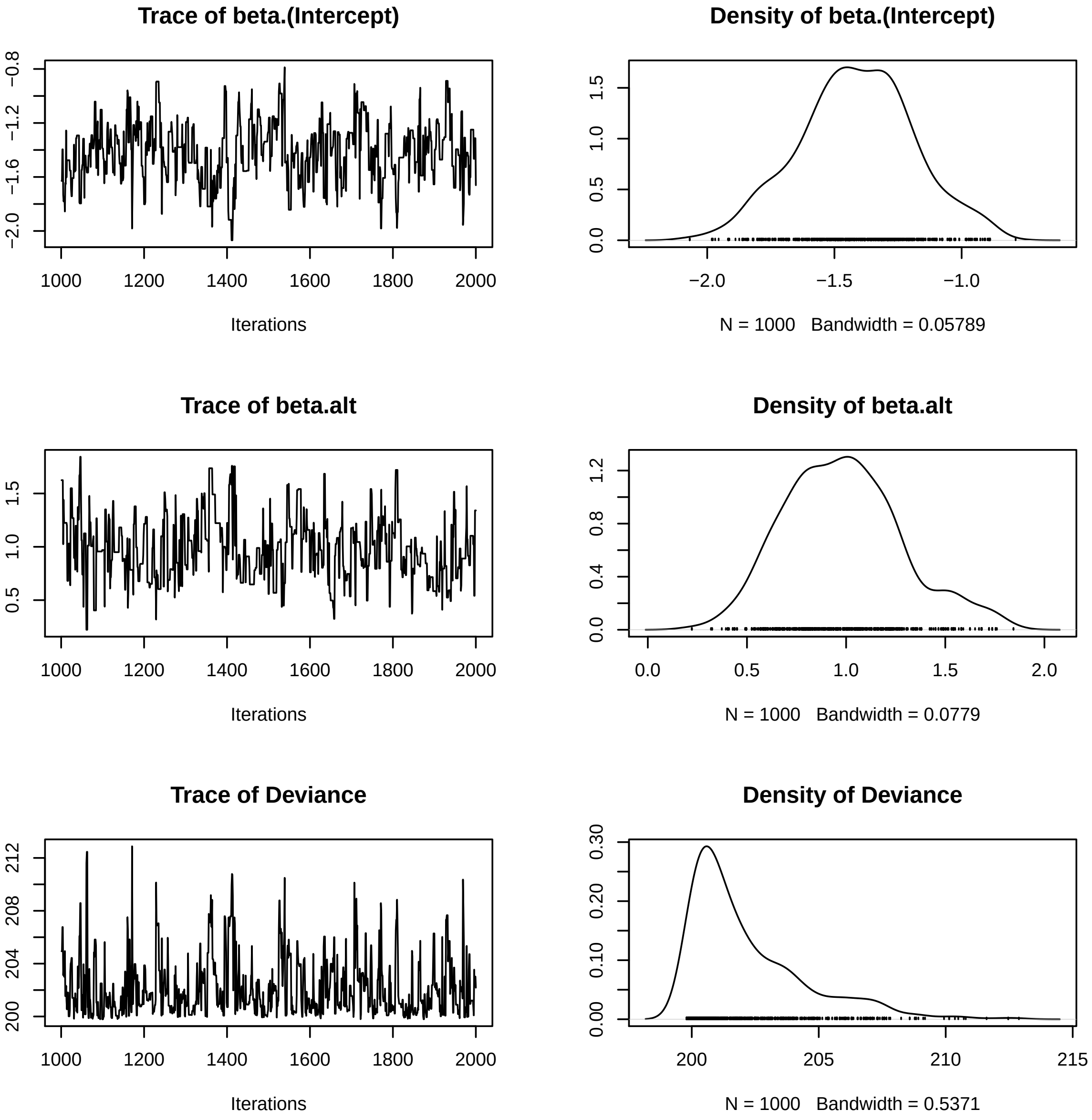


Figure 2.4: **Trace and density estimate for each variable of the MCMC.**

The second one, **theta.pred** is the set of sampled values from the predictive posterior (if parameter **save.p** is set to 1) or the predictive posterior mean (if **save.p** is set to 0) for each prediction. In our example, **save.p** is set to 1 and **theta.pred** is an **mcmc** object. Values in **theta.pred** can be used to plot the predicted probability of presence on the whole landscape and the uncertainty associated to predictions (Fig 2.5).

```
# Create a raster for predictions
theta.pred.mean <- raster(theta)
# Create rasters for uncertainty
theta.pred.2.5 <- theta.pred.97.5 <- raster(theta)
# Attribute predicted values to raster cells
theta.pred.mean[] <- apply(mod.hSDM.binomial$theta.pred,2,mean)
theta.pred.2.5[] <- apply(mod.hSDM.binomial$theta.pred,2,quantile,0.025)
theta.pred.97.5[] <- apply(mod.hSDM.binomial$theta.pred,2,quantile,0.975)
# Plot the predicted probability of presence and uncertainty
plot(theta.pred.mean,main="Mean",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
plot(theta.pred.2.5,main="Quantile 2.5 %",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
plot(theta.pred.97.5,main="Quantile 97.5 %",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
```

In our example, we can compare the predictions to the initial probability of presence computed from our model to check that our predictions are correct (Fig. 2.6).

```
# Comparing predictions to initial values
plot(theta[],theta.pred.mean[],cex.lab=1.4,xlim=c(0,1),ylim=c(0,1))
points(theta[],theta.pred.2.5[],cex.lab=1.4,col=grey(0.5))
points(theta[],theta.pred.97.5[],cex.lab=1.4,col=grey(0.5))
abline(a=0,b=1,col="red",lwd=2)
```

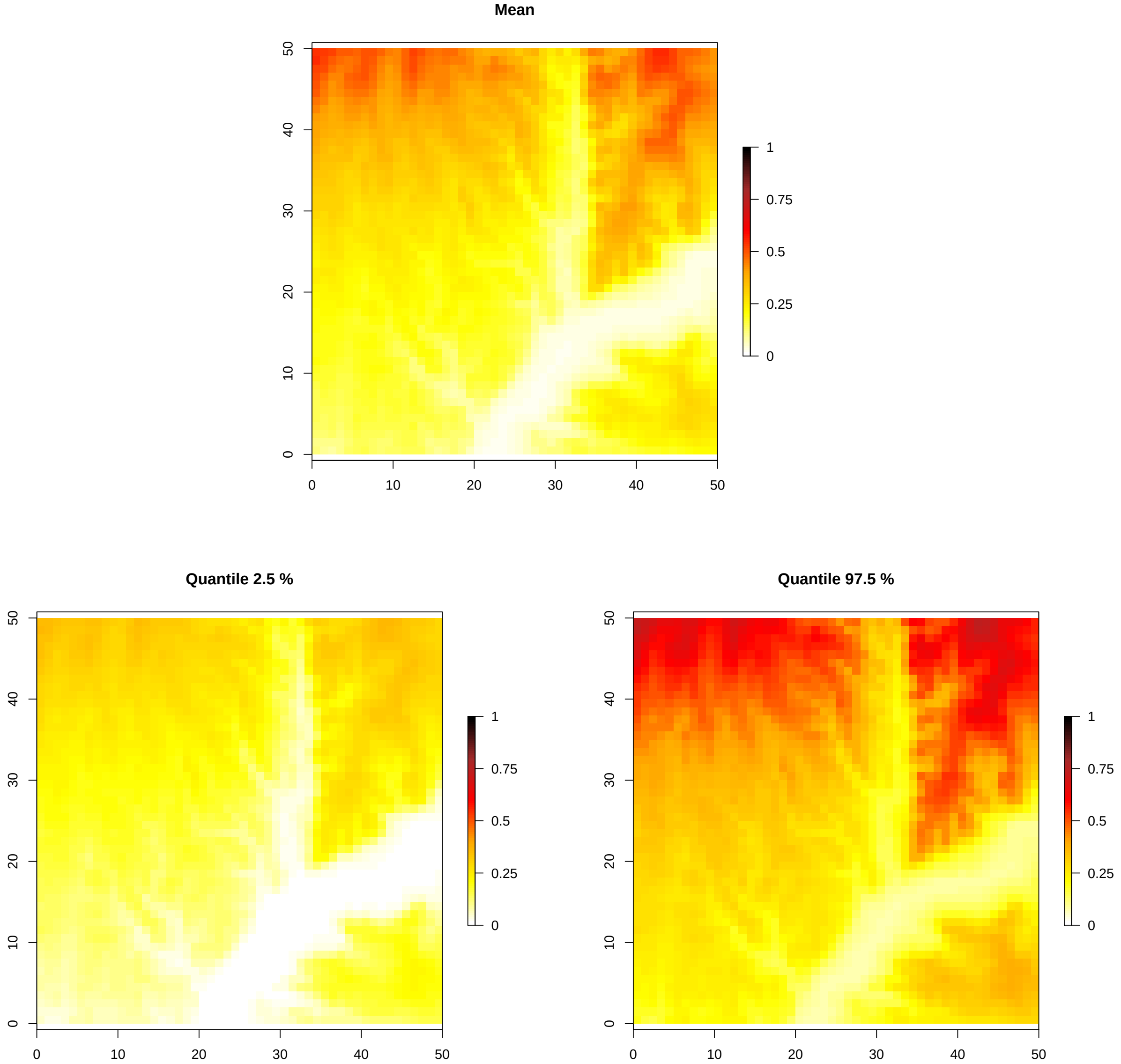


Figure 2.5: **Predicted probability of presence and uncertainty of predictions**. Mean probability of presence (top), predictions at 2.5% quantile (bottom left) and 97.5% quantile (bottom right) can be plotted from the `mcmc` object `plot.p.pred` returned by function `hSDM.binomial()`.

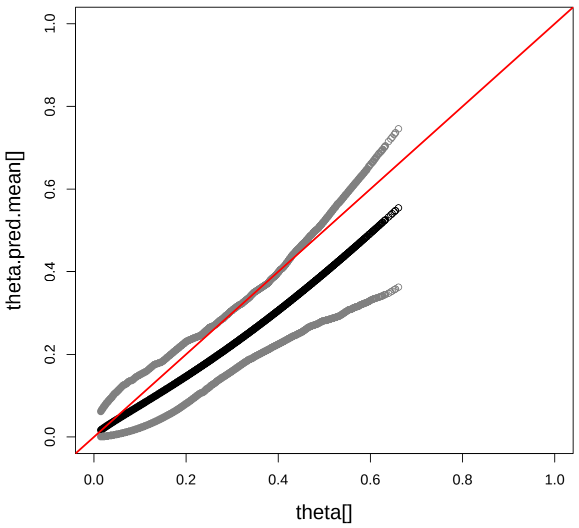


Figure 2.6: **Predicted vs. initial probabilities of presence**. Initial probabilities of presence are computed from the Binomial logistic regression model with target parameters.

2.2 Site-occupancy model

2.2.1 Mathematical formulation

Let's consider the random variable z_i describing habitat suitability at site i. The random variable z_i can take value 1 or 0 depending on the fact that the habitat is suitable ($z_i = 1$) or not ($z_i = 0$). Habitat at site i is described by environmental variables X_i. Random variable z_i can be assumed to follow a Bernoulli distribution of parameter θ_i (Eq. 2.3). In this case, θ_i is the probability that the habitat is suitable. Several visits at time t_1, t_2, etc., can occur at site i. Let's consider the random variable y_{it} representing the presence of the species at site i and time t. The species is observed at site i ($\sum_t y_{it} \geq 1$) only if the habitat is suitable ($z_i = 1$). The species is unobserved at site i ($\sum_t y_{it} = 0$) if the habitat is not suitable ($z_i = 0$), or if the habitat is suitable ($z_i = 1$) but the probability δ_{it} of detecting the species at site i and time t is inferior to 1. Thus, y_{it} is assumed to follow a Bernoulli distribution of parameter $z_i \delta_{it}$. Using a logit link function, δ_{it} can be expressed as a linear model combining explicative variables W_{it} and parameters γ (Eq. 2.3). Typically, explicative variables W_{it} are site characteristics (e.g., habitat variables) or survey characteristics (e.g., weather conditions). The function `hSDM.siteocc()` estimates the parameters β and γ of such a model.

$$
\begin{gathered}
\textbf{Ecological process:}\\
z_i \sim \mathcal{B}ernoulli(\theta_i)\\
\text{logit}(\theta_i) = X_i\beta\\
\\
\textbf{Observation process:}\\
y_{it} \sim \mathcal{B}ernoulli(z_i\delta_{it})\\
\text{logit}(\delta_{it}) = W_{it}\gamma
\end{gathered}
\tag{2.3}
$$

2.2.2 Data generation

To explore the characteristics of the `hSDM.siteocc()` function, we can generate a new virtual data-set on the basis of the site-occupancy model described above (Eq. 2.3). In the most general case, the observation protocol includes severals visits with varying survey conditions (e.g. weather conditions) to several sites with fixed sites characteristics (e.g. habitat variables). We will generate a virtual data-set following this protocole using the altitudinal data in the previous example for the Binomial model (Sec. 2.1).

We draw at random the number of visits at each site of the previous example (see Fig. 2.3 of Sec. 2.1).

```r
# Number of visits associated to each observation point
set.seed(seed)
visits <- rpois(nsite,lambda=3) # Mean number of visits ~3
# NB: Setting a too low mean number of visits per site (lambda < 3)
# leads to inaccurate parameter estimates
visits[visits==0] <- 1 # Number of visits must be > 0
# Vector of observation sites
sites <- vector()
for (i in 1:nsite) {
    sites <- c(sites,rep(i,visits[i]))
}
```

The survey conditions for each visit are determined by two explicative variables, w_1 and the altitude (variable denoted A). These two variables explain the observability of the species (Eq. 2.4).

$$
\begin{gathered}
y_{it} \sim \mathcal{B}ernoulli(z_i\delta_{it})\\
\text{logit}(\delta_{it}) = \gamma_0 + \gamma_1 w_{1it} + \gamma_2 A_{it}
\end{gathered}
\tag{2.4}
$$

We fix the intercept and the effects of these two variables: $\gamma_0 = -1$, $\gamma_1 = 1$ and $\gamma_2 = -1$ for determining the detection probability. In our case, the detection probability decreases with altitude ($\gamma_2 < 0$).

```r
# Explicative variables for observation process
nobs <- sum(visits)
set.seed(seed)
w1 <- rnorm(n=nobs,0,1)
W <- cbind(rep(1,nobs),w1,X.sites[sites,2])
# Target parameters for observation process
gamma.target <- matrix(c(-1,1,-1),ncol=1)
```

Using covariates and parameters for the two processes, we compute the probability that the habitat is suitable (θ_i) and the species detection probability (δ_i). We also draw the random variables z_i and y_i and construct the observation data-set.

```r
# Ecological process (suitability)
logit.theta.site <- X.sites %*% beta.target
theta.site <- inv.logit(logit.theta.site)
set.seed(seed)
Z <- rbinom(nsite,1,theta.site)

# Observation process (detectability)
logit.delta.obs <- W %*% gamma.target
delta.obs <- inv.logit(logit.delta.obs)
set.seed(seed)
Y <- rbinom(nobs,1,delta.obs*Z[sites])

# Data-sets
data.obs <- data.frame(Y,w1,alt=X.sites[sites,2],site=sites)
data.suit <- data.frame(alt=X.sites[,2])
```

2.2.3 Parameter inference using the `hSDM.siteocc()` function

The `hSDM.siteocc()` function estimates the parameter of a site-occupancy model in a Bayesian framework.

```r
mod.hSDM.siteocc <- hSDM.siteocc(# Observations
                                 presence=data.obs$Y,
                                 observability=~w1+alt,
                                 site=data.obs$site,
                                 data.observability=data.obs,
                                 # Habitat
                                 suitability=~alt,
                                 data.suitability=data.suit,
                                 # Predictions
                                 suitability.pred=data.pred,
                                 # Chains
                                 burnin=1000, mcmc=1000, thin=1,
                                 # Starting values
                                 beta.start=0,
                                 gamma.start=0,
                                 # Priors
                                 mubeta=0, Vbeta=1.0E6,
                                 mugamma=0, Vgamma=1.0E6,
                                 # Various
                                 seed=1234, verbose=1, save.p=1)
```

2.2.4 Analysis of the results

```
summary(mod.hSDM.siteocc$mcmc)

##
## Iterations = 1001:2000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                        Mean     SD Naive SE Time-series SE
## beta.(Intercept)   -0.8013 0.3357 0.010617        0.03161
## beta.alt            1.1533 0.4902 0.015501        0.04079
## gamma.(Intercept)  -1.2915 0.2261 0.007149        0.02448
## gamma.w1            0.9379 0.2273 0.007188        0.02099
## gamma.alt          -0.9588 0.2173 0.006871        0.01604
## Deviance          296.0651 3.2473 0.102688        0.28808
##
## 2. Quantiles for each variable:
##
##                        2.5%      25%      50%      75%     97.5%
## beta.(Intercept)   -1.4767  -1.0039  -0.8107  -0.5990  -0.08896
## beta.alt            0.4223   0.7532   1.0780   1.4936   2.21094
## gamma.(Intercept)  -1.7531  -1.4323  -1.2875  -1.1551  -0.77827
## gamma.w1            0.5312   0.7753   0.9254   1.0772   1.46189
## gamma.alt          -1.3678  -1.1046  -0.9737  -0.8099  -0.52155
## Deviance          291.8021 293.5787 295.4287 298.0085 303.22179
```

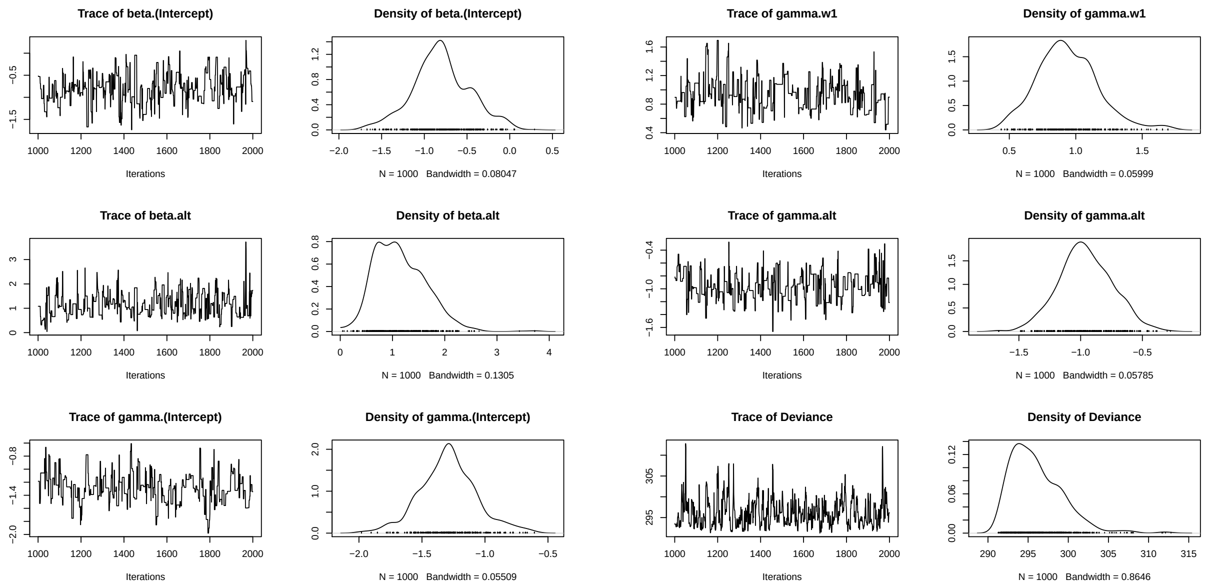


Figure 2.7: **Trace and density estimate for each variable of the MCMC.**

```
plot(mod.hSDM.siteocc$mcmc)
```

```
# Create a raster for predictions
theta.pred.mean <- raster(theta)
# Computing mean and quantiles for uncertainty
theta.pred.mean[] <- apply(mod.hSDM.siteocc$theta.pred,2,mean)
theta.pred.2.5 <- apply(mod.hSDM.siteocc$theta.pred,2,quantile,0.025)
theta.pred.97.5 <- apply(mod.hSDM.siteocc$theta.pred,2,quantile,0.975)
# Plot the predicted probability of presence
plot(theta.pred.mean,main="hSDM.siteocc",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
```

```
# Comparing predictions to initial values
plot(theta[],theta.pred.mean[],xlim=c(0,1),ylim=c(0,1),cex.lab=1.4)
points(theta[],theta.pred.2.5[],cex.lab=1.4,col=grey(0.5))
points(theta[],theta.pred.97.5[],cex.lab=1.4,col=grey(0.5))
abline(a=0,b=1,col="red",lwd=2)
```

Parameters estimates can be compared to results obtained with the `glm()` function assuming a perfect detection.

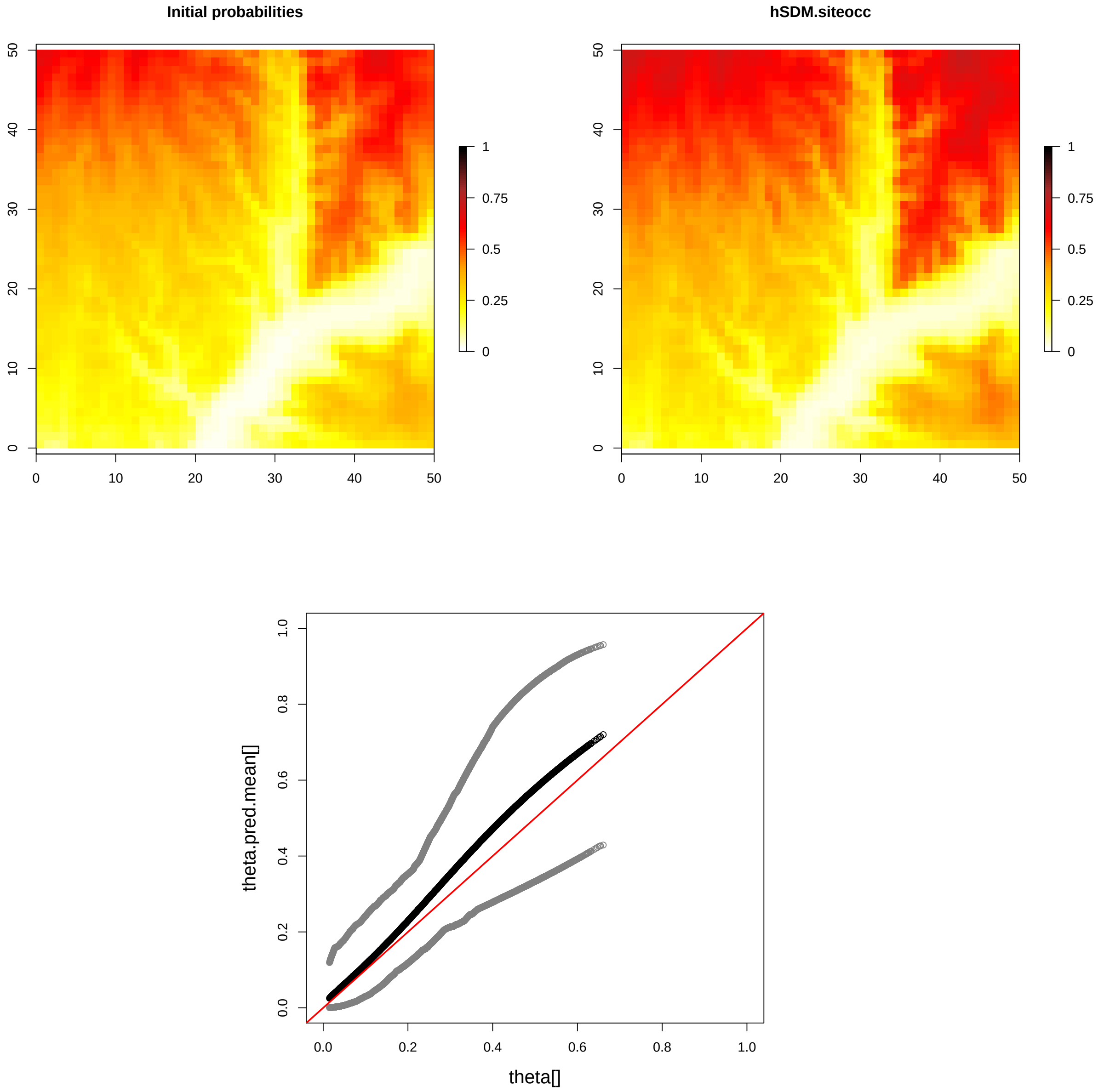


Figure 2.8: **Comparing predicted probability of presence with initial probabilities.**

```
#== glm results for comparison
mod.glm <- glm(Y~alt,family="binomial",data=data.obs)
summary(mod.glm)

##
## Call:
## glm(formula = Y ~ alt, family = "binomial", data = data.obs)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -0.5284  -0.4417  -0.4270  -0.4079   2.2650
##
## Coefficients:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -2.3175     0.1443 -16.056   <2e-16 ***
## alt          -0.1330     0.1289  -1.031    0.302
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##     Null deviance: 362.10  on 594  degrees of freedom
## Residual deviance: 361.08  on 593  degrees of freedom
## AIC: 365.08
##
## Number of Fisher Scoring iterations: 5
```

```
# Create a raster for predictions
theta.pred.glm <- raster(theta)
# Attribute predicted values to raster cells
theta.pred.glm[] <- predict.glm(mod.glm,newdata=data.pred,type="response")
# Plot the predicted probability of presence
plot(theta.pred.glm,main="GLM",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
```

```
# Comparing predictions to initial values
plot(theta[],theta.pred.glm[],
     xlim=c(0,1),ylim=c(0,1),cex.lab=1.4)
points(theta[],theta.pred.mean[],col=grey(0.5))
abline(a=0,b=1,col="red",lwd=2)
```

On Figure 2.9, we can see that using a GLM in the case of imperfect detection can lead to very inaccurate parameter estimates and predictions for the probability of presence of the species. This is particularly true when detection probability is negatively correlated to presence probability (through an explicative variable such as the altitude in our example). This has been clearly demonstrated in an article by Lahoz-Monfort *et al.* (2014).

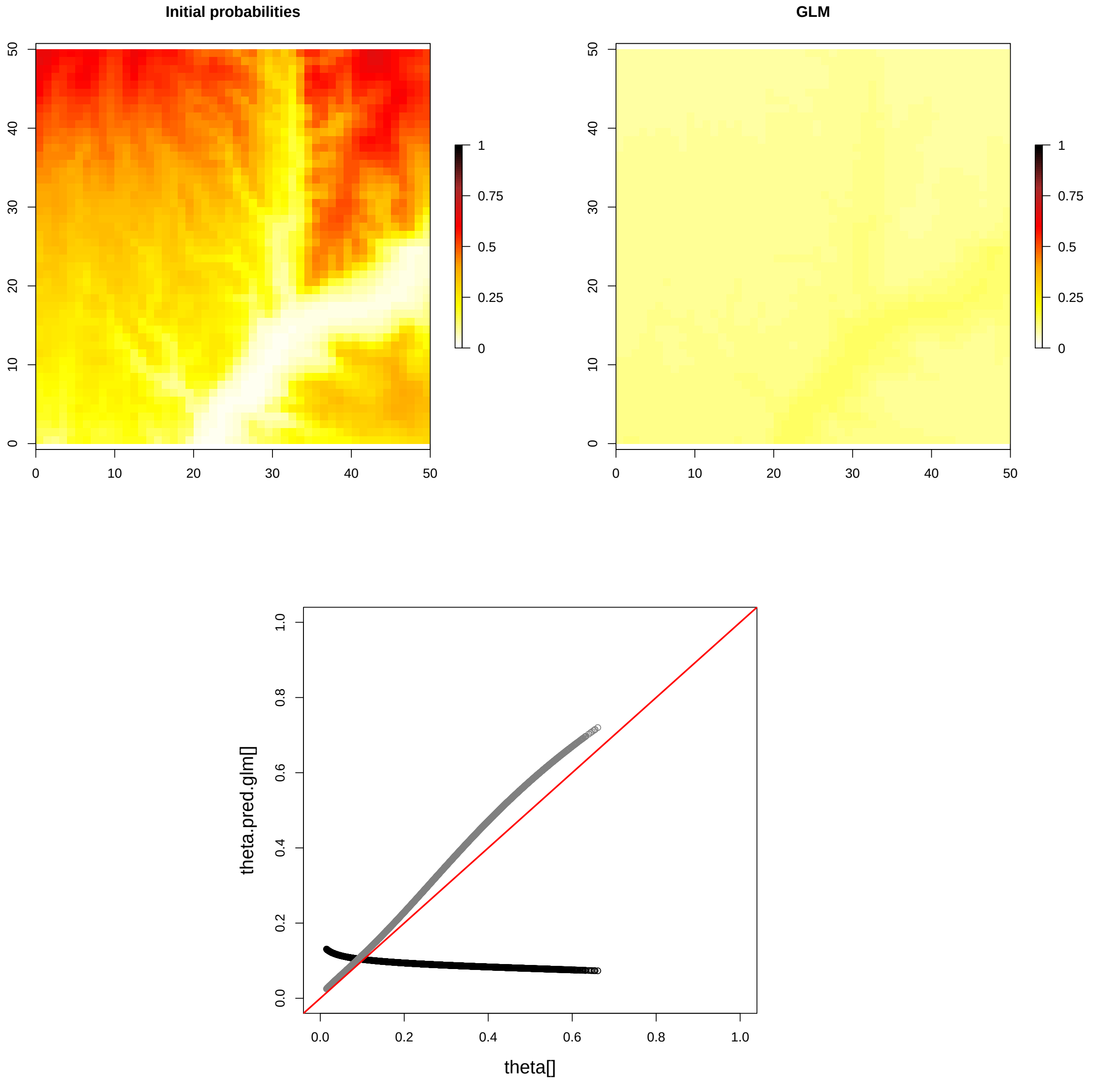


Figure 2.9: **Comparing predicted probability of presence using GLM with initial probabilities.** Grey dots figure the predictions with the `hSDM.siteocc()` function whereas black dots figure the prediction using the `glm()` function.

2.3 Binomial iCAR model

2.3.1 Mathematical formulation

2.3.2 Data generation with iCAR

```r
# Rasters must be projected to correctly compute the neighborhood
crs(alt) <- '+proj=utm +zone=1'
# Neighborhood matrix
neighbors.mat <- adjacent(alt, cells=c(1:ncells), directions=8,
                          pairs=TRUE, sorted=TRUE)
# Number of neighbors by cell
n.neighbors <- as.data.frame(table(as.factor(neighbors.mat[,1])))[,2]
# Adjacent cells
adj <- neighbors.mat[,2]
# Generate symmetric adjacency matrix, A
A <- matrix(0,ncells,ncells)
index.start <- 1
for (i in 1:ncells) {
    index.end <- index.start+n.neighbors[i]-1
    A[i,adj[c(index.start:index.end)]] <- 1
    index.start <- index.end+1
}
```

```r
# Function to draw in a multivariate normal
rmvn <- function(n, mu=0, V=matrix(1), seed=1234) {
    p <- length(mu)
    if (any(is.na(match(dim(V), p)))) {
        stop("Dimension problem!")
    }
    D <- chol(V)
    set.seed(seed)
    t(matrix(rnorm(n*p),ncol=p)%*%D+rep(mu,rep(n,p)))
}
```

```r
# Generate spatial random effects
Vrho.target <- 5 # Variance of spatial random effects
d <- 1  # Spatial dependence parameter = 1 for intrinsic CAR
Q <- diag(n.neighbors)-d*A + diag(.0001,ncells) # Add small constant to
                                                # make Q non-singular
covrho <- Vrho.target*solve(Q) # Covariance of rhos
rho <- c(rmvn(1,mu=rep(0,ncells),V=covrho,seed=seed)) # Spatial Random Effects
rho <- rho-mean(rho) # Centering rhos on zero
```

```
rho.rast <- rasterFromXYZ(xyz=cbind(coords,rho))
# Probability of presence
theta.cells <- inv.logit(X %*% beta.target + rho)
theta <- rasterFromXYZ(cbind(coords,theta.cells))
```

```
# Ecological process (suitability)
cells <- extract(alt,sites.sp,cell=TRUE)[,1]
logit.theta.site <- X.sites %*% beta.target + rho[cells]
theta.site <- inv.logit(logit.theta.site)
set.seed(seed)
Y <- rbinom(nsite,visits,theta.site)
# Data-sets
data.suit <- data.frame(Y,visits,alt=X.sites[,2],cells)
data.pred <- data.frame(alt=values(alt),cell=c(1:ncells))
# Transform observations into a spatial object
data.suit <- SpatialPointsDataFrame(coords=coordinates(sites.sp),
                                    data=data.suit)
```

```
# Plot spatial random effects
plot(rho.rast,main="Spatial random effects")
# Plot initial probabilities and observations
plot(theta,main="Initial probabilities (iCAR model)",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
points(data.suit[data.suit$Y>0,],pch=16)
points(data.suit[data.suit$Y==0,],pch=1)
```

2.3.3 Parameter inference using the hSDM.binomial.iCAR() function

```
Start <- Sys.time() # Start the clock
mod.hSDM.binomial.iCAR <- hSDM.binomial.iCAR(presences=data.suit$Y,
                                             trials=data.suit$visits,
                                             suitability=~alt,
                                             spatial.entity=data.suit$cells,
                                             data=data.suit,
                                             n.neighbors=n.neighbors,
                                             neighbors=adj,
                                             suitability.pred=data.pred,
                                             spatial.entity.pred=data.pred$cell,
                                             burnin=5000, mcmc=5000, thin=5,
```

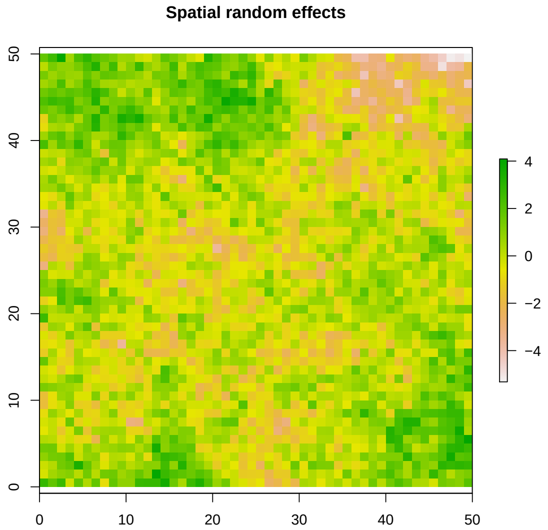


Figure 2.10: **Spatial random effects.**

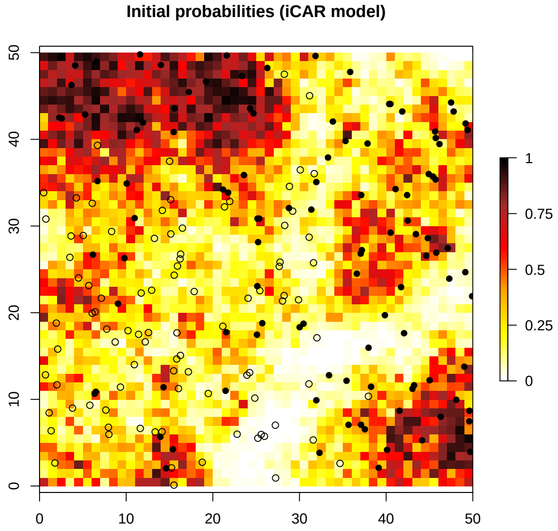


Figure 2.11: **Initial probability of presence and observations.** Presences (full circles) and absences (empty circles).

```
                                             beta.start=0,
                                             Vrho.start=1,
                                             priorVrho="1/Gamma",
                                             mubeta=0, Vbeta=1.0E6,
                                             shape=1, rate=1,
                                             Vrho.max=10,
                                             seed=1234, verbose=1,
                                             save.rho=1, save.p=0)
Time.hSDM <- difftime(Sys.time(),Start,units="sec") # Time difference
```

2.3.4 Analysis of the results with iCAR

```
summary(mod.hSDM.binomial.iCAR$mcmc)

##
## Iterations = 5001:9996
## Thinning interval = 5
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                      Mean      SD Naive SE Time-series SE
## beta.(Intercept)  -0.9929  0.1420 0.004490       0.009587
## beta.alt           0.7497  0.1943 0.006144       0.022300
## Vrho               2.8003  0.9797 0.030981       0.315369
## Deviance         327.8354 15.1139 0.477945       2.768131
##
## 2. Quantiles for each variable:
##
##                      2.5%     25%      50%      75%    97.5%
## beta.(Intercept)  -1.2754  -1.095  -1.0008  -0.8909  -0.7202
## beta.alt           0.4132   0.609   0.7363   0.8768   1.1585
## Vrho               1.3606   2.031   2.6470   3.4203   5.0378
## Deviance         297.8710 317.162 327.3254 338.7201 356.8067
```

```
# Predictions for spatial random effects
rho.pred <- apply(mod.hSDM.binomial.iCAR$rho.pred,2,mean)
rho.pred.rast <- rasterFromXYZ(cbind(coords,rho.pred))
plot(rho.pred.rast,main="Predictions rho")
# Predictions for probability of presence
```

```r
theta.pred <- mod.hSDM.binomial.iCAR$theta.pred
theta.pred.rast <- rasterFromXYZ(cbind(coords,theta.pred))
plot(theta.pred.rast,main="Predictions theta",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
# Predictions vs. initial spatial random effects
plot(rho[-cells],rho.pred[-cells],xlab="rho target",ylab="Predictions rho")
points(rho[cells],rho.pred[cells],col="blue",pch=16)
abline(a=0,b=1,col="red")
# Predictions vs. initial probabilities
plot(values(theta)[-cells],theta.pred[-cells],xlab="theta target",
     ylab="Predictions theta")
points(values(theta)[cells],theta.pred[cells],col="blue",pch=16)
abline(a=0,b=1,col="red")
```

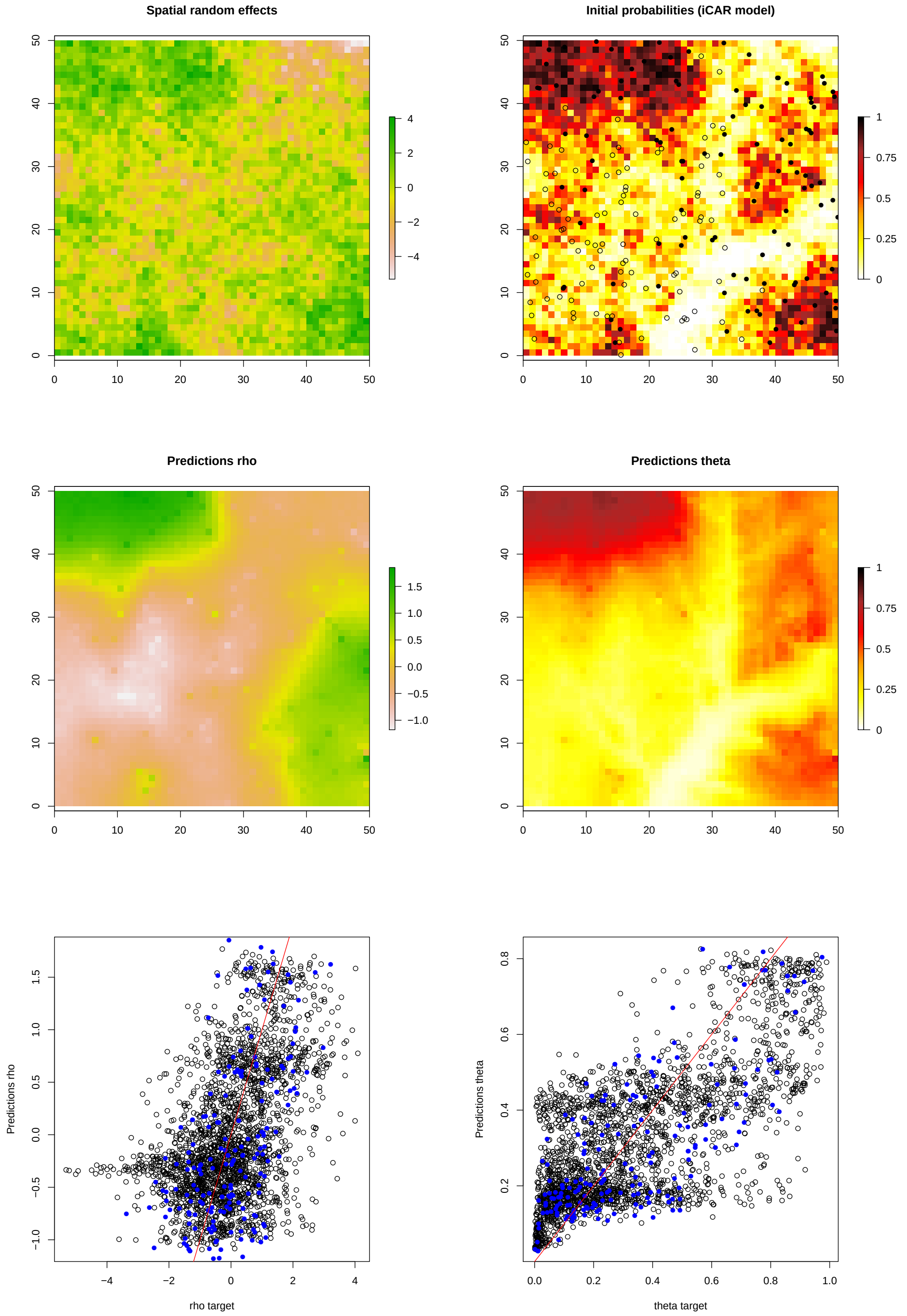


Figure 2.12: **Predictions vs. initial values**

2.3.5 Comparison with OpenBUGS results

```
# BUGS model
modelBUGS1.txt <-
"model {

# likelihood
for (n in 1:nobs) {
  y[n] ~ dbin(theta[n], visits[n])
  logit(theta[n]) <- Xbeta[n] + rho[IdCell[n]]
  Xbeta[n] <- beta[1] + beta[2]*x1[n]
}

# CAR prior distribution for spatial random effects:
rho[1:ncells] ~ car.normal(adj[], weights[], num[], tau)
for (k in 1:sumNumNeigh) {
  weights[k] <- 1 # set equal weights for all neighbors
}

# Other priors
for (i in 1:2) {
  beta[i] ~ dnorm(0,1.0E-6)
}
Vrho <- 1/tau
tau ~ dgamma(1,1)

}"

# Create model.txt file in the working directory
system(paste("echo \"",modelBUGS1.txt,"\" > modelBUGS1.txt",sep=""))

# Data for OpenBUGS
y <- data.suit$Y
visits <- data.suit$visits
IdCell <- data.suit$cells
x1 <- data.suit$alt
num <- n.neighbors
adj <- adj
nobs <- length(y)
ncells <- length(n.neighbors)
sumNumNeigh <- length(adj)
data <- list("y","visits","IdCell","x1","num",
             "adj","nobs","ncells","sumNumNeigh")

# Inits
```

Value	OpenBUGS	hSDM
β_0	-0.99	-0.99
β_{alt}	0.73	0.75
V_ρ	2.72	2.80
Deviance	328.62	327.84
Time (secs)	91	7

Table 2.1: **Comparison between hSDM and OpenBUGS outputs.**

```r
inits <- list(list(beta=rep(0,2),rho=rep(0,ncells),tau=1))

# OpenBUGS call
library(R2OpenBUGS)
Start <- Sys.time() # Start the clock
Open <- bugs(data,inits,
             model.file="modelBUGS1.txt",
             parameters=c("beta","Vrho","rho"),
             n.chains=1,
             OpenBUGS.pgm="/usr/bin/OpenBUGS",
             n.iter=2000,
             n.burnin=1000,
             n.thin=5,
             DIC=TRUE,
             debug=FALSE,
             clearWD=FALSE)
Time.OpenBUGS <- difftime(Sys.time(),Start,units="sec") # Time difference

# Time difference
ratio.time <- as.numeric(Time.OpenBUGS)/as.numeric(Time.hSDM)
ratio.time # For this example, hSDM is X times faster

#== Outputs
Open$DIC
Open$pD
beta.pred.Open <- apply(Open$sims.list$beta,2,mean)
Vrho.pred.Open <- mean(Open$sims.list$Vrho)
deviance.Open <- mean(Open$sims.list$deviance)
rho.OpenBUGS <- apply(Open$sims.list$rho,2,mean)
plot(rho.pred,rho.OpenBUGS)
abline(a=0,b=1,col="red")
```

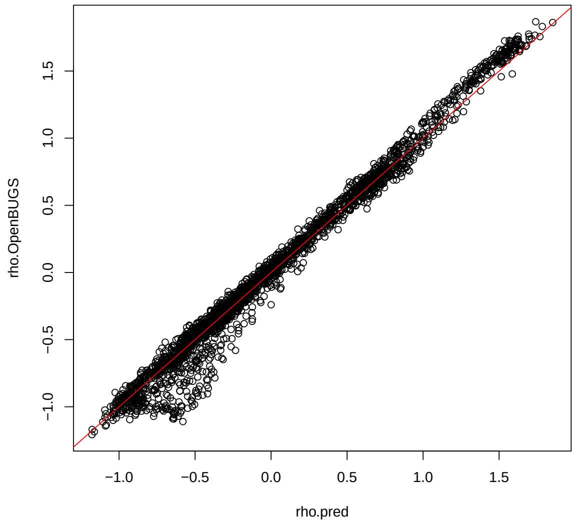


Figure 2.13: **Comparison between hSDM and OpenBUGS for spatial random effect estimates.**

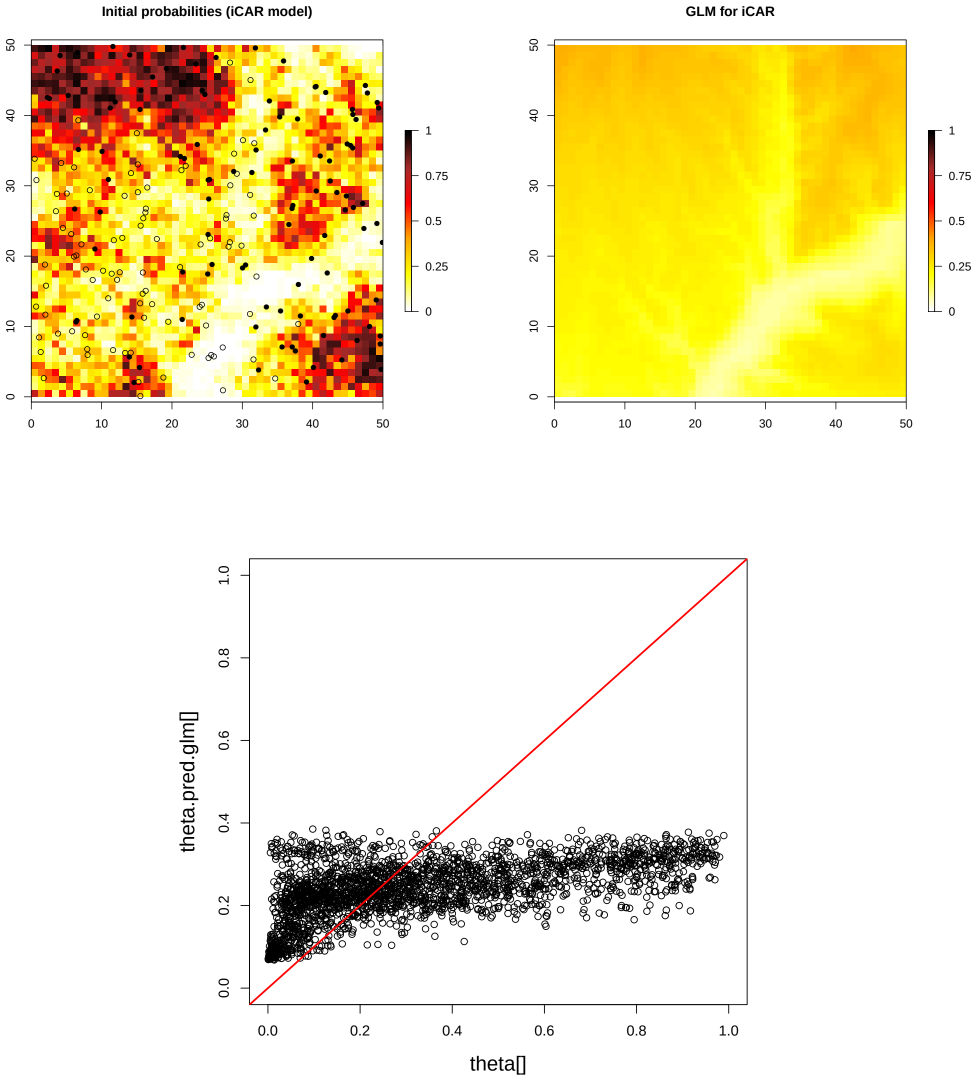
2.3.6 Comparison with GLM results

```
#== glm results for comparison
mod.glm <- glm(cbind(Y,visits)~alt,family="binomial",data=data.suit)
summary(mod.glm)

##
## Call:
## glm(formula = cbind(Y, visits) ~ alt, family = "binomial", data = data.suit)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -1.3707  -0.9457  -0.6015   0.4535   1.8110
##
## Coefficients:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.20339    0.08846 -13.604  < 2e-16 ***
## alt          0.44159    0.10239   4.313 1.61e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##     Null deviance: 157.26  on 199  degrees of freedom
## Residual deviance: 135.34  on 198  degrees of freedom
## AIC: 355.04
##
## Number of Fisher Scoring iterations: 4
```

```
# Create a raster for predictions
theta.pred.glm <- raster(theta)
# Attribute predicted values to raster cells
theta.pred.glm[] <- predict.glm(mod.glm,newdata=data.pred,type="response")
# Plot the predicted probability of presence
plot(theta.pred.glm,main="GLM for iCAR",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
```

```
# Comparing predictions to initial values
plot(theta[],theta.pred.glm[],
     xlim=c(0,1),ylim=c(0,1),cex.lab=1.4)
abline(a=0,b=1,col="red",lwd=2)
```


Initial probabilities (iCAR model)

GLM for iCAR

Figure 2.14: **Comparing predicted probability of presence using GLM with initial probabilities for a binomial model with iCAR process.**

2.4 Site-occupancy iCAR model

2.4.1 Mathematical formulation

2.4.2 Data generation

```
# Ecological process (suitability)
logit.theta.site <- X.sites %*% beta.target + rho[cells]
theta.site <- inv.logit(logit.theta.site)
set.seed(seed)
Z <- rbinom(nsite,1,theta.site)

# Observation process (detectability)
nobs <- sum(visits)
set.seed(seed)
Y <- rbinom(nobs,1,delta.obs*Z[sites])

# Data-sets
data.obs <- data.frame(Y,w1,alt=X.sites[sites,2],site=sites)
data.suit <- data.frame(alt=X.sites[,2],cell=cells)
```

2.4.3 Parameter inference using the hSDM.siteocc.iCAR() function

```
Start <- Sys.time() # Start the clock
mod.hSDM.siteocc.iCAR <- hSDM.siteocc.iCAR(# Observations
                    presence=data.obs$Y,
                    observability=~w1+alt,
                    site=data.obs$site, data.observability=data.obs,
                    # Habitat
                    suitability=~alt, data.suitability=data.suit,
                    # Spatial structure
                    spatial.entity=data.suit$cell,
                    n.neighbors=n.neighbors, neighbors=adj,
                    # Predictions
                    suitability.pred=data.pred,
                    spatial.entity.pred=data.pred$cell,
                    # Chains
                    burnin=5000, mcmc=5000, thin=5,
                    # Starting values
                    beta.start=0,
                    gamma.start=0,
                    Vrho.start=1,
                    # Priors
                    mubeta=0, Vbeta=1.0E6,
                    mugamma=0, Vgamma=1.0E6,
                    # priorVrho="1/Gamma",
                    # shape=1, rate=1,
                    priorVrho="Uniform",
                    Vrho.max=10,
                    # Various
                    seed=1234, verbose=1,
                    save.rho=1, save.p=0)
Time.hSDM <- difftime(Sys.time(),Start,units="sec") # Time difference
```

```
summary(mod.hSDM.siteocc.iCAR$mcmc)

##
## Iterations = 5001:9996
## Thinning interval = 5
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                        Mean      SD Naive SE Time-series SE
## beta.(Intercept)   -1.3887  0.4224 0.013357        0.03063
## beta.alt            1.0793  0.4787 0.015138        0.05328
## gamma.(Intercept)  -1.1084  0.2568 0.008121        0.01169
## gamma.w1            1.1206  0.2587 0.008180        0.01065
## gamma.alt          -0.5615  0.2236 0.007071        0.00881
## Vrho                6.8428  2.0419 0.064569        0.57398
## Deviance          253.1036 10.1066 0.319600        1.01861
##
## 2. Quantiles for each variable:
##
##                        2.5%      25%      50%      75%    97.5%
## beta.(Intercept)   -2.2137  -1.6727  -1.3879  -1.1172  -0.5645
## beta.alt            0.1648   0.7386   1.0730   1.3929   2.1004
## gamma.(Intercept)  -1.6208  -1.2980  -1.1016  -0.9277  -0.6422
## gamma.w1            0.6383   0.9490   1.1230   1.2783   1.6412
## gamma.alt          -0.9982  -0.7134  -0.5594  -0.4180  -0.1070
## Vrho                3.2623   5.1637   7.0166   8.6736   9.8196
## Deviance          233.3963 246.3764 252.9402 260.1291 274.6428
```

```
# Predictions for spatial random effects
rho.pred <- apply(mod.hSDM.siteocc.iCAR$rho.pred,2,mean)
rho.pred.rast <- rasterFromXYZ(cbind(coords,rho.pred))
plot(rho.pred.rast,main="Predictions rho")
# Predictions for probability of presence
theta.pred <- mod.hSDM.siteocc.iCAR$theta.pred
theta.pred.rast <- rasterFromXYZ(cbind(coords,theta.pred))
plot(theta.pred.rast,main="Predictions theta",col=colRP(nb),breaks=brks,
axis.args=arg,zlim=c(0,1))
# Predictions vs. initial spatial random effects
plot(rho[-cells],rho.pred[-cells],xlab="rho target",ylab="Predictions rho")
points(rho[cells],rho.pred[cells],col="blue",pch=16)
abline(a=0,b=1,col="red")
# Predictions vs. initial probabilities
plot(values(theta)[-cells],theta.pred[-cells],xlab="theta target",
ylab="Predictions theta")
points(values(theta)[cells],theta.pred[cells],col="blue",pch=16)
abline(a=0,b=1,col="red")
```

2.4.4 Comparison with OpenBUGS results

```
# BUGS model
modelBUGS.txt <-
"model {

# Suitability process
for (i in 1:nsite) {
  z[i] ~ dbern(theta[i])
  logit(theta[i]) <- Xbeta[i] + rho[IdCellforSite[i]]
  Xbeta[i] <- beta[1] + beta[2]*alt.suit[i]
}

# Observability process
for (n in 1:nobs) {
  y[n] ~ dbern(delta.prim[n])
  delta.prim[n] <- delta[n]*z[IdSiteforObs[n]]
  logit(delta[n]) <- gamma[1] + gamma[2]*w1[n] + gamma[3]*alt.obs[n]
}

# CAR prior distribution for spatial random effects:
rho[1:ncells] ~ car.normal(adj[], weights[], num[], tau)
for (k in 1:sumNumNeigh) {
  weights[k] <- 1 # set equal weights for all neighbors
```

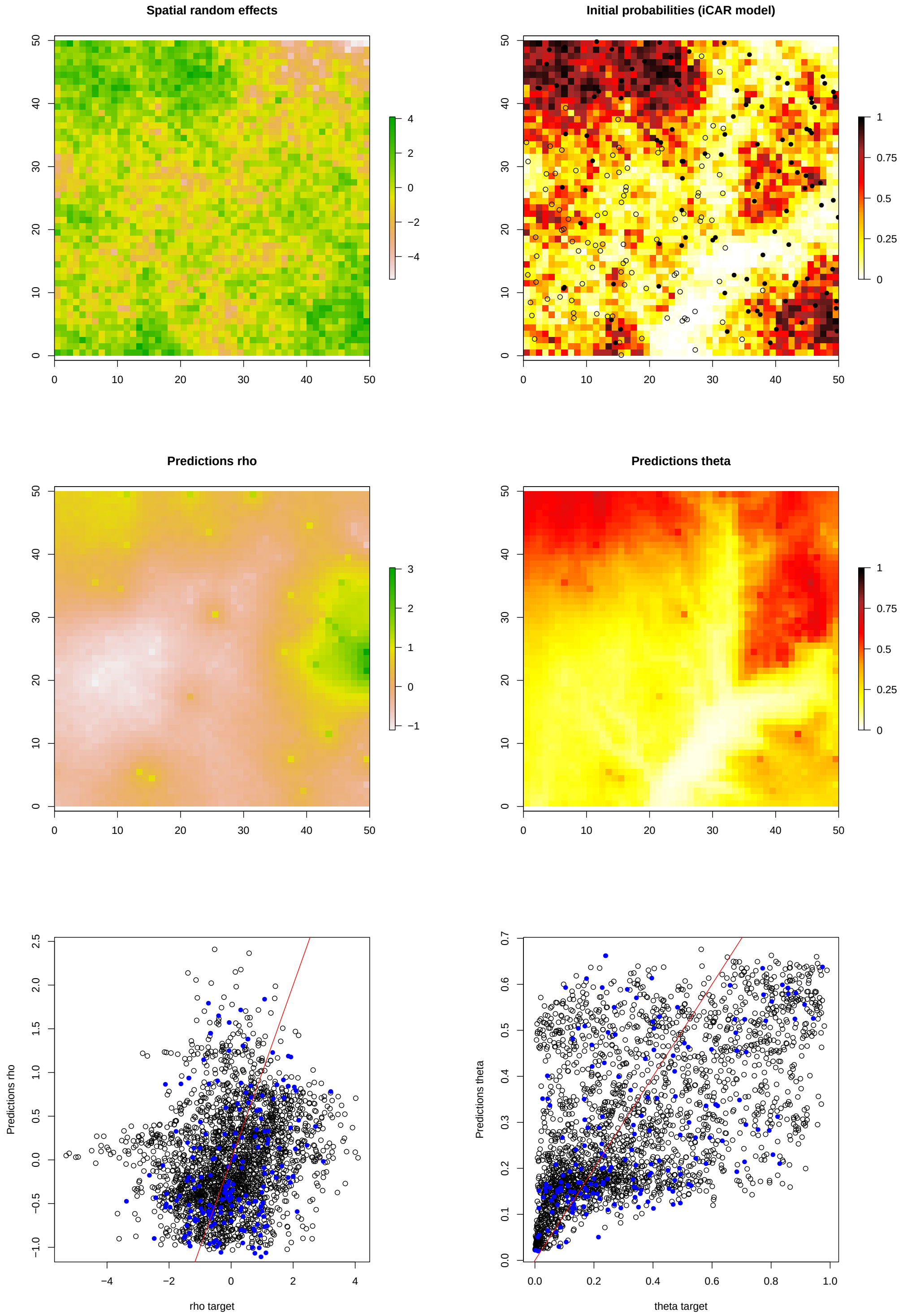


Figure 2.15: **Predictions vs. initial values**

```
}

# Other priors
for (i in 1:2) {
  beta[i] ~ dnorm(0,1.0E-6)
}
for (i in 1:3) {
  gamma[i] ~ dnorm(0,1.0E-6)
}
Vrho ~ dunif(0,10)
tau <- 1/Vrho

}"

# Create model.txt file in the working directory
system(paste("echo \"",modelBUGS.txt,"\" > modelBUGS.txt",sep=""))

# Data for OpenBUGS
y <- data.obs$Y
IdCellforSite <- data.suit$cell
IdSiteforObs <- data.obs$site
alt.suit <- data.suit$alt
w1 <- data.obs$w1
alt.obs <- data.obs$alt
num <- n.neighbors
adj <- adj
nobs <- length(y)
nsite <- length(IdCellforSite)
ncells <- length(n.neighbors)
sumNumNeigh <- length(adj)
data <- list("y","IdCellforSite","IdSiteforObs","alt.suit","w1","alt.obs","num",
"adj","nobs","nsite","ncells","sumNumNeigh")

# Inits
inits <- list(list(beta=rep(0,2),gamma=rep(0,3),rho=rep(0,ncells),Vrho=1))

# OpenBUGS call
library(R2OpenBUGS)
Start <- Sys.time() # Start the clock
Open <- bugs(data,inits,
             model.file="modelBUGS.txt",
             parameters=c("beta","gamma","Vrho","rho"),
             n.chains=1,
             OpenBUGS.pgm="/usr/bin/OpenBUGS",
             n.iter=2000,
```

Value	OpenBUGS	hSDM
β_0	-1.49	-1.39
β_{alt}	1.11	1.08
γ_0	-1.06	-1.11
γ_{w1}	1.13	1.12
γ_{alt}	-0.55	-0.56
V_ρ	6.38	6.84
Time (secs)	59	14

Table 2.2: **Comparison between hSDM and OpenBUGS outputs.**

```
             n.burnin=1000,
             n.thin=5,
             DIC=TRUE,
             debug=FALSE,
             clearWD=FALSE)
Time.OpenBUGS <- difftime(Sys.time(),Start,units="sec") # Time difference

# Time difference
ratio.time <- as.numeric(Time.OpenBUGS)/as.numeric(Time.hSDM)
ratio.time # For this example, hSDM is X times faster

#== Outputs
Open$DIC
Open$pD
beta.pred.Open <- apply(Open$sims.list$beta,2,mean)
gamma.pred.Open <- apply(Open$sims.list$gamma,2,mean)
Vrho.pred.Open <- mean(Open$sims.list$Vrho)
deviance.Open <- mean(Open$sims.list$deviance)
rho.OpenBUGS <- apply(Open$sims.list$rho,2,mean)
plot(rho.pred,rho.OpenBUGS)
abline(a=0,b=1,col="red")
```

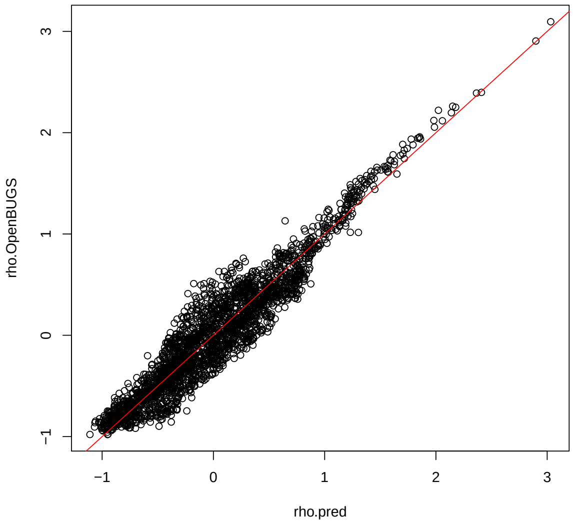


Figure 2.16: **Comparison between hSDM and OpenBUGS for spatial random effect estimates.**

2.4.5 Comparison with GLM results

```
#== glm results for comparison
mod.glm <- glm(y~alt,family="binomial",data=data.obs)
summary(mod.glm)

##
## Call:
## glm(formula = y ~ alt, family = "binomial", data = data.obs)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -0.4152  -0.4147  -0.4145  -0.4144   2.2352
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -2.410839   0.149237 -16.154   <2e-16 ***
## alt         -0.001029   0.144026  -0.007    0.994
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##     Null deviance: 338.53  on 594  degrees of freedom
## Residual deviance: 338.53  on 593  degrees of freedom
## AIC: 342.53
##
## Number of Fisher Scoring iterations: 5
```

```
# Create a raster for predictions
theta.pred.glm <- raster(theta)
# Attribute predicted values to raster cells
theta.pred.glm[] <- predict.glm(mod.glm,newdata=data.pred,type="response")
# Plot the predicted probability of presence
plot(theta.pred.glm,main="GLM for siteocc iCAR",col=colRP(nb),breaks=brks,
     axis.args=arg,zlim=c(0,1))
```

```
# Comparing predictions to initial values
plot(theta[],theta.pred.glm[],
     xlim=c(0,1),ylim=c(0,1),cex.lab=1.4)
abline(a=0,b=1,col="red",lwd=2)
```

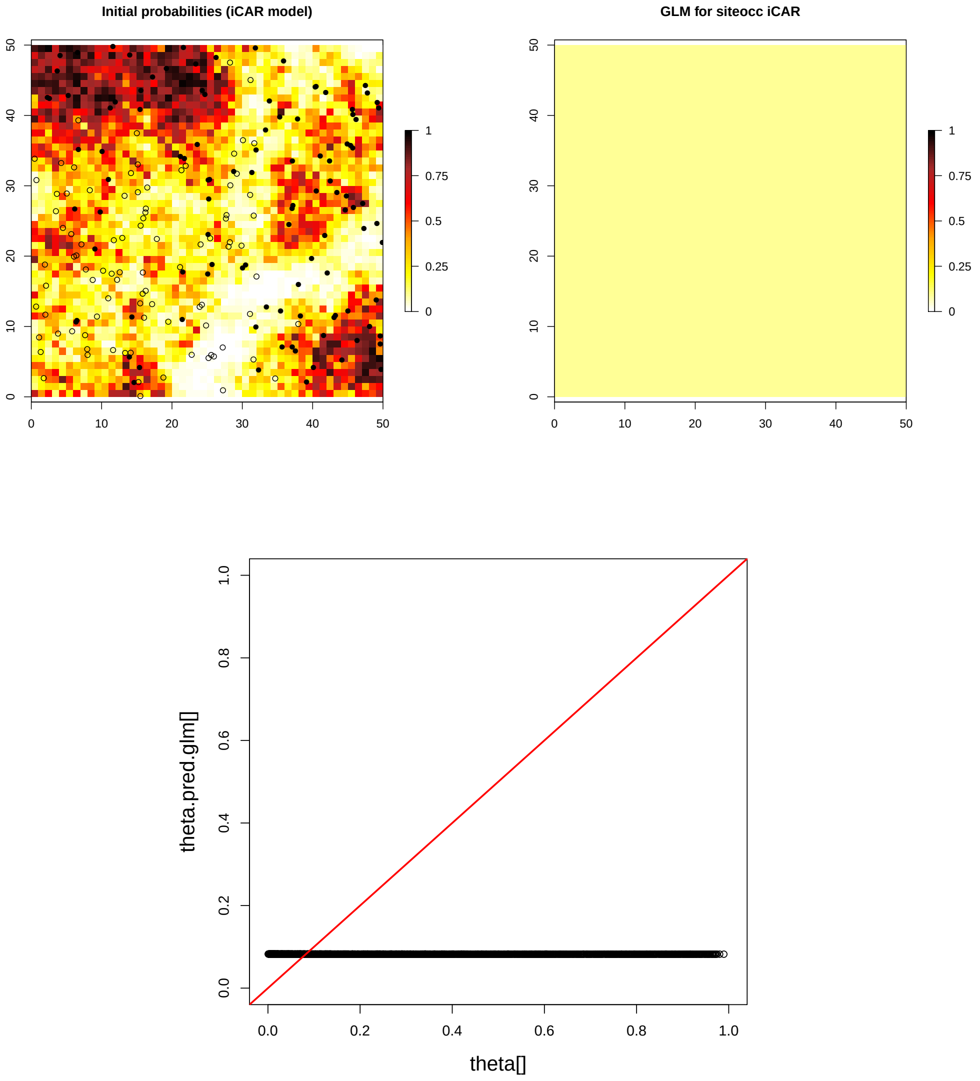


Figure 2.17: **Comparing predicted probability of presence using GLM with initial probabilities for a site-occupancy model with iCAR process.**

CHAPTER 3

Abundance data

CHAPTER 4

Additional examples with real data

4.1 Binomial iCAR model with tens of thousands spatial cells

This example illustrates the use of the `hSDM.binomial.iCAR()` function on a large region (tens of thousands grid cells). The data-set includes presence-absence observations for *Protea punctata* Meisn. (Fig. 4.1) in the Cap Floristic Region. The data-set also includes environmental variables for 36909 one minute by one minute grid cells on the whole South Africa's Cap Floristic Region (Fig. 4.2).

```r
# Libraries
require(sp)
require(raster)
library(hSDM)

# Load data
data(cfr.env, package="hSDM")
dim(cfr.env) # 36909 cells
data(punc10, package="hSDM")
dim(punc10) # 2934 observations

# Standardize predictors
for (i in 3:8) {
    m <- cfr.env[,i]-mean(cfr.env[,i], na.rm=T)
    cfr.env[,i] <- m/sd(cfr.env[,i], na.rm=T)
}
```

Figure 4.1: Photography of *Protea punctata* Meisn.

```r
# Make both data sets spatial objects
cfr.env <- SpatialPixelsDataFrame(points=cfr.env[c("lon","lat")],
                                  tol=0.175039702866343,
                                  data=cfr.env[,-c(1,2)])
fullgrid(cfr.env) <- TRUE
coordinates(punc10) <- c(2,3)

# Plot the whole data set
spplot(cfr.env,sp.layout=list('sp.points',
                   punc10[punc10$Occurrence==1,],
                   col='black',pch='o'),
       col.regions=rainbow(100,start=0.67,end=0))
```

```r
# Get the indices of cells where presences and absences have been observed.
cfr.env.rast <- stack(cfr.env)
pres <- extract(cfr.env.rast, SpatialPoints(punc10[punc10$Occurrence==1,]),
                cellnumbers=TRUE)[,1]
abs <- extract(cfr.env.rast, SpatialPoints(punc10[punc10$Occurrence==0,]),
               cellnumbers=TRUE)[,1]

# Make the data frame used in regressions
ncelltot <- length(cfr.env) # Including NULL cells
d <- data.frame(lon=coordinates(cfr.env)[,1],lat=coordinates(cfr.env)[,2],
                Y=rep(0,ncelltot),
                trials=rep(0,ncelltot),
                cell.orig=1:ncelltot,
                cfr.env@data)
```

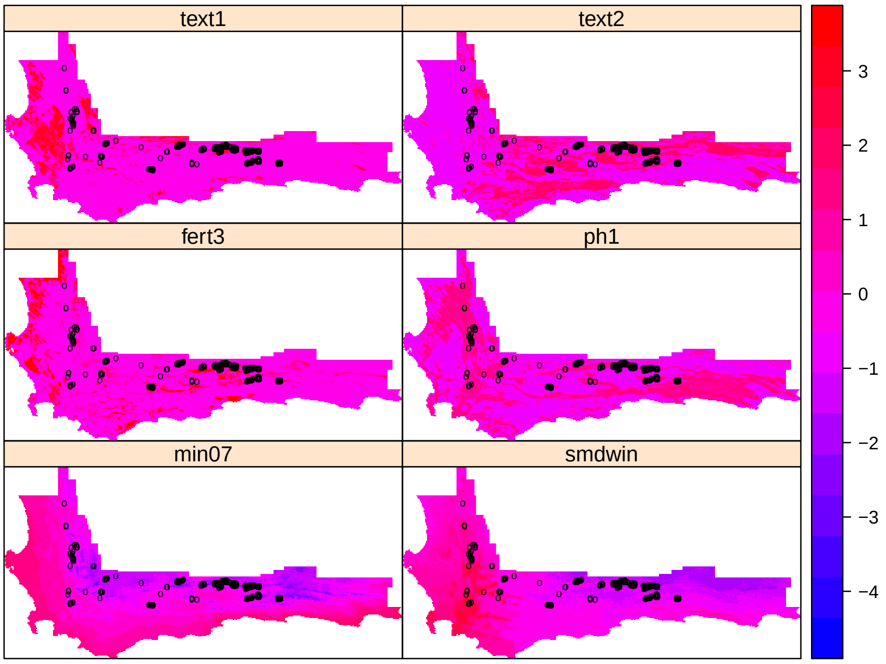


Figure 4.2: **Values of environmental variables in the Cap Floristic Region.** Points of presence of *Protea punctata* are represented by a circle.

```
d$Y[pres] <- 1
d$trials[c(pres,abs)] <- 1

# Remove NAs
to.remove <- which(!complete.cases(d))
d <- d[-to.remove,]
summary(d)

# Make d a spatial object for later use
coordinates(d) <- c(1,2)

# Find cells' neighborhood with function 'adjacent' from the 'raster' package
plot(cfr.env.rast)
sel.cell <- d$cell.orig
neighbors.mat <- adjacent(cfr.env.rast, cells=sel.cell, directions=8,
                          pairs=TRUE, target=sel.cell, sorted=TRUE)
n.neighbors <- as.data.frame(table(as.factor(neighbors.mat[,1])))[,2]
neighbors.orig <- neighbors.mat[,2]

# Sorting cells from 1 to dim(d)[1] (dim(d)[1]=36907)
s.cell <- sort(unique(d$cell.orig))
d$cell <- match(d$cell.orig,s.cell)
s.neighbors <- sort(unique(neighbors.orig))
neighbors <- match(neighbors.orig,s.neighbors)
```

```
# glm, just to compare
mod.glm <- glm(cbind(Y,trials-Y)~min07+smdwin,data=d, family="binomial")
summary(mod.glm)

# hSDM
mod.hSDM.binomial.iCAR <- hSDM.binomial.iCAR(presences=d$Y[d$trials>0],
                                             trials=d$trials[d$trials>0],
                                             suitability=~min07+smdwin,
                                             spatial.entity=d$cell[d$trials>0],
                                             data=d[d$trials>0,],
                                             n.neighbors=n.neighbors,
                                             neighbors=neighbors,
                                             suitability.pred=d,
                                             spatial.entity.pred=d$cell,
                                             burnin=1000,
                                             mcmc=1000, thin=1,
                                             beta.start=c(0,0,0),
                                             Vrho.start=10,
                                             priorVrho="1/Gamma",
                                             mubeta=0, Vbeta=1.0E6,
                                             shape=2, rate=1,
                                             Vrho.max=10,
                                             seed=1234, verbose=1, save.rho=0)
```

```
# Outputs
summary(mod.hSDM.binomial.iCAR$mcmc)

##
## Iterations = 1001:2000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                       Mean      SD Naive SE Time-series SE
## beta.(Intercept)  -6.7924  0.2721 0.008605        0.05725
## beta.min07        -2.7341  0.1630 0.005153        0.03472
## beta.smdwin        0.7583  0.1404 0.004439        0.02668
## Vrho               6.7782  1.0610 0.033552        0.67466
## Deviance         489.1038 20.4751 0.647480        4.02088
##
## 2. Quantiles for each variable:
##
##                       2.5%     25%      50%      75%   97.5%
## beta.(Intercept)  -7.4383  -6.969  -6.7523  -6.6060  -6.363
## beta.min07        -3.0927  -2.840  -2.7185  -2.6345  -2.420
## beta.smdwin        0.4662   0.674   0.7581   0.8437   1.007
## Vrho               5.3646   5.934   6.5480   7.6397   8.843
## Deviance         451.8252 474.131 488.0859 502.8298 533.916

# Put output together
out <- data.frame(d,pred=mod.hSDM.binomial.iCAR$theta.pred,
                  sp.ef=mod.hSDM.binomial.iCAR$rho.pred)

# Plot results
coordinates(out) <- coordinates(d)
out <- SpatialPixelsDataFrame(out,tol=0.175039702866343,data=data.frame(out))
fullgrid(out) <- TRUE
p1 <- spplot(out['pred'],col.regions=rainbow(100,start=0.67,end=0),
             sp.layout=list('sp.points',punc10[punc10$Occurrence==1,],
                 col='black',pch='o'))
```

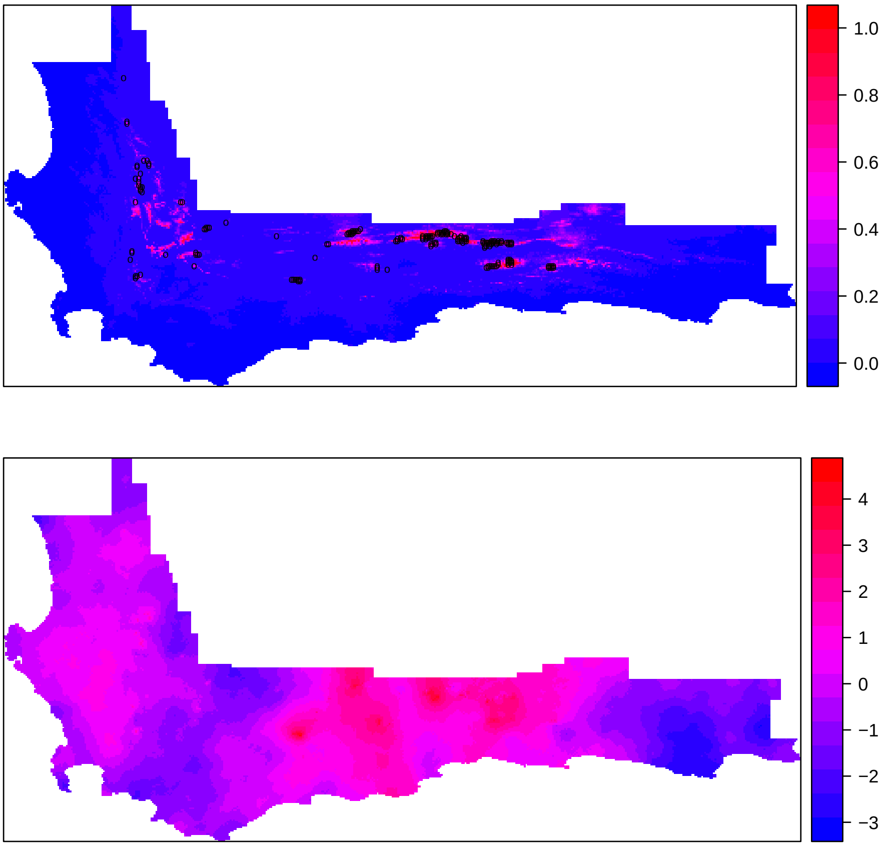


Figure 4.3: **Predicted probability of presence (top) and estimated spatial random effects (bottom).** Points of presence of *Protea punctata* are represented by a circle.

```
p2 <- spplot(out['sp.ef'],col.regions=rainbow(100,start=0.67,end=0))
print(p1,position=c(0,0.5,1,1),more=T)
print(p2,position=c(0,0,1,0.5))
```

Using function `hSDM.binomial.iCAR()`, we were able to estimate the spatial random effect of 36907 cells (Fig. 4.3) and we demonstrated that the use of this function is not limited (through memory problem or a much too long computation time) by the number of spatial grid cells. Nevertheless, in this particular example, it is very difficult to reach convergence for the variance of the spatial random effects (see MCMC outputs above). This is likely due to the low information content of binary maps and the relatively low number of observations (2934). As previously underlined by Dormann *et al.* (2007), we argue that binomial intrinsic CAR models require further study and caution in their use. The **hSDM** R package offers tools to help ecologist explore the behavior and performance of such models.

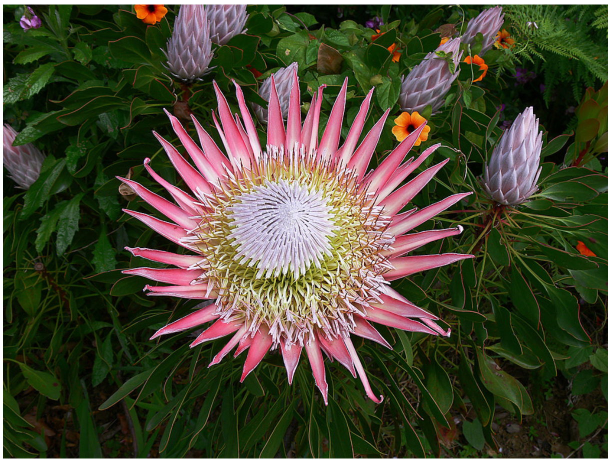


Figure 4.4: Photography of *Protea cynaroides* (L.) L..

4.2 Binomial iCAR model with data from Latimer *et al.* (2006)

In the Appendix B of their scientific article, Latimer *et al.* (2006) provide some code to fit what they called "Model 2", a Binomial iCAR model using presence/absence data for species *Protea cynaroides* (L.) L., a common *Protea* and the national flower of South Africa (Fig. 4.4).

For the purpose of their example, Latimer *et al.* (2006) provide data for a small region including 476 one minute by one minute grid cells. This region is is a small corner of South Africa's Cape Floristic Region, and includes very high plant species diversity and a World Biosphere Reserve. Contrary to the previous example, the data-set includes several visits at the same site.

```r
# Library
library(hSDM)

# Load data
data(datacells.Latimer2006,package="hSDM")
datacells.Latimer2006$cell <- c(1:dim(datacells.Latimer2006)[1])
data(neighbors.Latimer2006,package="hSDM")

# Format data
p <- datacells.Latimer2006$y[datacells.Latimer2006$n>0]
t <- datacells.Latimer2006$n[datacells.Latimer2006$n>0]
s <- datacells.Latimer2006$cell[datacells.Latimer2006$n>0]
data.obs <- datacells.Latimer2006[datacells.Latimer2006$n>0,]
```

```
# Model
Start <- Sys.time() # Start the clock
mod.hSDM.Lat2006.iCAR <- hSDM.binomial.iCAR(presences=p,
                         trials=t,
                         suitability=~rough+julmint+pptcv+smdsum+evi+ph1,
                         spatial.entity=s,
                         data=data.obs,
                         n.neighbors=datacells.Latimer2006$num,
                         neighbors=neighbors.Latimer2006,
                         suitability.pred=datacells.Latimer2006,
                         spatial.entity.pred=datacells.Latimer2006$cell,
                         burnin=5000,
                         mcmc=5000, thin=5,
                         beta.start=0,
                         Vrho.start=10,
                         priorVrho="1/Gamma",
                         mubeta=0, Vbeta=1.0E6,
                         shape=0.001, rate=0.001,
                         Vrho.max=1000,
                         seed=1234, verbose=1,
                         save.rho=0,save.p=0)
Time.hSDM <- difftime(Sys.time(),Start,units="sec") # Time difference

# Some outputs
summary(mod.hSDM.Lat2006.iCAR$rho.pred)
summary(mod.hSDM.Lat2006.iCAR$theta.latent)
summary(mod.hSDM.Lat2006.iCAR$theta.pred)
```

```
# Parameter estimates
summary(mod.hSDM.Lat2006.iCAR$mcmc)

##
## Iterations = 5001:9996
## Thinning interval = 5
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                         Mean      SD Naive SE Time-series SE
## beta.(Intercept)  -1.87424  0.1867 0.005905        0.02306
## beta.rough         0.04654  0.1929 0.006100        0.03137
## beta.julmint      -0.68919  0.1907 0.006032        0.03595
## beta.pptcv         -0.50551  0.3131 0.009900        0.07505
## beta.smdsum        -0.05816  0.2581 0.008162        0.06383
## beta.evi           -0.12120  0.2250 0.007116        0.03272
## beta.ph1            1.18415  0.3666 0.011594        0.07490
## Vrho               10.01343  1.6786 0.053082        0.14259
## Deviance          741.74700 23.2539 0.735353        1.33653
##
## 2. Quantiles for each variable:
##
##                      2.5%       25%       50%       75%    97.5%
## beta.(Intercept)  -2.2863  -1.98541  -1.85755  -1.75081  -1.5319
## beta.rough        -0.3059  -0.09902   0.04951   0.18855   0.4036
## beta.julmint      -1.0113  -0.81231  -0.70643  -0.59932  -0.2302
## beta.pptcv        -1.1328  -0.70159  -0.50666  -0.29266   0.1193
## beta.smdsum       -0.5741  -0.23491  -0.05943   0.12900   0.4283
## beta.evi          -0.5819  -0.26339  -0.12097   0.01707   0.3810
## beta.ph1           0.5368   0.92446   1.17545   1.41019   1.9645
## Vrho               7.1367   8.79720   9.92110  11.08064  13.5447
## Deviance         695.1199 725.74487 742.33633 758.12635 786.8725
```

Contrary to the previous example, and due to the higher information content associated to the fact that each site is visited several times, it was easier to reach convergence for the variance of the spatial random effects in this example.

```
# BUGS model
modelBUGS2.txt <-
"model {

# Likelihood
for (i in 1:N_nonzeroy) {
  y[ind[i]] ~ dbin(p[ind[i]], n[ind[i]])
}

for(i in 1:N_LOC){
  logit(p[i]) <- rho[i]+xbeta[i]+mu
  xbeta[i]<-beta[1]*rough[i] + beta[2]*julmint[i] + beta[3]*pptcv[i] +
            beta[4]*smdsum[i] + beta[5]*evi[i] + beta[6]*ph1[i]
}

# CAR prior distribution for spatial random effects:
rho[1:N_LOC] ~ car.normal(adj[], weights[], num[], tau)
for(k in 1:sumNumNeigh) {
  weights[k] <- 1 # set equal weights for all neighbors
}
```

```
# Other priors
mu ~ dnorm(0,0.1)
for (i in 1:6) {
  beta[i] ~ dnorm(0, 0.2)
}
vrho <- 1/tau
tau ~ dgamma(0.001,0.001)

}"

# Create model.txt file in the working directory
system(paste("echo \"",modelBUGS2.txt,"\" > modelBUGS2.txt",sep=""))

# Data for OpenBUGS
y <- datacells.Latimer2006$y
n <- datacells.Latimer2006$n
rough <- datacells.Latimer2006$rough
julmint <- datacells.Latimer2006$julmint
pptcv <- datacells.Latimer2006$pptcv
smdsum <- datacells.Latimer2006$smdsum
evi <- datacells.Latimer2006$evi
ph1 <- datacells.Latimer2006$ph1
num <- datacells.Latimer2006$num
adj <- neighbors.Latimer2006
ind <- which(datacells.Latimer2006$n!=0)
N_LOC <- length(y)
N_nonzeroy <- length(ind)
sumNumNeigh <- length(adj)

data <- list("y","n","rough","julmint","pptcv","smdsum",
             "evi","ph1","num",
             "adj","ind","N_LOC","N_nonzeroy","sumNumNeigh")

# Inits
inits <- list(list(mu=1,beta=rep(1.5,6),rho=rep(0,N_LOC),tau=1))

# OpenBUGS call
library(R2OpenBUGS)
Start <- Sys.time() # Start the clock
Open <- bugs(data,inits,
            model.file="modelBUGS2.txt",
            parameters=c("mu","beta","vrho"),
            n.chains=1,
            OpenBUGS.pgm="/usr/bin/OpenBUGS",
            n.iter=2000,
            n.burnin=1000,
            n.thin=5,
            DIC=TRUE,
            debug=FALSE,
            clearWD=FALSE)
Time.OpenBUGS <- difftime(Sys.time(),Start,units="sec") # Time difference

# Time difference
ratio.time <- as.numeric(Time.OpenBUGS)/as.numeric(Time.hSDM)
```

```
# Parameter estimates with OpenBUGS
print(Open$summary[,c(1,2)])

##                  mean         sd
## mu        -1.85205700  0.1598051
## beta[1]    0.03595761  0.1455205
## beta[2]   -0.74706210  0.2354220
## beta[3]   -0.49305137  0.2673517
## beta[4]   -0.12947751  0.3064259
## beta[5]   -0.14999565  0.1899236
## beta[6]    1.15288960  0.2608238
## vrho       9.59598700  1.5356158
## deviance 740.95200000 21.0887086
```

For this example, hSDM and OpenBUGS gave similar estimates for model parameters. For the same number of iterations (10000), and for a relatively low number of grid cells (476), hSDM was more than twice as fast as OpenBUGS.

4.3 ZIB model with data from Latimer *et al.* (2006)

Because sites have been visited several times, the same data-set can be used to fit a ZIB model accounting for imperfect detection. If the observation conditions were different from one visit to another, we would have to use the `hSDM.siteocc()` function which uses a mixture model combining two Bernoulli processes. But in this case, the observation conditions are not specified and can be supposed to be the same so that we can use the `hSDM.ZIB()` function of the **hSDM** package. The `hSDM.ZIB()` function uses a mixture model combining a Binomial process for observability and a Bernoulli process for suitability.

```
# Model
mod.hSDM.Lat2006.ZIB <- hSDM.ZIB(presences=p,
                                 trials=t,
                                 suitability=~rough+julmint+pptcv+smdsum+evi+ph1,
                                 observability=~1,
                                 data=data.obs,
                                 suitability.pred=datacells.Latimer2006,
                                 burnin=1000,
                                 mcmc=1000, thin=1,
                                 beta.start=0,
                                 gamma.start=0,
                                 mubeta=0, Vbeta=1.0E6,
                                 mugamma=0, Vgamma=1.0E6,
                                 seed=1234, verbose=1,
                                 save.p=0)

# Some outputs
summary(mod.hSDM.Lat2006.ZIB$prob.p.pred)
summary(mod.hSDM.Lat2006.ZIB$prob.p.latent)
summary(mod.hSDM.Lat2006.ZIB$prob.q.latent)
```

```
# Parameter estimates
summary(mod.hSDM.Lat2006.ZIB$mcmc)

##
## Iterations = 1001:2000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                         Mean      SD Naive SE Time-series SE
## beta.(Intercept)   3.376e-01 0.22592 0.007144       0.024106
## beta.rough        -7.023e-03 0.26532 0.008390       0.023803
## beta.julmint       8.855e-01 0.31619 0.009999       0.040362
## beta.pptcv        -4.258e-01 0.33632 0.010635       0.044614
## beta.smdsum        6.609e-01 0.32246 0.010197       0.038242
## beta.evi          -9.290e-01 0.30885 0.009767       0.027722
## beta.ph1           1.607e+00 0.34856 0.011022       0.035347
## gamma.(Intercept)  1.259e-01 0.03747 0.001185       0.003638
## Deviance           1.838e+03 4.15851 0.131504       0.408601
##
## 2. Quantiles for each variable:
##
##                         2.5%        25%        50%    75%  97.5%
## beta.(Intercept)    -0.06711    0.17945  3.156e-01 0.4737 0.7671
## beta.rough          -0.56028   -0.17994 -2.721e-03 0.1628 0.4449
## beta.julmint          0.22677    0.69281  9.022e-01    1.1097    1.4876
## beta.pptcv           -1.10536   -0.61322 -3.971e-01   -0.2145    0.2101
## beta.smdsum           0.05880    0.44203  6.429e-01    0.8748    1.3067
## beta.evi             -1.63302   -1.14023 -8.925e-01   -0.6909   -0.4173
## beta.ph1              0.91858    1.38330  1.596e+00    1.8395    2.3208
## gamma.(Intercept)     0.04765    0.09901  1.235e-01    0.1497    0.1992
## Deviance           1831.80407 1834.72720  1.837e+03 1839.9540 1847.4970
```

```
# Detection probability
gamma.hat <- mean(mod.hSDM.Lat2006.ZIB$mcmc[,"gamma.(Intercept)"])
delta.est <- inv.logit(gamma.hat)
delta.est

## [1] 0.5314216
```

Using this type of model, we can estimate the detection probability of the species (`delta.est`= 0.53).

4.4 ZIB iCAR model with data from Latimer *et al.* (2006)

```
# Model
mod.hSDM.Lat2006.ZIB.iCAR <- hSDM.ZIB.iCAR(presences=p,
                         trials=t,
                         suitability=~rough+julmint+pptcv+smdsum+evi+ph1,
                         observability=~1,
                         spatial.entity=s,
                         data=data.obs,
                         n.neighbors=datacells.Latimer2006$num,
                         neighbors=neighbors.Latimer2006,
                         suitability.pred=datacells.Latimer2006,
                         spatial.entity.pred=datacells.Latimer2006$cell,
                         burnin=5000,
                         mcmc=5000, thin=5,
                         beta.start=0,
                         gamma.start=0,
                         Vrho.start=10,
                         priorVrho="Uniform",
                         mubeta=0, Vbeta=1.0E6,
                         mugamma=0, Vgamma=1.0E6,
                         shape=2, rate=1,
                         Vrho.max=10,
                         seed=1234, verbose=1,
                         save.rho=0,save.p=0)

# Some outputs
summary(mod.hSDM.Lat2006.ZIB.iCAR$prob.p.pred)
summary(mod.hSDM.Lat2006.ZIB.iCAR$prob.p.latent)
summary(mod.hSDM.Lat2006.ZIB.iCAR$prob.q.latent)
```

```
# Parameter estimates
summary(mod.hSDM.Lat2006.ZIB.iCAR$mcmc)

##
## Iterations = 5001:9996
## Thinning interval = 5
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                        Mean       SD Naive SE Time-series SE
## beta.(Intercept)     0.7138  0.26719 0.008449       0.014766
## beta.rough           0.5643  0.39828 0.012595       0.046211
## beta.julmint        -1.1857  0.59331 0.018762       0.069454
## beta.pptcv          -0.7958  0.49922 0.015787       0.061846
## beta.smdsum         -0.4783  0.62096 0.019636       0.088051
## beta.evi            -0.5099  0.38857 0.012288       0.023951
## beta.ph1             1.3835  0.42089 0.013310       0.035438
## gamma.(Intercept)    0.1299  0.03698 0.001170       0.001329
## Vrho                 9.1243  0.76955 0.024335       0.061263
## Deviance          1729.7004 10.98519 0.347382       0.845395
##
## 2. Quantiles for each variable:
##
##                         2.5%       25%       50%        75%      97.5%
## beta.(Intercept)     0.21252    0.5418    0.7078    0.90554    1.22941
## beta.rough          -0.15347    0.2965    0.5564    0.81978    1.41734
## beta.julmint        -2.37556   -1.5903   -1.1581   -0.77204   -0.09995
## beta.pptcv          -1.68890   -1.1230   -0.8478   -0.46587    0.26083
## beta.smdsum         -1.56522   -0.8984   -0.5346   -0.08909    0.84548
## beta.evi            -1.27733   -0.7641   -0.4957   -0.23088    0.17985
## beta.ph1             0.61176    1.0899    1.3566    1.67052    2.17121
## gamma.(Intercept)    0.06067    0.1043    0.1309    0.15590    0.19941
## Vrho                 7.11220    8.7303    9.3438    9.73560    9.98959
## Deviance          1710.18198 1721.6650 1729.2054 1737.04701 1752.44302
```

```
# Detection probability
gamma.hat <- mean(mod.hSDM.Lat2006.ZIB.iCAR$mcmc[,"gamma.(Intercept)"])
delta.est <- inv.logit(gamma.hat)
delta.est

## [1] 0.5324361
```

4.5 Abundance models with data from Kéry & Andrew Royle (2010)

4.5.1 Presentation of the data

The data-set from Kéry & Andrew Royle (2010) includes repeated count data for the Willow tit (*Poecile montanus*, a pesserine bird, see Fig. 4.5) in Switzerland on the period 1999-2003. Data come from the Swiss national breeding bird survey MHB (Monitoring Haüfige Brutvögel). MHB is based on 264 1-km^2 sampling units (quadrats) laid out as a grid (Fig. 4.6). Since 1999, every quadrat has been surveyed two to three times during most breeding seasons (15 April to 15 July). The Willow tit is a widespread but moderately rare bird species. It has a weak song and elusive behaviour and can be rather difficult to detect.

This data-set is available in the **hSDM** R package. It can be loaded with the `data` command and formated to be used with hSDM functions.

```
# Load libraries
library(hSDM)
library(sp)
library(raster)

# Load Kéry et al. 2010 data
data(data.Kery2010,package="hSDM")
head(data.Kery2010)

# Normalized variables
elev.mean <- mean(data.Kery2010$elevation)
elev.sd <- sd(data.Kery2010$elevation)
juldate.mean <- mean(c(data.Kery2010$juldate1,
                      data.Kery2010$juldate2,
                      data.Kery2010$juldate3),na.rm=TRUE)
juldate.sd <- sd(c(data.Kery2010$juldate1,
                  data.Kery2010$juldate2,
                  data.Kery2010$juldate3),na.rm=TRUE)
data.Kery2010$elevation <- (data.Kery2010$elevation-elev.mean)/elev.sd
```

Figure 4.5: **Willow tit (*Poecile montanus*).**

```
data.Kery2010$juldate1 <- (data.Kery2010$juldate1-juldate.mean)/juldate.sd
data.Kery2010$juldate2 <- (data.Kery2010$juldate2-juldate.mean)/juldate.sd
data.Kery2010$juldate3 <- (data.Kery2010$juldate3-juldate.mean)/juldate.sd

# Landscape and observation sites
sites.sp <- SpatialPointsDataFrame(coords=data.Kery2010[c("coordx","coordy")],
                                   data=data.Kery2010[,-c(1,2)])
xmin <- min(data.Kery2010$coordx)
xmax <- max(data.Kery2010$coordx)
ymin <- min(data.Kery2010$coordy)
ymax <- max(data.Kery2010$coordy)
ext <- extent(c(xmin,xmax,ymin,ymax))
ncol <- round((xmax-xmin)/10)
nrow <- round((ymax-ymin)/10)
landscape <- raster(ncols=ncol,nrows=nrow,ext)
values(landscape) <- runif(ncell(landscape),0,1)
landscape.po <- rasterToPolygons(landscape)
plot(landscape.po)
plot(sites.sp,add=TRUE,col="red",pch=16)
# Neighborhood
# Rasters must be projected to correctly compute the neighborhood
crs(landscape) <- '+proj=utm +zone=1'
# Cell for each site
cells <- extract(landscape,sites.sp,cell=TRUE)[,1]
# Neighborhood matrix
ncells <- ncell(landscape)
neighbors.mat <- adjacent(landscape, cells=c(1:ncells), directions=8,
                          pairs=TRUE, sorted=TRUE)
# Number of neighbors by cell
```

```
n.neighbors <- as.data.frame(table(as.factor(neighbors.mat[,1])))[,2]
# Adjacent cells
adj <- neighbors.mat[,2]

# Arranging data
# data.obs
nsite <- length(data.Kery2010$coordx)
count <- c(data.Kery2010$count1,data.Kery2010$count2,data.Kery2010$count3)
juldate <- c(data.Kery2010$juldate1,data.Kery2010$juldate2,
             data.Kery2010$juldate3)
site <- rep(1:nsite,3)
data.obs <- data.frame(count,juldate,site)
data.obs <- data.obs[!is.na(data.obs$juldate),]
# data.suit
data.suit <- data.Kery2010[c("coordx","coordy","elevation","forest")]
data.suit$cells <- cells
data.suit <- data.suit[-139,] # Removing site 139 with no juldate
```

4.5.2 Simple Poisson model

```
# hSDM.poisson
data.pois <- data.obs
data.pois$elevation <- data.suit$elevation[as.numeric(as.factor(data.obs$site))]
mod.Kery2010.pois <- hSDM.poisson(counts=data.pois$count,
                                  suitability=~elevation+I(elevation^2),
                                  data=data.pois,beta.start=0)
```

```
# Outputs
summary(mod.Kery2010.pois$mcmc)

##
## Iterations = 5001:14991
## Thinning interval = 10
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                           Mean      SD Naive SE Time-series SE
## beta.(Intercept)       0.02814 0.06428 0.002033       0.003726
## beta.elevation         3.08127 0.15347 0.004853       0.017159
```

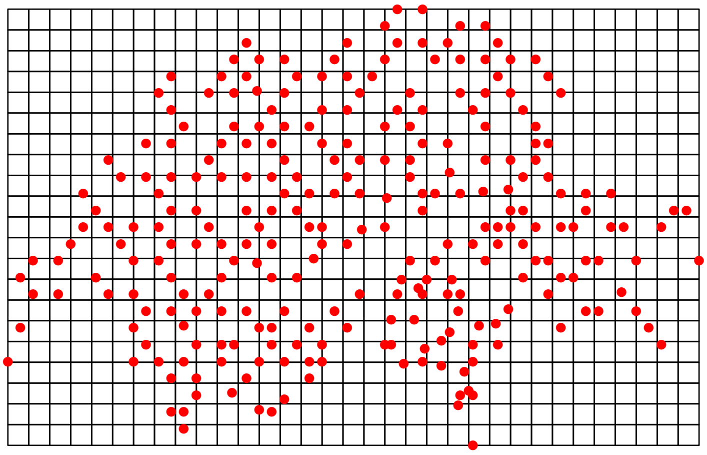


Figure 4.6: **Location of the 264 1-km^2 quadrats of the Swiss national breeding bird survey.** Points are located on a grid of 10-km^2 cells. The grid is covering the geographical extent of the observation points.

```
## beta.I(elevation^2)   -1.79995 0.10235 0.003236       0.010673
## Deviance            2157.88058 2.40508 0.076055       0.116160
##
## 2. Quantiles for each variable:
##
##                           2.5%        25%        50%        75%     97.5%
## beta.(Intercept)      -0.09261   -0.01438    0.02764    0.07104    0.1562
## beta.elevation         2.80721    2.97833    3.07749    3.17837    3.3823
## beta.I(elevation^2)   -2.00237   -1.86256   -1.79905   -1.73075   -1.6108
## Deviance            2155.19932 2156.14125 2157.27804 2158.97142 2164.3795
```

```
# Predictions
npred <- 100
nsamp <- dim(mod.Kery2010.pois$mcmc)[1]
# Abundance-elevation
elev.seq <- seq(500,3000,length.out=npred)
elev.seq.n <- (elev.seq-elev.mean)/elev.sd
beta <- as.matrix(mod.Kery2010.pois$mcmc[,1:3])
tbeta <- t(beta)
X <- matrix(c(rep(1,npred),elev.seq.n,elev.seq.n^2),ncol=3)
N <- matrix(NA,nrow=nsamp,ncol=npred)
for (i in 1:npred) {
    N[,i] <- exp(X[i,] %*% tbeta)
}
N.est.pois <- apply(N,2,mean)
N.q1.pois <- apply(N,2,quantile,0.025)
N.q2.pois <- apply(N,2,quantile,0.975)
```

4.5.3 N-mixture model with imperfect detection

```
# hSDM.Nmixture
mod.Kery2010.Nmix <- hSDM.Nmixture(# Observations
                     counts=data.obs$count,
                     observability=~juldate+I(juldate^2),
                     site=data.obs$site,
                     data.observability=data.obs,
                     # Habitat
                     suitability=~elevation+I(elevation^2),
                     data.suitability=data.suit,
                     # Predictions
                     suitability.pred=NULL,
                     # Chains
                     burnin=10000, mcmc=5000, thin=5,
                     # Starting values
                     beta.start=0,
                     gamma.start=0,
                     # Priors
                     mubeta=0, Vbeta=1.0E6,
                     mugamma=0, Vgamma=1.0E6,
                     # Various
                     seed=1234, verbose=1,
                     save.p=0, save.N=0)
```

```
# Outputs
summary(mod.Kery2010.Nmix$mcmc)

##
## Iterations = 10001:14996
## Thinning interval = 5
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                           Mean       SD Naive SE Time-series SE
## beta.(Intercept)       0.6726  0.08660 0.002739       0.007342
## beta.elevation         2.7879  0.19608 0.006200       0.023100
## beta.I(elevation^2)   -1.7905  0.14436 0.004565       0.018337
## gamma.(Intercept)      0.2537  0.10346 0.003272       0.008333
## gamma.juldate         -0.2253  0.08493 0.002686       0.004897
## gamma.I(juldate^2)     0.2658  0.08202 0.002594       0.005667
## Deviance            1887.5828 27.73003 0.876900       2.195556
##
## 2. Quantiles for each variable:
##
##                            2.5%       25%       50%       75%      97.5%
## beta.(Intercept)       0.50177    0.6142    0.6744    0.7296    0.83792
## beta.elevation         2.41646    2.6443    2.7935    2.9233    3.17012
## beta.I(elevation^2)   -2.07261   -1.8875   -1.7856   -1.6886   -1.51417
## gamma.(Intercept)      0.05384    0.1768    0.2596    0.3280    0.44389
## gamma.juldate         -0.38921   -0.2820   -0.2230   -0.1683   -0.05706
## gamma.I(juldate^2)     0.09516    0.2089    0.2669    0.3209    0.41889
## Deviance            1837.06989 1868.2134 1885.6799 1906.7686 1942.45453
```

```
# Predictions
nsamp <- dim(mod.Kery2010.Nmix$mcmc)[1]
# Abundance-elevation
beta <- as.matrix(mod.Kery2010.Nmix$mcmc[,1:3])
tbeta <- t(beta)
N <- matrix(NA,nrow=nsamp,ncol=npred)
for (i in 1:npred) {
    N[,i] <- exp(X[i,] %*% tbeta)
}
N.est.Nmix <- apply(N,2,mean)
N.q1.Nmix <- apply(N,2,quantile,0.025)
N.q2.Nmix <- apply(N,2,quantile,0.975)
# Detection-Julian date
juldate.seq <- seq(100,200,length.out=npred)
juldate.seq.n <- (juldate.seq-juldate.mean)/juldate.sd
gamma <- as.matrix(mod.Kery2010.Nmix$mcmc[,4:6])
tgamma <- t(gamma)
W <- matrix(c(rep(1,npred),juldate.seq.n,juldate.seq.n^2),ncol=3)
delta <- matrix(NA,nrow=nsamp,ncol=npred)
for (i in 1:npred) {
    delta[,i] <- inv.logit(X[i,] %*% tgamma)
}
delta.est.Nmix <- apply(delta,2,mean)
delta.q1.Nmix <- apply(delta,2,quantile,0.025)
delta.q2.Nmix <- apply(delta,2,quantile,0.975)
```

4.5.4 Nmixture model with iCAR process

```
# hSDM.Nmixture.iCAR
mod.Kery2010.Nmix.iCAR <- hSDM.Nmixture.iCAR(# Observations
                            counts=data.obs$count,
                            observability=~juldate+I(juldate^2),
                            site=data.obs$site,
                            data.observability=data.obs,
                            # Habitat
                            suitability=~elevation+I(elevation^2),
                            data.suitability=data.suit,
                            # Spatial structure
                            spatial.entity=data.suit$cells,
                            n.neighbors=n.neighbors, neighbors=adj,
                            # Chains
                            burnin=20000, mcmc=10000, thin=10,
                            # Starting values
                            beta.start=0,
                            gamma.start=0,
                            Vrho.start=1,
                            # Priors
                            mubeta=0, Vbeta=1.0E6,
                            mugamma=0, Vgamma=1.0E6,
                            priorVrho="1/Gamma",
                            shape=1, rate=1,
                            # Various
                            seed=1234, verbose=1,
                            save.rho=0, save.p=0, save.N=0)
```

```
# Outputs
summary(mod.Kery2010.Nmix.iCAR$mcmc)

##
## Iterations = 20001:29991
## Thinning interval = 10
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                          Mean       SD Naive SE Time-series SE
## beta.(Intercept)       0.3037  0.29294 0.009264       0.033554
## beta.elevation         2.1858  0.52575 0.016626       0.109007
## beta.I(elevation^2)   -1.9443  0.31587 0.009989       0.051676
## gamma.(Intercept)     -0.7980  0.17325 0.005479       0.048075
## gamma.juldate         -0.1653  0.06898 0.002181       0.004864
## gamma.I(juldate^2)     0.1451  0.05597 0.001770       0.003551
## Vrho                  15.2809  3.51718 0.111223       0.362266
## Deviance            1383.3447 45.30455 1.432656       7.774908
##
## 2. Quantiles for each variable:
##
##                           2.5%       25%       50%       75%     97.5%
## beta.(Intercept)      -0.26973    0.1131    0.2992    0.4970    0.8584
## beta.elevation         1.28847    1.8279    2.1260    2.4716    3.5030
## beta.I(elevation^2)   -2.63988   -2.1388   -1.9197   -1.7269   -1.3687
## gamma.(Intercept)     -1.10129   -0.9177   -0.8203   -0.6720   -0.4640
## gamma.juldate         -0.29742   -0.2094   -0.1668   -0.1206   -0.0243
## gamma.I(juldate^2)     0.04049    0.1070    0.1458    0.1805    0.2670
## Vrho                   9.69374   12.8070   14.8371   17.2770   23.6666
## Deviance            1300.66478 1351.5389 1381.0295 1411.1528 1479.4193
```

```
# Spatial random effects
rho.pred <- mod.Kery2010.Nmix.iCAR$rho.pred
r.rho.pred <- rasterFromXYZ(cbind(coordinates(landscape),rho.pred))
plot(r.rho.pred)
# Mean abundance by site
ma <- apply(sites.sp@data[,3:5],1,mean,na.rm=TRUE)
points(sites.sp,pch=".",cex=2)
points(sites.sp,pch=1,cex=ma/2)
```

```
# Predictions
nsamp <- dim(mod.Kery2010.Nmix.iCAR$mcmc)[1]
# Abundance-elevation
beta <- as.matrix(mod.Kery2010.Nmix.iCAR$mcmc[,1:3])
tbeta <- t(beta)
N <- matrix(NA,nrow=nsamp,ncol=npred)
# Simplified way of obtaining samples for rho
rho.samp <- sample(rho.pred,nsamp,replace=TRUE)
for (i in 1:npred) {
    N[,i] <- exp(X[i,] %*% tbeta + rho.samp)
}
N.est.Nmix.iCAR <- apply(N,2,mean)
N.q1.Nmix.iCAR <- apply(N,2,quantile,0.025)
N.q2.Nmix.iCAR <- apply(N,2,quantile,0.975)

# Detection-Julian date
gamma <- as.matrix(mod.Kery2010.Nmix.iCAR$mcmc[,4:6])
tgamma <- t(gamma)
delta <- matrix(NA,nrow=nsamp,ncol=npred)
for (i in 1:npred) {
    delta[,i] <- inv.logit(X[i,] %*% tgamma)
}
delta.est.Nmix.iCAR <- apply(delta,2,mean)
delta.q1.Nmix.iCAR <- apply(delta,2,quantile,0.025)
delta.q2.Nmix.iCAR <- apply(delta,2,quantile,0.975)
```

4.5.5 Comparing predictions from the three different models

```
# Expected abundance - Elevation
par(mar=c(4,4,1,1),cex=1.4,tcl=+0.5)
plot(elev.seq,N.est.pois,type="l",
     xlim=c(500,3000),
     ylim=c(0,7),
```

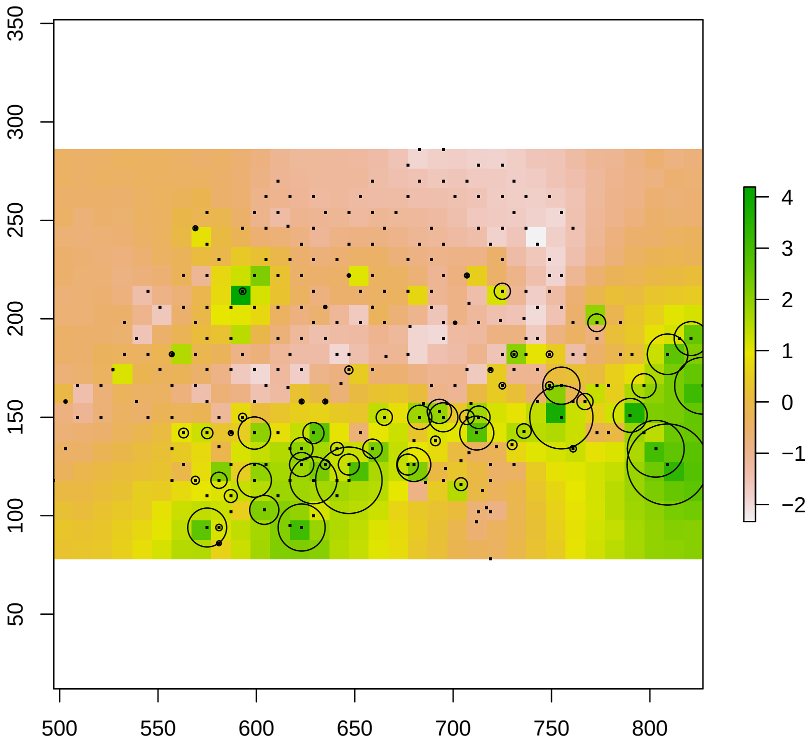


Figure 4.7: **Estimated spatial random effects.** Locations of observation quadrats are represented by dots. The mean abundance on each quadrat is represented by a circle of size proportional to abundance.

```
     lwd=2,
     xlab="Elevation (m a.s.l.)",
     ylab="Expected abundance",
     axes=FALSE)
#lines(elev.seq,N.q1.pois,lty=3,lwd=1)
#lines(elev.seq,N.q2.pois,lty=3,lwd=1)
axis(1,at=seq(500,3000,by=500),labels=seq(500,3000,by=500))
axis(2,at=seq(0,7,by=1),labels=seq(0,7,by=1))
# Nmix
lines(elev.seq,N.est.Nmix,lwd=2,col="red")
#lines(elev.seq,N.q1.Nmix,lty=3,lwd=1,col="red")
#lines(elev.seq,N.q2.Nmix,lty=3,lwd=1,col="red")
# Nmix.iCAR
lines(elev.seq,N.est.Nmix.iCAR,lwd=2,col="dark green")
#lines(elev.seq,N.q1.Nmix.iCAR,lty=3,lwd=1,col="dark green")
#lines(elev.seq,N.q2.Nmix.iCAR,lty=3,lwd=1,col="dark green")
```

```
# Detection probability - Julian date
par(mar=c(4,4,1,1),cex=1.4,tcl=+0.5)
plot(juldate.seq,delta.est.Nmix,type="l",
     xlim=c(100,200),
     ylim=c(0,1),
     lwd=2,
     col="red",
     xlab="Julian date",
     ylab="Detection probability",
     axes=FALSE)
lines(juldate.seq,delta.q1.Nmix,lty=3,lwd=1,col="red")
lines(juldate.seq,delta.q2.Nmix,lty=3,lwd=1,col="red")
axis(1,at=seq(100,200,by=20),labels=seq(100,200,by=20))
axis(2,at=seq(0,1,by=0.2),labels=seq(0,1,by=0.2))
# Nmix.iCAR
lines(juldate.seq,delta.est.Nmix.iCAR,lwd=2,col="dark green")
lines(juldate.seq,delta.q1.Nmix.iCAR,lty=3,lwd=1,col="dark green")
lines(juldate.seq,delta.q2.Nmix.iCAR,lty=3,lwd=1,col="dark green")
```

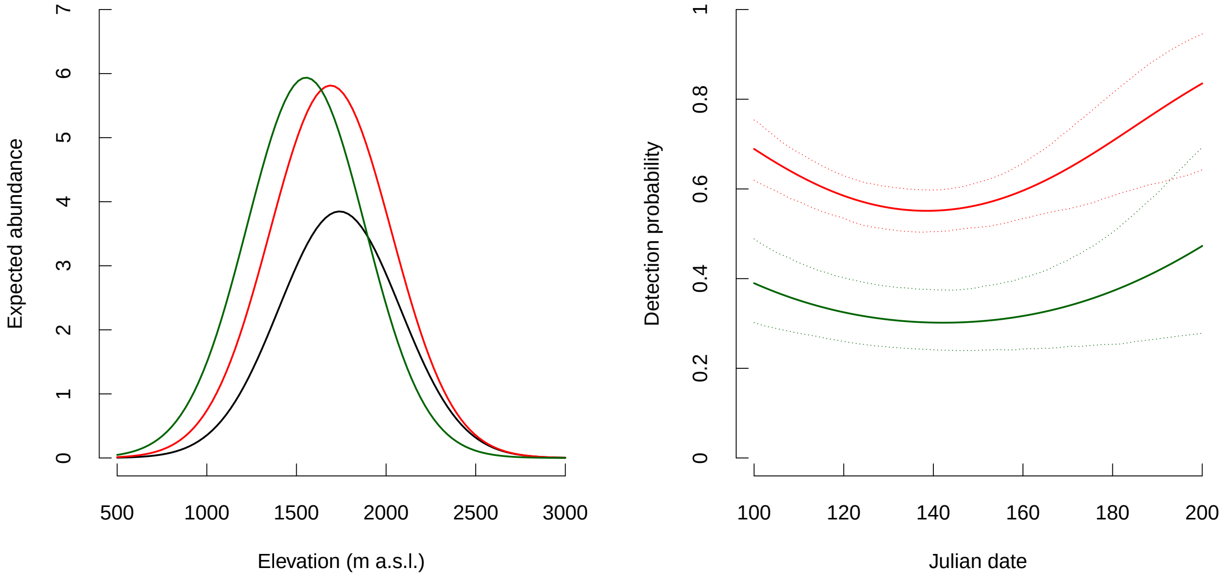


Figure 4.8: **Comparing predictions from the three different models.** The three different models are: Poisson (black), N-mixture (red) and N-mixture with iCAR process (green). The plain lines represent the predictive posterior mean of the abundance or of the probability of detection while the dashed lines represent the quantiles at 95% of the predictive posterior given parameter uncertainty.

CHAPTER 5

Some technical aspects of parameter inference

5.1 Likelihood for site-occupancy models

As previously detailed in the mathematical formulation of the site-occupancy model, let's consider the random variable z_i describing habitat suitability at site i. The random variable z_i can take value 1 or 0 depending on the fact that the habitat is suitable ($z_i = 1$) or not ($z_i = 0$). Random variable z_i can be assumed to follow a Bernoulli distribution of parameter θ_i. In this case, θ_i is the probability that the habitat is suitable. Several visits at time t_1, t_2, etc., can occur at site i. Let's consider the random variable y_{it} representing the presence of the species at site i and time t. The species is observed at site i ($\sum_t y_{it} \geq 1$) only if the habitat is suitable ($z_i = 1$). The species is unobserved at site i ($\sum_t y_{it} = 0$) if the habitat is not suitable ($z_i = 0$), or if the habitat is suitable ($z_i = 1$) but the probability δ_{it} of detecting the species at site i and time t is inferior to 1. Given H_i the set of observations (list of presence/absence) at site i, the likelihood L for site-occupancy models can be computed as follow (Eq. 5.1).

$$
\begin{array}{ll}
L = \prod_i \mathrm{p}(H_i) & \\
& \\
\text{if } \sum_t y_{it} \geq 1 & \mathrm{p}(H_i) = \mathrm{p}(z_i = 1) \prod_t \mathrm{p}(y_{it}) \\
& \mathrm{p}(H_i) = \theta_i \prod_{t=1} \mathrm{p}(y_{it}) \\
& \text{with } \mathrm{p}(y_{it} = 1) = \delta_{it} \text{ and } \mathrm{p}(y_{it} = 0) = 1 - \delta_{it} \\
& \\
\text{if } \sum_t y_{it} = 0 & \mathrm{p}(H_i) = \mathrm{p}(z_i = 0) + \mathrm{p}(z_i = 1) \prod_t \mathrm{p}(y_{it} = 0) \\
& \mathrm{p}(H_i) = (1 - \theta_i) + \theta_i \prod_t (1 - \delta_{it})
\end{array}
\tag{5.1}
$$

For site-occupancy models, there is a strong advantage of visiting a site several times.

When a site is visited several times for observation, if the species has been observed at least once during the different visits, we can assert that the habitat at this site is suitable. And the fact that the species can be unobserved at this site is only due to imperfect detection. For more details, please refer to the original paper by MacKenzie *et al.* (2002) and the very pedagogical note by Bailey & Adams (2005).

5.2 Random walk for estimating latent variables in N-mixture models

For N-mixture models, in the **hSDM** package, the abundances N_i at site i are considered as latent variables. N_i are estimated using a (simple) reflecting random walk Metropolis algorithm (Hastings, 1970). Hastings (1970) suggests the following probabilities for the proposal value $N^\star$ (Eq. 5.2).

$$
\begin{aligned}
&\text{If } N = 0 \\
&\qquad \mathrm{p}(N^\star = 0 | N = 0) = 1/2 \qquad \mathrm{p}(N^\star = 1 | N = 0) = 1/2 \\
&\text{If } N > 0 \\
&\qquad \mathrm{p}(N^\star = i+1 | N = i) = 1/2 \quad \mathrm{p}(N^\star = i-1 | N = i) = 1/2
\end{aligned}
\tag{5.2}
$$

In practice, if N_i are small, this choice seems to work fairly well and fast to approximate the probability distributions of N_i, since it suffices that the chain visits only the first few integers.

The approach used in the **hSDM** package for estimating parameters of N-mixture models is different to the one proposed by Royle (2004) where the integral other N_i values for the likelihood computation is approximated by a sum (see Eq. 3 in Royle (2004)). In practice, the summation over N_i is restricted to a finite but large bound K. K should be set high enough so that it does not affect the parameter estimates, but computation time increases with K. In a Bayesian framework with MCMC methods, this approach (although leading to equivalent parameter estimates for large values of K) is much slower than the approach considering latent variables. For a comparison between the two approaches, a function called `hSDM.Nmixture.K()`, which uses the approach by summation with bound K, is available in the **hSDM** package.

5.3 Adaptive Metropolis within Gibbs

Except for the variance of the spatial random effects of the iCAR models, for which we proposed conjugate priors, we used an adaptive Metropolis algorithm (Metropolis *et al.*, 1953; Robert & Casella, 2004) within Gibbs sampler (Casella & George, 1992; Gelfand & Smith, 1990) to draw the samples of the posterior distribution for model's parameters.

The proposal distribution in the Metropolis algorithm is a Normal distribution centered on the current parameter value and with standard deviation σ. The standard deviation σ is set to 1 at the beginning of the MCMC and is continuously adjusted so that the acceptance rate is 0.44 for non-hierarchical models (`hSDM.binomial()` and `hSDM.poisson()` functions) and 0.234 for hierarchical models (other hSDM functions). These values of acceptance rate (0.44 for low-dimensional models and 0.234 for high-dimensional models) ensure a better efficiency of the Metropolis algorithm and a faster MCMC convergence (Roberts *et al.*, 1997; Roberts & Rosenthal, 2009; Roberts *et al.*, 2001).

The actualized value $\sigma^\star$ of the standard deviation of the proposal distribution is computed from the current acceptance rate A, the optimal acceptance rate r (0.44 or 0.234) and the current standard deviation σ (Eq. 5.3).

$$\begin{array}{rl} \text{if } A \geq r & \sigma^\star = \sigma(2-(1-A)/(1-r)) \\ \text{else} & \sigma^\star = \sigma/(2-A/r) \end{array} \tag{5.3}$$

The tuning of the proposal is only done during the burnin period. After the burnin period, the standard deviation of the proposal distribution is fixed at the current value. The adaptive Metropolis within Gibbs is written in C code and compiled to optimize computation efficiency.

5.4 Intrinsic conditional autoregressive (iCAR) model

To capture the spatial autocorrelation, we employ a Gaussian intrinsic conditional autoregressive (iCAR) model (Besag, 1974). To specify this model, we assume that the conditional distribution of the spatial random effect ρ_j in cell j, given values for the spatial random effect in all other cells $j' \neq j$, depends only on the spatial random effect of the neighbouring cells of j. Here, we specify that cell j' is a neighbor of j if their boundaries intersect (Fig. 5.1). In the actual version of the iCAR process used in the **hSDM** R package, the spatial effect for any given cell depends only on the values of ρ for the cells in its neighborhood, and the neighborhood encompasses only the height immediately adjacent cells ("king movement" in chess). The neighborhood could alternatively be defined to be larger, and different weights could be assigned to cells at different distances. Formally, the Gaussian iCAR model for the spatial random effect at cell i can be presented by a conditional distribution (Eq. 5.4).

$$\begin{array}{l} \mathrm{p}(\rho_j|\rho_{j'}) \sim \mathcal{N}ormal(\mu_j, V_\rho/n_j) \\ \\ \mu_j\text{: mean of } \rho_{j'} \text{ in the neighborhood of } j. \\ V_\rho\text{: variance of the spatial random effects.} \\ n_j\text{: number of neighbors for cell } j. \end{array} \tag{5.4}$$

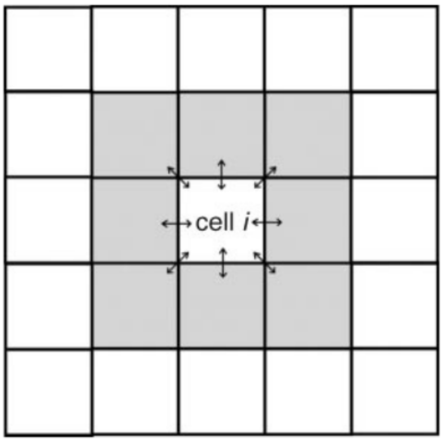


Figure 5.1: **Diagram of the grid cell neighborhood used in the intrinsic conditional autoregressive (iCAR) models**

The variance of the spatial random effects V_ρ is also a parameter to be estimated. We use a conjugate prior to infer V_ρ and we propose two prior distributions: an Inverse-Gamma distribution with shape and rate parameters or a Uniform distribution with zero for the lower bound of the interval and one parameter for the upper bound.

5.5 Difference between site-occupancy and ZIB models

Both site-occupancy or ZIB models (with `hSDM.siteocc()` or `hSDM.ZIB()` functions respectively) can be used to model the presence-absence of a species taking into account imperfect detection. The site-occupancy model can be used in all cases but can be less convenient and slower to fit when the repeated visits at each site are made under the exact same observation conditions. In this particular case, a Binomial distribution can be used for the observation process and we suggest the use of a ZIB model for computational efficiency (see example in Section 4.3).

On the contrary, when the data-set includes several visits at each site under different observation conditions, a Bernoulli distribution must be used for the observation process (not a Binomial distribution). In this case, the ZIB models must not be used. For `hSDM.ZIB()` functions, the fact that the observations are done on a same site is implicitely assumed by the data structure (see `presences` and `trials` arguments for each observation/site). Thus, for `hSDM.ZIB()` functions, there is no `site` argument to specify the site for each observation such as for `hSDM.siteocc()` functions.

5.6 Difference between N-mixture and ZIP models

For counts data with imperfect detection, both N-mixture and ZIP models can be used (with `hSDM.Nmixture()` or `hSDM.ZIP()` functions respectively). But the interpretation of the underlying processes and the structure of the data that can be used differ between the two models.

For the N-mixture model, the suitability process is modelled by a Poisson distribution. In this case, we interpret the number of individuals at one site as a function of environmental variables and we assume that there is more individuals when the habitat is more suitable. In a second step, the observability process is modelled by a Binomial distribution. We only see a fraction of the individuals present at one site due to observation conditions (Eq. 5.5).

For the N-mixture model, several visits can occur at one site under different observation conditions (see response variable y, explicative variables W and probability δ indexed on both i and t).

$$\begin{aligned}
&\textbf{Ecological process:} \\
&\qquad N_i \sim \mathcal{P}oisson(\lambda_i) \\
&\qquad \log(\lambda_i) = X_i\beta \\
&\textbf{Observation process:} \\
&\qquad y_{it} \sim \mathcal{B}inomial(N_i, \delta_{it}) \\
&\qquad \mathrm{logit}(\delta_{it}) = W_{it}\gamma
\end{aligned} \tag{5.5}$$

For the ZIP model, the suitability process is modelled by a Bernoulli distribution. In this case, we interpret the habitat at a particular site to be suitable for the species ($z_i = 1$) or not ($z_i = 0$). Then, the process determining the number of individuals observed at suitable sites (the abundance) is modelled by a Poisson distribution. Thus, this second process can include both ecological or detection factors explaining the abundance of the species at suitable sites (Eq. 5.6). Flores *et al.* (2009) provide a good example of the application of a ZIP model to the distribution of tree saplings.

$$\begin{aligned}
&\textbf{Suitability process:} \\
&\qquad z_i \sim \mathcal{B}ernoulli(\theta_i) \\
&\qquad \mathrm{logit}(\theta_i) = X_i\beta \\
&\textbf{Abundance process:} \\
&\qquad y_i \sim \mathcal{P}oisson(z_i, \lambda_i) \\
&\qquad \log(\lambda_i) = W_i\gamma
\end{aligned} \tag{5.6}$$

Note that ZIP models cannot be used when the data-set includes several visits by site. The likelihood of the ZIP models does not account for the fact that if the species is observed at least once at one site during the visits, then the habitat at this site is obviously suitable. Thus, such as for `hSDM.ZIB()` functions, `hSDM.ZIP()` functions do not have a `site` argument to specify the site for each observation (which is the case for `hSDM.Nmixture()` functions).

5.7 Difference between `site` and `spatial.entity`

For site-occupancy and N-mixture models taking into account both imperfect detection and spatial correlation, the user must make the difference between the `site` argument which indicates the site where the repeated observations have been made, and the `spatial.entity` argument which indicates the spatial entity for the spatial correlation process. These two spatial levels are clearly distinct. Thus, several sites (places visited) can be located in the same spatial entity (region, state, etc.).

Of course, in some particular cases, the site and the spatial entity can be confounded. Nonetheless, it is recommended to choose a resonable spatial scale (not too fine) for the spatial correlation process. With a limited number of spatial entities, there is a possibility to have more observations in each spatial entity. This should increase the amount of information for estimating spatial random effects and also speed up the computation with fewer spatial random effects to estimate. But the number of spatial entities should also be large enough to be able to estimate the variance of the spatial random effects. For example, Maas & Hox (2005) suggest a minimum of 50 levels for a random effect factor.

5.8 Computing the neighborhood for iCAR model

Section to be written...

- **raster** package
- The landscape raster must be projected (otherwise, torus system)
- function `adjacent()`

5.9 Forecasting species distribution under future climate change

Section to be written...

- How to obtain predictions
- What about the spatial random effects, do we include them ?

5.10 Computation time

When comparing OpenBUGS and hSDM outputs, computation times are given for guidance. The computer used for performing the statistical analysis had 4 processors of 2.5 GHz and 8Go of RAM. There is no parallelization implemented when running the Gibbs sampler, so that only one processor is used. The operating system installed on the computer was Linux Debian 9.0.

5.11 Package development, git and Sourceforge

Section to be written...

- Git repository: `https://github.com/ghislainv/hSDM`
- Web site on Sourceforge: `https://ecology.ghislainv.fr/hSDM`
- Number of line of code

Development work to be done:

- Analytically estimate the latent variables in N-mixture models
- Probit link function for Binomial model
- Random site effect for observability process
- Multispecies approach (see `jSDM` R package)

CHAPTER 6

Conclusion

Section to be written...

- Advantages of hSDM
  - User friendly
  - Speed
  - Can handle large data-sets
- Recommendations
  - Fitting complex models imply the use of data-sets providing sufficient information (in number of observations, in number of repetitions, etc.).
  - Users must be careful especially with non-identifiable over-parametrized model.
  - Using hierarchical Bayesian species distribution models is only an option. Be careful with “statistical machismo” (see http://dynamicecology.wordpress.com/2012/09/11/statistical-machismo/ and Hodges & Reich (2010) for example).

CHAPTER 7

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