

Better GDM

The Problem

The idea of GDM, modelling matrices of dissimilarity, was suggested by Ferrier (2002). Recently, White et al. (2023) suggested improvements to generalized dissimilarity modelling. Here we will develop an alternative, based on modelling the data rather than the distances between data.

The ecological problem is to explain how beta diversity, i.e. variation between sites, is affected by predictors, such as the environment. This can be done using GDM, which regresses distances between communities against the environmental covariates. Here we suggest an alternative approach.

The Model

We assume we have a site by species matrix, Y , with each row being observations of species (abundance, presence etc.), and each column being a site. So Y_{ij} is the observation for the i^{th} species ($i = 1, \dots, S$) and j^{th} species ($j = 1, \dots, N$). For each site we have P covariates, x_{jk} ($k = 1, \dots, P$), so these are in a $N \times P$ matrix X .

We assume we model this data using a GLM, i.e. we assume Y_{ij} follows some distribution in the exponential family, with expected value $\mu = g(\eta)$, where $g(\cdot)$ is a link function, and η is a linear predictor:

$$\eta_{ij} = \alpha_i + \kappa_j + \beta_{ij}$$

For identifiability we assume $\sum_j \kappa_j = 0$ and $\sum_j \beta_j = 0$

So α_i is the mean commonness of a species, and κ is the abundance at a site: we will assume this is not interesting, as it is affected by the sampling process. β_{ij} is where beta diversity lies (at least compositional beta diversity). The total beta diversity can be measured as $\text{Var}(\beta) = \sigma_\beta^2$. We can clearly model β_{ij} further, e.g. for a single covariate x_j

$$\beta_{ij} = \beta_0 + \delta_i x_j + \epsilon_{ij}$$

i.e. each species has its own response to x .

Then,

$$\begin{aligned} \text{Var}(\beta) &= \text{Var}(\beta_0 + \delta_i x_j + \epsilon_{ij}) \\ &= \frac{1}{(S-1)(N-1)} \sum_{i=1}^S \sum_{j=1}^N (\delta_i (x_j - \bar{x}) + \epsilon_{ij})^2 \\ &= \frac{1}{(S-1)(N-1)} \left(\sum_{i=1}^S \sum_{j=1}^N \delta_i^2 (x_j - \bar{x})^2 + \sum_{i=1}^S \sum_{j=1}^N \epsilon_{ij}^2 \right) \\ &= \frac{1}{(S-1)} \sum_{i=1}^S \delta_i^2 \frac{1}{(N-1)} \sum_{j=1}^N (x_j - \bar{x})^2 + \frac{1}{(S-1)(N-1)} \sum_{i=1}^S \sum_{j=1}^N \epsilon_{ij}^2 \\ &= \frac{1}{(S-1)} \sum_{i=1}^S \delta_i^2 \text{Var}(x) + \text{Var}(\epsilon_{ij}) \\ &= \frac{\text{Var}(x)}{(S-1)} \sum_{i=1}^S (\delta_i - \bar{\delta} + \bar{\delta})^2 + \text{Var}(\epsilon_{ij}) \\ &= \frac{\text{Var}(x)}{(S-1)} \sum_{i=1}^S (\delta_i - \bar{\delta})^2 - S\bar{\delta}^2 + \text{Var}(\epsilon_{ij}) \\ &= \text{Var}(\delta_i) \text{Var}(x_j) + \frac{S}{S-1} \bar{\delta}^2 \text{Var}(x) + \text{Var}(\epsilon_{ij}) \end{aligned}$$

because $\sum_i (\delta_i - \bar{\delta} + \bar{\delta})^2 = \sum_i (\delta_i - \bar{\delta})^2 + \sum_i (\delta_i - \bar{\delta})\bar{\delta} + \sum_i \bar{\delta}^2 = \sum_i (\delta_i - \bar{\delta})^2 + \bar{\delta}(\sum_i \delta_i - S\bar{\delta}) + S\bar{\delta}^2 = \sum_i (\delta_i - \bar{\delta})^2 + S\bar{\delta}^2$.

So, we can model the species abundance as a function of the environment. We can extend this to more than one covariate, if they are assumed to have independent effects between species (i.e. δ_{ik} is independent of δ_{il} for species i and covariates k and l).

Relationship to Distance

If we have two vectors of biodiversity, η_1 and η_2 then the distance between them is just the Euclidean distance:

$$D_{12} = \|\eta_1 - \eta_2\| = \sqrt{\sum_{i=1}^S (\eta_{i1} - \eta_{i2})^2}$$

So that

$$\begin{aligned}
D_{12}^2 &= \sum_{i=1}^S (\eta_{i1} - \eta_{i2})^2 \\
&= \sum_{i=1}^S (\alpha_i + \kappa_1 + \beta_{i1} - (\alpha_i + \kappa_2 + \beta_{i2}))^2 \\
&= \sum_{i=1}^S ((\kappa_1 - \kappa_2) + (\beta_{i1} - \beta_{i2}))^2 \\
&= \sum_{i=1}^S ((\kappa_1 - \kappa_2)^2 + (\kappa_1 - \kappa_2)(\beta_{i1} - \beta_{i2}) + (\beta_{i1} - \beta_{i2})^2) \\
&= S(\kappa_1 - \kappa_2)^2 + (\kappa_1 - \kappa_2) \sum_{i=1}^S (\beta_{i1} - \beta_{i2}) + \sum_{i=1}^S (\beta_{i1} - \beta_{i2})^2 \\
&= S(\kappa_1 - \kappa_2)^2 + \sum_{i=1}^S (\beta_{i1} - \beta_{i2})^2 \\
&= S(\kappa_1 - \kappa_2)^2 + \sum_{i=1}^S \beta_{i1}^2 - 2 \sum_{i=1}^S \beta_{i1} \beta_{i2} + \sum_{i=1}^S \beta_{i2}^2 \\
&= S(\kappa_1 - \kappa_2)^2 + (S - 1) (\text{Var}(\beta_{.1}) + \text{Var}(\beta_{.2}) - 2\text{Cov}(\beta_{.1}\beta_{.2}))
\end{aligned}$$

Where the $(\kappa_1 - \kappa_2) \sum_{i=1}^S (\beta_{i1} - \beta_{i2})$ term disappears because, by construction, $\sum_{i=1}^S \beta_{ij} = 0$. $\text{Var}_{ij}(X)$ is the variance of X in populations i and j .

If we are interested in compositional diversity, we can ignore the terms involving the κ s, so the distance is just a function of the second moments of β .

Examples

We use two of the three examples from White et al. (2023). The third is presence/absence data, so is less interesting, as ϵ_{ij} is the residual, which is thoroughly uninteresting in Bernoulli trials.

First we need some bookkeeping, to list the libraries and create a function to ...

```
library(zen4R) # used to download SA data
library(INLA)
library(gdm)
library(taxize)
```

```

# Define PC priors, to stop the models exploding horribly
PCHyper <- list(prec = list(prior="pc.prec", param=c(0.1,0.001)))
PCHyper2 <- list(prec = list(prior="pc.prec", param=c(0.2,0.01)))

# Number of simulations from posterior to calculate statistics
nsim <- 1000

# Function to calculate variance components
CalcPostVar <- function(INLASamp, data) {
  # Extract main effects of covariates
  LatentNames <- attr(INLASamp$latent, "dimnames")[[1]]
  RFNames <- paste(c(gsub("Precision for ", "", names(INLASamp$hyperpar)),
                    "(Intercept)", "Predictor"), collapse="|")
  FxNames <- LatentNames[!grepl(RFNames, LatentNames)]
  RFNames <- gsub(":", "", FxNames)
  # Calculate/extract parts of variance terms
  VarHyper <- 1/INLASamp$hyperpar
  wh.delta <- sapply(RFNames, function(wh, nm) grep(wh, nm), nm=names(VarHyper))
  VarDelta <- VarHyper[wh.delta]
  Var0th <- VarHyper[!seq_along(VarHyper)%in%wh.delta]

  VarX <- var(data[, RFNames])
  S <- nlevels(data$Species)

  # Deltabar
  Fx.wh <- which(attr(INLASamp$latent, "dimnames")[[1]]%in%FxNames)
  Deltabar <- INLASamp$latent[Fx.wh]
  names(Deltabar) <- attr(INLASamp$latent, "dimnames")[[1]][Fx.wh]

  AllVars <- c(MeanDelta = t(Deltabar)%*%VarX%*%Deltabar,
               VarDelta = sum(VarDelta*diag(VarX)), # not sure this is right
               Var0th)
  return(AllVars)
}

```

Example 1: South African flora

This is data with 288 species and 413 sites. The data is given in wide format, so we need to convert it to long. The data can be downloaded from [Zenodo](#).

```

#|output: false

# Download the data, if it hasn't already been done.
if(!dir.exists("data/philawhite-spGDMM-code-d8279ee/data/")) {
  download_zenodo("10.5281/zenodo.10091441", path="data")
  unzip("data/spGDMM-code-spGDMM_v1.zip", exdir="data")
}

Data <- read.csv("data/philawhite-spGDMM-code-d8279ee/data/sa_species_data.csv")

# SpNames <- gsub("\\\\.", " ", names(Data)[grep("\\\\.", names(Data))])
SpNames <- names(Data)[grep("\\\\.", names(Data))]
# FamNames <- names(FamData)[!names(FamData)%in%names(Data)]

# Discover that not all family names from GBIF are the same as the family data
# FamData <- read.csv("philawhite-spGDMM-code-d8279ee/data/sa_family_data.csv")
# FamNames <- names(FamData)[!names(FamData)%in%names(Data)]
# Family[!Family%in%FamNames]

SpData.wide <- Data[, SpNames]
IsZero <- apply(SpData.wide, 2, function(x) mean(x==0))

UseNames <- names(IsZero)[IsZero<0.99]
RemoveNames <- SpNames[!SpNames%in%UseNames]
NamesToLong <- names(Data)[!names(Data)%in%RemoveNames]

SAData.long <- reshape(Data[,NamesToLong], direction = "long", varying = UseNames,
  v.names = "Percent", timevar="SpeciesID")
SAData.long$Species <- SpNames[SAData.long$SpeciesID]
SAData.long$Percent2 <- pmax(0.1, SAData.long$Percent)
SAData.long$Abund <- log(SAData.long$Percent2/(100-SAData.long$Percent2))

SA.EnvCov <- c("gmap", "RFL_CONC", "HeatLoadIndex30m", "tmean13c",
  # "Elevation30m",
  "SoilConductivitymSm", "SoilTotalNPercent")

ScCov <- apply(SAData.long[,SA.EnvCov], 2, scale)
colnames(ScCov) <- paste0(colnames(ScCov), ".sc")

SAData <- cbind(SAData.long, ScCov)

```

```
# Get family names from GBIF
Classification <- classification(SpNames, db = 'gbif', rows=1)
```

== 288 queries =====

Retrieving data for taxon 'Adenogramma.glomerata'

Found: Adenogramma.glomerata

Retrieving data for taxon 'Albuca.concordiana'

Found: Albuca.concordiana

Retrieving data for taxon 'Albuca.sp.'

Found: Albuca.sp.

Retrieving data for taxon 'Aloe.microstigma'

Found: Aloe.microstigma

Retrieving data for taxon 'Amphiglossa.tomentosa'

Found: Amphiglossa.tomentosa

Retrieving data for taxon 'Amphiglossa.triflora'

Found: Amphiglossa.triflora

Retrieving data for taxon 'Anginon.fruticosum'

Found: Anginon.fruticosum

Retrieving data for taxon 'Anisodontea.triloba'

Found: Anisodontea.triloba

Retrieving data for taxon 'Anthospermum.aethiopicum'

Found: Anthospermum.aethiopicum

Retrieving data for taxon 'Anthospermum.spathulatum'

Found: Anthospermum.spathulatum

Retrieving data for taxon 'Antimima.triquetra'

Found: Antimima.triquetra

Retrieving data for taxon 'Aptosimum.indivisum'

Found: Aptosimum.indivisum

Retrieving data for taxon 'Aptosimum.spinescens'

Found: Aptosimum.spinescens

Retrieving data for taxon 'Arctopus.echinatus'

Found: Arctopus.echinatus

Retrieving data for taxon 'Arctotheca.calendula'

Found: Arctotheca.calendula

Retrieving data for taxon 'Arctotis.acaulis'

Found: Arctotis.acaulis

Retrieving data for taxon 'Aridaria.noctiflora'

Found: Aridaria.noctiflora

Retrieving data for taxon 'Aristida.vestita'

Found: Aristida.vestita

Retrieving data for taxon 'Asparagus.capensis'

Found: Asparagus.capensis

Retrieving data for taxon 'Asparagus.retrofractus'

Found: Asparagus.retrofractus

Retrieving data for taxon 'Asparagus.rubicundus'

Found: Asparagus.rubicundus

Retrieving data for taxon 'Asparagus.striatus'

Found: *Asparagus.striatus*

Retrieving data for taxon '*Atriplex.lindleyi*'

Found: *Atriplex.lindleyi*

Retrieving data for taxon '*Atriplex.semibaccata*'

Found: *Atriplex.semibaccata*

Retrieving data for taxon '*Augea.capensis*'

Found: *Augea.capensis*

Retrieving data for taxon '*Babiana.sambucina.var.longibracteata*'

Found: *Babiana.sambucina.var.longibracteata*

Retrieving data for taxon '*Berkheya.glabrata*'

Found: *Berkheya.glabrata*

Retrieving data for taxon '*Bromus.pectinatus*'

Found: *Bromus.pectinatus*

Retrieving data for taxon '*Brunsvigia.bosmaniae*'

Found: *Brunsvigia.bosmaniae*

Retrieving data for taxon 'Bulbine.nutans'

Found: Bulbine.nutans

Retrieving data for taxon 'Bulbine.succulenta'

Found: Bulbine.succulenta

Retrieving data for taxon 'Cannomois.parviflora'

Found: Cannomois.parviflora

Retrieving data for taxon 'Chaenostoma.caeruleum'

Found: Chaenostoma.caeruleum

Retrieving data for taxon 'Cheiridopsis.namaquensis'

Found: Cheiridopsis.namaquensis

Retrieving data for taxon 'Chlorophytum.undulatum'

Found: Chlorophytum.undulatum

Retrieving data for taxon 'Chrysocoma.ciliata'

Found: Chrysocoma.ciliata

Retrieving data for taxon 'Cladoraphis.spinosa'

Found: Cladoraphis.spinosa

Retrieving data for taxon 'Cleretum.bellidiforme'

Found: Cleretum.bellidiforme

Retrieving data for taxon 'Cliffortia.arborea'

Found: Cliffortia.arborea

Retrieving data for taxon 'Cliffortia.ruscifolia'

Found: Cliffortia.ruscifolia

Retrieving data for taxon 'Colchicum.crispum'

Found: Colchicum.crispum

Retrieving data for taxon 'Colchicum.volutare'

Found: Colchicum.volutare

Retrieving data for taxon 'Convolvulus.capensis'

Found: Convolvulus.capensis

Retrieving data for taxon 'Conyza.scabrida'

Found: Conyza.scabrida

Retrieving data for taxon 'Corymbium.africanum.subsp.scabridum'

Found: Corymbium.africanum.subsp.scabridum

Retrieving data for taxon 'Cotula.microglossa'

Found: Cotula.microglossa

Retrieving data for taxon 'Cotula.nudicaulis'

Found: Cotula.nudicaulis

Retrieving data for taxon 'Cotyledon.orbiculata'

Found: Cotyledon.orbiculata

Retrieving data for taxon 'Crassula.barbata'

Found: Crassula.barbata

Retrieving data for taxon 'Crassula.muscosa'

Found: Crassula.muscosa

Retrieving data for taxon 'Crassula.rupestris'

Found: Crassula.rupestris

Retrieving data for taxon 'Crassula.umbella'

Found: Crassula.umbella

Retrieving data for taxon 'Cymbopogon.marginatus'

Found: Cymbopogon.marginatus

Retrieving data for taxon 'Cyphia.digitata'

Found: Cyphia.digitata

Retrieving data for taxon 'Cyphia.volubilis'

Found: Cyphia.volubilis

Retrieving data for taxon 'Didelta.spinosa'

Found: Didelta.spinosa

Retrieving data for taxon 'Dimorphotheca.cuneata'

Found: Dimorphotheca.cuneata

Retrieving data for taxon 'Dimorphotheca.pinnata'

Found: Dimorphotheca.pinnata

Retrieving data for taxon 'Dimorphotheca.pluvialis'

Found: Dimorphotheca.pluvialis

Retrieving data for taxon 'Dimorphotheca.sinuata'

Found: Dimorphotheca.sinuata

Retrieving data for taxon 'Diospyros.austro.africana'

Found: Diospyros.austro.africana

Retrieving data for taxon 'Dodonaea.viscosa.var..angustifolia'

Found: Dodonaea.viscosa.var..angustifolia

Retrieving data for taxon 'Drosanthemum.floribundum'

Found: Drosanthemum.floribundum

Retrieving data for taxon 'Ehrharta.bulbosa'

Found: Ehrharta.bulbosa

Retrieving data for taxon 'Ehrharta.calycina'

Found: Ehrharta.calycina

Retrieving data for taxon 'Ehrharta.melicoides'

Found: Ehrharta.melicoides

Retrieving data for taxon 'Ehrharta.ramosa.subsp.ramosa'

Found: *Ehrharta.ramosa.subsp.ramosa*

Retrieving data for taxon '*Erepsia.saturata*'

Found: *Erepsia.saturata*

Retrieving data for taxon '*Erica.inaequalis*'

Found: *Erica.inaequalis*

Retrieving data for taxon '*Erica.plumosa*'

Found: *Erica.plumosa*

Retrieving data for taxon '*Eriocephalus.africanus*'

Found: *Eriocephalus.africanus*

Retrieving data for taxon '*Eriocephalus.decussatus*'

Found: *Eriocephalus.decussatus*

Retrieving data for taxon '*Eriocephalus.ericoides*'

Found: *Eriocephalus.ericoides*

Retrieving data for taxon '*Eriocephalus.microphyllus*'

Found: *Eriocephalus.microphyllus*

Retrieving data for taxon 'Erioccephalus.namaquensis'

Found: Erioccephalus.namaquensis

Retrieving data for taxon 'Erioccephalus.pauperrimus'

Found: Erioccephalus.pauperrimus

Retrieving data for taxon 'Erioccephalus.punctulatus'

Found: Erioccephalus.punctulatus

Retrieving data for taxon 'Erioccephalus.purpureus'

Found: Erioccephalus.purpureus

Retrieving data for taxon 'Erioccephalus.spinescens'

Found: Erioccephalus.spinescens

Retrieving data for taxon 'Eriospermum.capense'

Found: Eriospermum.capense

Retrieving data for taxon 'Erodium.cicutarium'

Found: Erodium.cicutarium

Retrieving data for taxon 'Euchlora.hirsuta'

Found: *Euchlora.hirsuta*

Retrieving data for taxon '*Euphorbia.decussata*'

Found: *Euphorbia.decussata*

Retrieving data for taxon '*Euphorbia.mauritanica*'

Found: *Euphorbia.mauritanica*

Retrieving data for taxon '*Euryops.lateriflorus*'

Found: *Euryops.lateriflorus*

Retrieving data for taxon '*Euryops.multifidus*'

Found: *Euryops.multifidus*

Retrieving data for taxon '*Felicia.australis*'

Found: *Felicia.australis*

Retrieving data for taxon '*Felicia.filifolia*'

Found: *Felicia.filifolia*

Retrieving data for taxon '*Felicia.hirta*'

Found: *Felicia.hirta*

Retrieving data for taxon 'Felicia.macrorrhiza'

Found: Felicia.macrorrhiza

Retrieving data for taxon 'Felicia.ovata'

Found: Felicia.ovata

Retrieving data for taxon 'Felicia.rogersii'

Found: Felicia.rogersii

Retrieving data for taxon 'Festuca.scabra'

Found: Festuca.scabra

Retrieving data for taxon 'Ficinia.bulbosa'

Found: Ficinia.bulbosa

Retrieving data for taxon 'Ficinia.deusta'

Found: Ficinia.deusta

Retrieving data for taxon 'Ficinia.indica'

Found: Ficinia.indica

Retrieving data for taxon 'Ficinia.nigrescens'

Found: *Ficinia.nigrescens*

Retrieving data for taxon '*Fingerhuthia.africana*'

Found: *Fingerhuthia.africana*

Retrieving data for taxon '*Foveolina.dichotoma*'

Found: *Foveolina.dichotoma*

Retrieving data for taxon '*Galenia.africana*'

Found: *Galenia.africana*

Retrieving data for taxon '*Galenia.filiiformis*'

Found: *Galenia.filiiformis*

Retrieving data for taxon '*Galenia.fruticosa*'

Found: *Galenia.fruticosa*

Retrieving data for taxon '*Galenia.namaensis*'

Found: *Galenia.namaensis*

Retrieving data for taxon '*Galenia.sarcophylla*'

Found: *Galenia.sarcophylla*

Retrieving data for taxon 'Gazania.krebsiana'

Found: Gazania.krebsiana

Retrieving data for taxon 'Gazania.lichtensteinii'

Found: Gazania.lichtensteinii

Retrieving data for taxon 'Gazania.rigida'

Found: Gazania.rigida

Retrieving data for taxon 'Gnidia.scabra'

Found: Gnidia.scabra

Retrieving data for taxon 'Gorteria.diffusa'

Found: Gorteria.diffusa

Retrieving data for taxon 'Gymnodiscus.capillaris'

Found: Gymnodiscus.capillaris

Retrieving data for taxon 'Helichrysum.asperum'

Found: Helichrysum.asperum

Retrieving data for taxon 'Helichrysum.hamulosum'

Found: *Helichrysum.hamulosum*

Retrieving data for taxon '*Helichrysum.moeserianum*'

Found: *Helichrysum.moeserianum*

Retrieving data for taxon '*Helichrysum.obtusum*'

Found: *Helichrysum.obtusum*

Retrieving data for taxon '*Helichrysum.revolutum*'

Found: *Helichrysum.revolutum*

Retrieving data for taxon '*Helichrysum.stellatum*'

Found: *Helichrysum.stellatum*

Retrieving data for taxon '*Heliophila.amplexicaulis*'

Found: *Heliophila.amplexicaulis*

Retrieving data for taxon '*Heliophila.collina*'

Found: *Heliophila.collina*

Retrieving data for taxon '*Heliophila.crithmifolia*'

Found: *Heliophila.crithmifolia*

Retrieving data for taxon 'Heliophila.pinnata'

Found: Heliophila.pinnata

Retrieving data for taxon 'Hermannia.althaeifolia'

Found: Hermannia.althaeifolia

Retrieving data for taxon 'Hermannia.coccocarpa'

Found: Hermannia.coccocarpa

Retrieving data for taxon 'Hermannia.cuneifolia'

Found: Hermannia.cuneifolia

Retrieving data for taxon 'Hermannia.spinosa'

Found: Hermannia.spinosa

Retrieving data for taxon 'Hirpicium.alienatum'

Found: Hirpicium.alienatum

Retrieving data for taxon 'Hoodia.gordonii'

Found: Hoodia.gordonii

Retrieving data for taxon 'Ifloga.ambigua'

Found: Ifloga.ambigua

Retrieving data for taxon 'Ifloga.glomerata'

Found: Ifloga.glomerata

Retrieving data for taxon 'Indigofera.nigromontana'

Found: Indigofera.nigromontana

Retrieving data for taxon 'Ixia.rapunculoides'

Found: Ixia.rapunculoides

Retrieving data for taxon 'Lapeirousia.jacquinii'

Found: Lapeirousia.jacquinii

Retrieving data for taxon 'Lapeirousia.plicata'

Found: Lapeirousia.plicata

Retrieving data for taxon 'Lasiopogon.muscoides'

Found: Lasiopogon.muscoides

Retrieving data for taxon 'Lasiospermum.brachyglossum'

Found: Lasiospermum.brachyglossum

Retrieving data for taxon 'Leipoldtia.schultzei'

Found: Leipoldtia.schultzei

Retrieving data for taxon 'Leucadendron.brunioides'

Found: Leucadendron.brunioides

Retrieving data for taxon 'Leucadendron.remotum'

Found: Leucadendron.remotum

Retrieving data for taxon 'Leucadendron.salignum'

Found: Leucadendron.salignum

Retrieving data for taxon 'Leysera.gnaphalodes'

Found: Leysera.gnaphalodes

Retrieving data for taxon 'Leysera.gnaphaloides'

Found: Leysera.gnaphaloides

Retrieving data for taxon 'Leysera.tenella'

Found: Leysera.tenella

Retrieving data for taxon 'Limeum.aethiopicum'

Found: *Limeum.aethiopicum*

Retrieving data for taxon '*Linum.africanum*'

Found: *Linum.africanum*

Retrieving data for taxon '*Lycium.cinereum*'

Found: *Lycium.cinereum*

Retrieving data for taxon '*Malephora.crassa*'

Found: *Malephora.crassa*

Retrieving data for taxon '*Massonia.depressa*'

Found: *Massonia.depressa*

Retrieving data for taxon '*Melianthus.comosus*'

Found: *Melianthus.comosus*

Retrieving data for taxon '*Melolobium.candicans*'

Found: *Melolobium.candicans*

Retrieving data for taxon '*Mesembryanthemum.guerichianum*'

Found: *Mesembryanthemum.guerichianum*

Retrieving data for taxon 'Mesembryanthemum.stenandrum'

Found: Mesembryanthemum.stenandrum

Retrieving data for taxon 'Microloma.sagittatum'

Found: Microloma.sagittatum

Retrieving data for taxon 'Monoculus.monstrosus'

Found: Monoculus.monstrosus

Retrieving data for taxon 'Montinia.caryophyllacea'

Found: Montinia.caryophyllacea

Retrieving data for taxon 'Moraea.bifida'

Found: Moraea.bifida

Retrieving data for taxon 'Moraea.brachygyne'

Found: Moraea.brachygyne

Retrieving data for taxon 'Moraea.ciliata'

Found: Moraea.ciliata

Retrieving data for taxon 'Moraea.falcifolia'

Found: *Moraea.falcifolia*

Retrieving data for taxon '*Muraltia.divaricata*'

Found: *Muraltia.divaricata*

Retrieving data for taxon '*Muraltia.spinosa*'

Found: *Muraltia.spinosa*

Retrieving data for taxon '*Nemesia.cheiranthus*'

Found: *Nemesia.cheiranthus*

Retrieving data for taxon '*Nemesia.leipoldtii*'

Found: *Nemesia.leipoldtii*

Retrieving data for taxon '*Oedera.genistifolia*'

Found: *Oedera.genistifolia*

Retrieving data for taxon '*Oedera.sedifolia*'

Found: *Oedera.sedifolia*

Retrieving data for taxon '*Oedera.squarrosa*'

Found: *Oedera.squarrosa*

Retrieving data for taxon 'Olea.europaea'

Found: Olea.europaea

Retrieving data for taxon 'Ornithogalum.tanquanum'

Found: Ornithogalum.tanquanum

Retrieving data for taxon 'Osteospermum.acanthospermum'

Found: Osteospermum.acanthospermum

Retrieving data for taxon 'Osteospermum.incanum.subsp.incanum'

Found: Osteospermum.incanum.subsp.incanum

Retrieving data for taxon 'Osteospermum.leptolobum'

Found: Osteospermum.leptolobum

Retrieving data for taxon 'Osteospermum.scariosum'

Found: Osteospermum.scariosum

Retrieving data for taxon 'Osteospermum.sinuatum'

Found: Osteospermum.sinuatum

Retrieving data for taxon 'Otholobium.candicans'

Found: Otholobium.candicans

Retrieving data for taxon 'Othonna.auriculifolia'

Found: Othonna.auriculifolia

Retrieving data for taxon 'Othonna.hederifolia'

Found: Othonna.hederifolia

Retrieving data for taxon 'Othonna.rechingeri'

Found: Othonna.rechingeri

Retrieving data for taxon 'Othonna.undulosa'

Found: Othonna.undulosa

Retrieving data for taxon 'Oxalis.flava'

Found: Oxalis.flava

Retrieving data for taxon 'Oxalis.luteola'

Found: Oxalis.luteola

Retrieving data for taxon 'Oxalis.massoniana.var.massoniana'

Found: Oxalis.massoniana.var.massoniana

Retrieving data for taxon 'Oxalis.obtusa'

Found: Oxalis.obtusa

Retrieving data for taxon 'Oxalis.pes.caprae'

Found: Oxalis.pes.caprae

Retrieving data for taxon 'Oxalis.pocockiae'

Found: Oxalis.pocockiae

Retrieving data for taxon 'Paranomus.bracteolaris'

Found: Paranomus.bracteolaris

Retrieving data for taxon 'Passerina.truncata'

Found: Passerina.truncata

Retrieving data for taxon 'Pelargonium.articulatum'

Found: Pelargonium.articulatum

Retrieving data for taxon 'Pelargonium.crithmifolium'

Found: Pelargonium.crithmifolium

Retrieving data for taxon 'Pelargonium.magentium'

Found: Pelargonium.magentum

Retrieving data for taxon 'Pelargonium.praemorsum'

Found: Pelargonium.praemorsum

Retrieving data for taxon 'Pelargonium.rapaceum'

Found: Pelargonium.rapaceum

Retrieving data for taxon 'Pelargonium.reflexum'

Found: Pelargonium.reflexum

Retrieving data for taxon 'Pelargonium.scabrum'

Found: Pelargonium.scabrum

Retrieving data for taxon 'Pelargonium.triste'

Found: Pelargonium.triste

Retrieving data for taxon 'Pentameris.pallida'

Found: Pentameris.pallida

Retrieving data for taxon 'Pentameris.rupestris'

Found: Pentameris.rupestris

Retrieving data for taxon 'Pentzia.incana'

Found: Pentzia.incana

Retrieving data for taxon 'Pentzia.spinescens'

Found: Pentzia.spinescens

Retrieving data for taxon 'Pharnaceum.aurantium'

Found: Pharnaceum.aurantium

Retrieving data for taxon 'Pharnaceum.ciliare'

Found: Pharnaceum.ciliare

Retrieving data for taxon 'Phylica.agathosmoides'

Found: Phylica.agathosmoides

Retrieving data for taxon 'Phylica.rigidifolia'

Found: Phylica.rigidifolia

Retrieving data for taxon 'Plantago.cafra'

Found: Plantago.cafra

Retrieving data for taxon 'Poa.bulbosa'

Found: Poa.bulbosa

Retrieving data for taxon 'Polycarena.aurea'

Found: Polycarena.aurea

Retrieving data for taxon 'Polygala.myrtifolia'

Found: Polygala.myrtifolia

Retrieving data for taxon 'Polygala.scabra'

Found: Polygala.scabra

Retrieving data for taxon 'Protea.laurifolia'

Found: Protea.laurifolia

Retrieving data for taxon 'Protea.repens'

Found: Protea.repens

Retrieving data for taxon 'Pteronia.adenocarpa'

Found: Pteronia.adenocarpa

Retrieving data for taxon 'Pteronia.divaricata'

Found: Pteronia.divaricata

Retrieving data for taxon 'Pteronia.empetrifolia'

Found: Pteronia.empetrifolia

Retrieving data for taxon 'Pteronia.glabrata'

Found: Pteronia.glabrata

Retrieving data for taxon 'Pteronia.glauca'

Found: Pteronia.glauca

Retrieving data for taxon 'Pteronia.glomerata'

Found: Pteronia.glomerata

Retrieving data for taxon 'Pteronia.incana'

Found: Pteronia.incana

Retrieving data for taxon 'Pteronia.pallens'

Found: Pteronia.pallens

Retrieving data for taxon 'Pteronia.paniculata'

Found: Pteronia.paniculata

Retrieving data for taxon 'Pteronia.villosa'

Found: Pteronia.villosa

Retrieving data for taxon 'Restio.capensis'

Found: Restio.capensis

Retrieving data for taxon 'Restio.longiaristatus'

Found: Restio.longiaristatus

Retrieving data for taxon 'Restio.macer'

Found: Restio.macer

Retrieving data for taxon 'Restio.monanthos'

Found: Restio.monanthos

Retrieving data for taxon 'Restio.rudolfii'

Found: Restio.rudolfii

Retrieving data for taxon 'Restio.vimineus'

Found: Restio.vimineus

Retrieving data for taxon 'Romulea.sabulosa'

Found: Romulea.sabulosa

Retrieving data for taxon 'Rosenia.glandulosa'

Found: Rosenia.glandulosa

Retrieving data for taxon 'Rosenia.oppositifolia'

Found: Rosenia.oppositifolia

Retrieving data for taxon 'Ruschia.cradockensis'

Found: Ruschia.cradockensis

Retrieving data for taxon 'Ruschia.intricata'

Found: Ruschia.intricata

Retrieving data for taxon 'Salsola.aphylla'

Found: Salsola.aphylla

Retrieving data for taxon 'Salsola.kali'

Found: Salsola.kali

Retrieving data for taxon 'Salvia.disermas'

Found: Salvia.disermas

Retrieving data for taxon 'Sarcocaulon.crassicaule'

Found: Sarcocaulon.crassicaule

Retrieving data for taxon 'Satyrium.erectum'

Found: Satyrium.erectum

Retrieving data for taxon 'Schismus.schismoides'

Found: Schismus.schismoides

Retrieving data for taxon 'Scirpoides.dioecus'

Found: Scirpoides.dioecus

Retrieving data for taxon 'Searsia.angustifolia'

Found: Searsia.angustifolia

Retrieving data for taxon 'Searsia.burchellii'

Found: Searsia.burchellii

Retrieving data for taxon 'Searsia.lancea'

Found: Searsia.lancea

Retrieving data for taxon 'Searsia.longispina'

Found: Searsia.longispina

Retrieving data for taxon 'Searsia.undulata'

Found: Searsia.undulata

Retrieving data for taxon 'Selago.albida'

Found: Selago.albida

Retrieving data for taxon 'Selago.articulata'

Found: Selago.articulata

Retrieving data for taxon 'Selago.glabrata'

Found: Selago.glabrata

Retrieving data for taxon 'Senecio.arenarius'

Found: Senecio.arenarius

Retrieving data for taxon 'Senecio.burchellii'

Found: Senecio.burchellii

Retrieving data for taxon 'Senecio.cardaminifolius'

Found: Senecio.cardaminifolius

Retrieving data for taxon 'Senecio.erosus'

Found: *Senecio.erosus*

Retrieving data for taxon '*Senecio.radicans*'

Found: *Senecio.radicans*

Retrieving data for taxon '*Septulina.glauca*'

Found: *Septulina.glauca*

Retrieving data for taxon '*Silene.clandestina*'

Found: *Silene.clandestina*

Retrieving data for taxon '*Stachys.rugosa*'

Found: *Stachys.rugosa*

Retrieving data for taxon '*Stipagrostis.ciliata*'

Found: *Stipagrostis.ciliata*

Retrieving data for taxon '*Stipagrostis.namaquensis*'

Found: *Stipagrostis.namaquensis*

Retrieving data for taxon '*Stipagrostis.obtusa*'

Found: *Stipagrostis.obtusa*

Retrieving data for taxon 'Stipagrostis.zeyheri'

Found: Stipagrostis.zeyheri

Retrieving data for taxon 'Struthiola.ciliata.subsp.incana'

Found: Struthiola.ciliata.subsp.incana

Retrieving data for taxon 'Sutherlandia.frutescens'

Found: Sutherlandia.frutescens

Retrieving data for taxon 'Tenaxia.dura'

Found: Tenaxia.dura

Retrieving data for taxon 'Tenaxia.stricta'

Found: Tenaxia.stricta

Retrieving data for taxon 'Tetragonia.fruticosa'

Found: Tetragonia.fruticosa

Retrieving data for taxon 'Tetragonia.microptera'

Found: Tetragonia.microptera

Retrieving data for taxon 'Tetragonia.nigrescens'

Found: *Tetragonia.nigrescens*

Retrieving data for taxon '*Thamnochortus.platypteris*'

Found: *Thamnochortus.platypteris*

Retrieving data for taxon '*Thesium.hispidulum*'

Found: *Thesium.hispidulum*

Retrieving data for taxon '*Thesium.lineatum*'

Found: *Thesium.lineatum*

Retrieving data for taxon '*Trachyandra.divaricata*'

Found: *Trachyandra.divaricata*

Retrieving data for taxon '*Trachyandra.falcata*'

Found: *Trachyandra.falcata*

Retrieving data for taxon '*Tribolium.hispidum*'

Found: *Tribolium.hispidum*

Retrieving data for taxon '*Tribolium.uniolae*'

Found: *Tribolium.uniolae*

Retrieving data for taxon 'Tylecodon.paniculatus'

Found: Tylecodon.paniculatus

Retrieving data for taxon 'Tylecodon.reticulatus'

Found: Tylecodon.reticulatus

Retrieving data for taxon 'Tylecodon.wallichii'

Found: Tylecodon.wallichii

Retrieving data for taxon 'Ursinia.anthemoides'

Found: Ursinia.anthemoides

Retrieving data for taxon 'Ursinia.cakilefolia'

Found: Ursinia.cakilefolia

Retrieving data for taxon 'Ursinia.chrysanthemoides'

Found: Ursinia.chrysanthemoides

Retrieving data for taxon 'Ursinia.pilifera'

Found: Ursinia.pilifera

Retrieving data for taxon 'Viscum.capense'

Found: *Viscum.capense*

Retrieving data for taxon '*Wiborgia.monoptera*'

Found: *Wiborgia.monoptera*

Retrieving data for taxon '*Wiborgiella.leipoldtiana*'

Found: *Wiborgiella.leipoldtiana*

Retrieving data for taxon '*Willdenowia.arescens*'

Found: *Willdenowia.arescens*

Retrieving data for taxon '*Willdenowia.incurvata*'

Found: *Willdenowia.incurvata*

Retrieving data for taxon '*Zaluzianskya.cohabitans*'

Found: *Zaluzianskya.cohabitans*

Retrieving data for taxon '*Zaluzianskya.pusilla*'

Found: *Zaluzianskya.pusilla*

Retrieving data for taxon '*Zaluzianskya.violacea*'

Found: *Zaluzianskya.violacea*

Retrieving data for taxon 'Zygophyllum.foetidum'

Found: Zygophyllum.foetidum

Retrieving data for taxon 'Zygophyllum.lichtensteinianum'

Found: Zygophyllum.lichtensteinianum

Retrieving data for taxon 'Zygophyllum.pygmaeum'

Found: Zygophyllum.pygmaeum

Retrieving data for taxon 'Zygophyllum.retrofractum'

Found: Zygophyllum.retrofractum

== Results =====

- Total: 288
- Found: 288
- Not Found: 0

```
Family <- unlist(lapply(Classification, function(lst) lst$name[lst$rank=="family"]))

SADData$Family <- unlist(sapply(SADData$Species, function(Sp, fam) {
#   cat(Spp, "\n")
  ff <- which(Sp==names(fam))
  if(length(ff)==0) {
    res <- "AAAAAGH"
  } else {
    res <- fam[ff]
  }
  res
}, fam=Family))

# any(SADData$Family=="AAAAAGH")
```

```
SADData$Family <- factor(SADData$Family)
SADData$Species <- factor(SADData$Species)
SADData$plot <- factor(SADData$plot)
```

Covariates:

- gmap: mean annual precipitation
- RFL_CONC: rainfall concentration
- Elevation30m: elevation (at 30m resolution)
- HeatLoadIndex30m: heat load index (at 30m resolution)
- tmean13c: mean annual temperature
- SoilConductivitymSm: soil conductivity
- SoilTotalNPercent: Nitrogen concentration in soil (%)

We remove elevation because of the high correlation with tmean13c (-0.94), and all species that occur in <1% of sites, giving 146 species out of the original 288.

We fit the model with INLA, and use relatively tight PC priors to control the estimates of the environmental effects (without doing this everything is horribly unstable).

```
# Create formula for INLA
SA.Formula <- formula(
  paste0("Abund ~ f(Species, hyper = PCHyper) + f(plot, hyper = PCHyper) + ",
    paste(
      c(paste0(SA.EnvCov, ".sc"),
        apply(paste0(SA.EnvCov, ".sc"), function(eu) {
          paste0("f(Species.", eu, ", ", eu, ", hyper = PCHyper)")
        })), collapse=" + "))
)

SAenvInd <- data.frame(apply(SA.EnvCov, function(nm, dat) assign(nm, dat),
  dat=SADData$Species))
names(SAenvInd) <- paste0("Species.", names(SAenvInd), ".sc")

SADData <- cbind(SADData, SAenvInd)

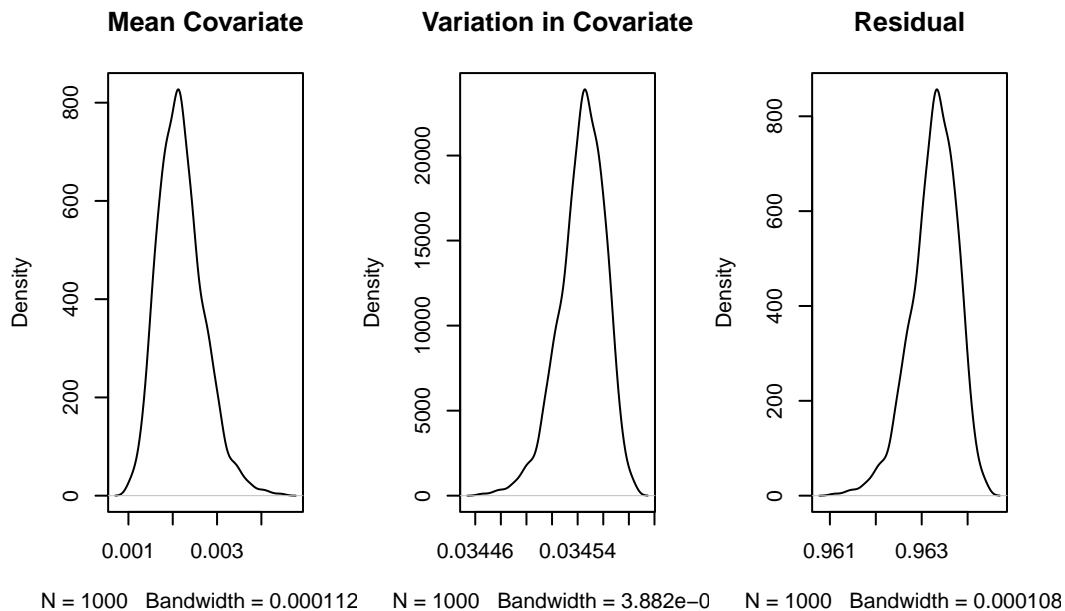
# int.strategy = "ccd" or int.strategy = "grid"
# Fit the model
SAinla <- inla(SA.Formula, data=SADData, control.compute=list(config = TRUE),
  control.inla=list(int.strategy = "ccd"))
SASumm <-summary(SAinla)
```

This will calculate the statistics

```
SAsamps <- inla.posterior.sample(nsim, SAinla)

SAPosts <- data.frame(t(apply(SAsamps, CalcPostVar, data=SAData)))
Use <- !names(SAPosts)%in%paste0("Precision.for.", c("Species", "plot"))
SA.PropVar <- sweep(SAPosts[,Use], 1, rowSums(SAPosts[,Use]), "/")
names(SA.PropVar) <- gsub("Precision.for.the.Gaussian.observations", "VarEps",
                          names(SA.PropVar), fixed=TRUE)

par(mfrow=c(1,3))
plot(density(SA.PropVar$MeanDelta), main="Mean Covariate")
plot(density(SA.PropVar$VarDelta), main="Variation in Covariate")
plot(density(SA.PropVar$VarEps), main="Residual")
```



```
# Summary
SA.SummVars <- cbind(
  Mode=MCMCglmm::posterior.mode(coda::as.mcmc(SA.PropVar)),
  coda::HPDinterval(coda::as.mcmc(SA.PropVar), prob = 0.95)
)
```

We find that 3.67% of the variation in beta diversity is explained by the covariates, with a 95% HPDI of 3.58% - 3.77%.

Example 2: The Inevitable BCI Data

This is counts of trees on an island that only exists to let ecologists take a holiday in the jungle. The data can be downloaded from Condit et al. (2002).

```
BCI.Env <- read.csv("philawhite-spGDMM-code-d8279ee/data/Panama_env.csv")
BCI.Sp <- read.csv("philawhite-spGDMM-code-d8279ee/data/Panama_species.csv")

# Stupid naming
# "species" is actually site. And the format of the names is different between files
# This is why "data scientist" has a lower job satisfaction than "statistician"
BCI.Sp$site.no. <- sprintf("P%02d", as.numeric(gsub("P", "", BCI.Sp$species)))
BCI.Sp$species <- NULL

BCI.EnvCov <- c("precip", "elev", "age")
Pres <- apply(BCI.Sp, 2, function(x) sum(x>0))
sp.tmp <- BCI.Sp[,which(Pres>10)]
dat.tmp <- cbind(BCI.Env, sp.tmp)
SpNames <- names(sp.tmp)[!names(sp.tmp)%in%c("species", "site.no.")]
BCIData <- reshape(dat.tmp, direction = "long", varying = SpNames, v.names = "Count")
BCIData$Species <- factor(SpNames[BCIData$time])
BCIData$Site <- factor(BCIData$site.no.)
BCIData$SiteSpecies <- paste0(BCIData$Site, BCI.Sp$species)
# Scale env
Scale.tmp <- apply(BCIData[,BCI.EnvCov], 2, scale)
colnames(Scale.tmp) <- paste0(colnames(Scale.tmp), ".sc")
BCIData <- cbind(BCIData, Scale.tmp)
```

We can fit the model in INLA:

```
BCI.Formula <- formula(
  paste0("Count ~ f(Species, hyper = PCHyper) + f(Site, hyper = PCHyper) + ",
  paste(
    c(paste0(BCI.EnvCov, ".sc"),
      sapply(paste0(BCI.EnvCov, ".sc"), function(eu) {
        paste0("f(Species.", eu, ", ", eu, ", hyper = PCHyper)")
      })), collapse=" + "), " + f(OD, hyper = PCHyper)")
)

BCIenvInd <- data.frame(sapply(BCI.EnvCov, function(nm, dat) assign(nm, dat),
  dat=BCIData$Species))
names(BCIenvInd) <- paste0("Species.", names(BCIenvInd), ".sc")
```

```

BCIData <- cbind(BCIData, BCIenvInd)
BCIData$OD <- factor(1:nrow(BCIData))

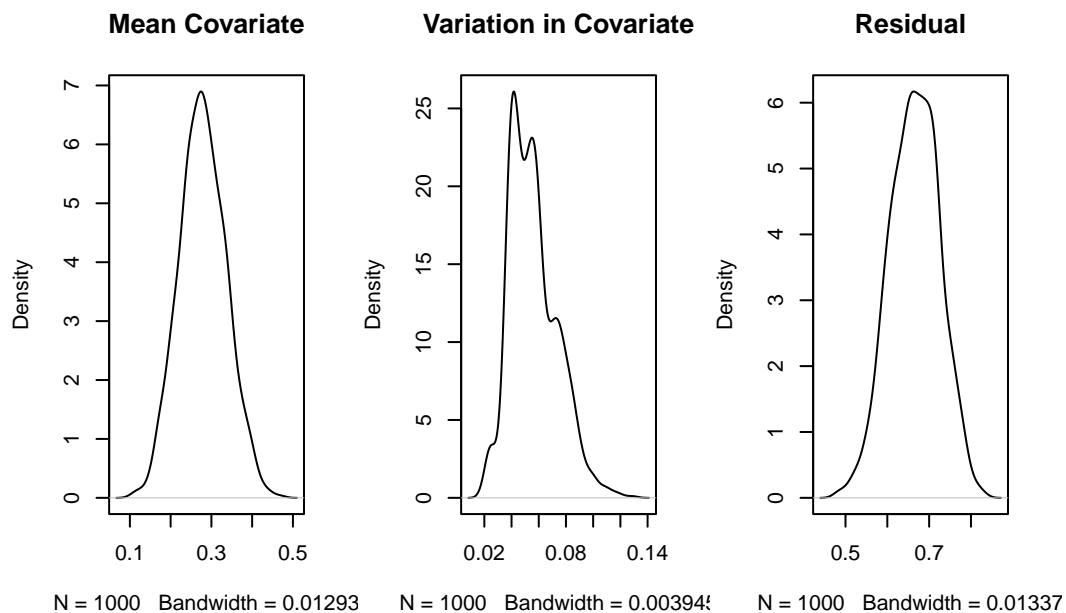
# Fit the model
BCIinla <- inla(BCI.Formula, data=BCIData, control.compute=list(config = TRUE),
               family="poisson")
BCISumm <- summary(BCIinla)

BCIsamps <- inla.posterior.sample(nsim, BCIinla)

BCI.Posts <- data.frame(t(sapply(BCIsamps, CalcPostVar, data=BCIData)))
Use <- !names(BCI.Posts)%in%paste0("Precision.for.", c("Species", "Site"))
BCI.PropVar <- sweep(BCI.Posts[,Use], 1, rowSums(BCI.Posts[,Use]), "/")
names(BCI.PropVar)[3] <- "VarEps"

par(mfrow=c(1,3))
plot(density(BCI.PropVar$MeanDelta), main="Mean Covariate")
plot(density(BCI.PropVar$VarDelta), main="Variation in Covariate")
plot(density(BCI.PropVar$VarEps), main="Residual")

```



```

BCI.SummVars <- cbind(
  Mode=MCMCglmm::posterior.mode(coda::as.mcmc(BCI.PropVar)),
  coda::HPDinterval(coda::as.mcmc(BCI.PropVar), prob = 0.95)
)

```


We find that 29.63% of the variation in beta diversity is explained by the covariates, with a 95% HPDI of 21.59% - 44.13%.

Example 3: Australian Plants

This is occurrence of plants in Southwest Australia, the `southwest` data in the `gdm` package. The data are not well documented, with several presences per species per site. Absence data is not given. Fortunately, the environmental data does not vary within a site.

```
data("southwest")

SW.EnvCov <- names(southwest)[!names(southwest)%in%c("species","site", "Lat", "Long")]

Pres <- table(southwest$species)
sp.keep <- names(Pres[Pres>50]) #reduce to 10?

southwest.small <- southwest[southwest$species%in%sp.keep,]
southwest.small$species <- factor(southwest.small$species)
SW.pres <- expand.grid(species=unique(southwest.small$species),
                      site=unique(southwest.small$site))
SW.pres$Presence <- apply(SW.pres, 1, function(wh, dat) {
  any(dat$site==wh["site"] & dat$species==wh["species"])
}, dat=southwest.small)

# Extract environmental variables
SWenv <- data.frame(apply(southwest.small[,SW.EnvCov], 2, function(x, dat) {
  tapply(x, list(dat$site), function(xx) xx[1])
}, dat=southwest.small))
env.site <- rownames(SWenv)
SWenv <- data.frame(apply(SWenv, 2, scale))
names(SWenv) <- paste0(colnames(SWenv), ".sc")
SWenv$site <- env.site

SW.data <- merge(SW.pres, SWenv)
SW.data$Presence <- as.numeric(SW.data$Presence)

# Check to see if there is variation in environment between sites. There isn't.
# SDs <- by(southwest.small, list(southwest.small$site), function(df, vars) {
#   apply(df[,vars], 2, sd)
```

```
# }, vars=SW.EnvCov)
# table(unlist(SDs))
```

We can fit the model in INLA:

```
SW.Formula <- formula(
  paste0("Presence ~ f(species, hyper = PCHyper) + f(site, hyper = PCHyper) + ",
    paste(
      c(paste0(SW.EnvCov, ".sc"),
        sapply(paste0(SW.EnvCov, ".sc"), function(eu) {
          paste0("f(Species.", eu, ", ", " ", eu, ", ", hyper = PCHyper)")
        })), collapse=" + "))
)

SWenvInd <- data.frame(sapply(SW.EnvCov, function(nm, dat) assign(nm, dat),
  dat=SW.data$species))
names(SWenvInd) <- paste0("Species.", names(SWenvInd), ".sc")
SW.data <- cbind(SW.data, SWenvInd)

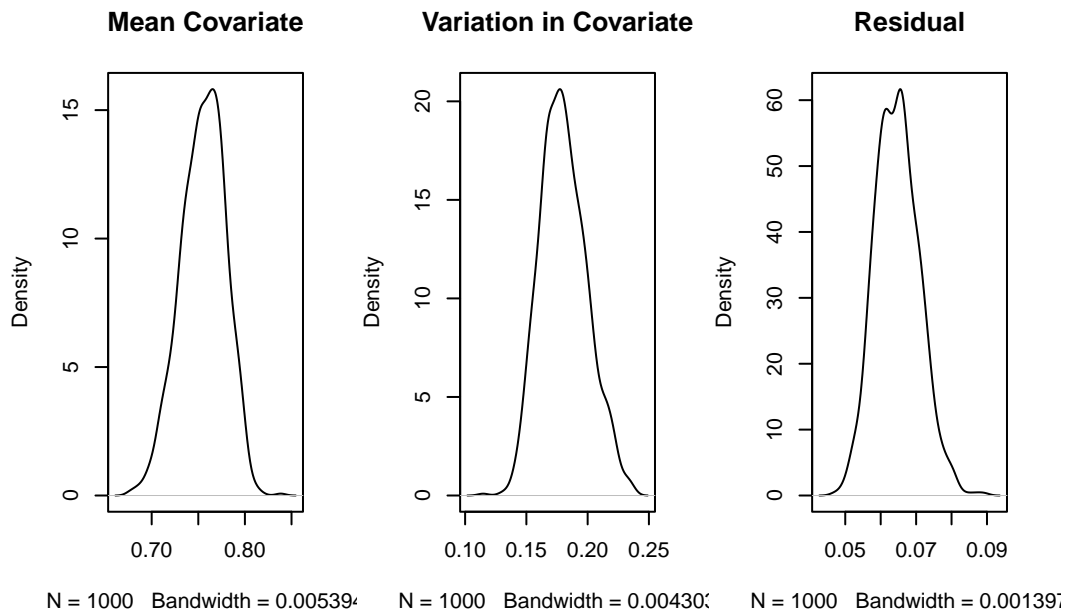
# Fit the model
SWinla <- inla(SW.Formula, data=SW.data, control.compute=list(config = TRUE),
  family="binomial", Ntrials = 1)
SWSumm <-summary(SWinla)
```

And now...

```
SWsamps <- inla.posterior.sample(nsim, SWinla)

SW.Posts <- data.frame(t(sapply(SWsamps, CalcPostVar, data=SW.data)))
SW.Posts$logitVar <- pi/3
Use <- !names(SW.Posts)%in%paste0("Precision.for.", c("species", "site"))
SW.PropVar <- sweep(SW.Posts[,Use], 1, rowSums(SW.Posts[,Use]), "/")
names(SW.PropVar)[3] <- "VarEps"

par(mfrow=c(1,3))
plot(density(SW.PropVar$MeanDelta), main="Mean Covariate")
plot(density(SW.PropVar$VarDelta), main="Variation in Covariate")
plot(density(SW.PropVar$VarEps), main="Residual")
```



```
SW.SummVars <- cbind(
  Mode=MCMCglmm::posterior.mode(coda::as.mcmc(SW.PropVar)),
  coda::HPDinterval(coda::as.mcmc(SW.PropVar), prob = 0.95)
)
```

We find that 93.4% of the variation in beta diversity is explained by the covariates, with a 95% HPDI of 92.4% - 94.77%.

References

- Condit, Richard, Nigel Pitman, Egbert G. Leigh, Jérôme Chave, John Terborgh, Robin B. Foster, Percy Núñez, et al. 2002. "Beta-Diversity in Tropical Forest Trees." *Science* 295 (5555): 666–69. <https://doi.org/10.1126/science.1066854>.
- Ferrier, Simon. 2002. "Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here?" *Systematic Biology* 51 (2): 331–63. <https://doi.org/10.1080/10635150252899806>.
- White, Philip A., Henry A. Frye, Jasper A. Slingsby, John A. Silander Jr, and Alan E. Gelfand. 2023. "Generative Spatial Generalized Dissimilarity Mixed Modelling (spGDMM): An Enhanced Approach to Modelling Beta Diversity." *Methods in Ecology and Evolution* n/a (n/a). <https://doi.org/https://doi.org/10.1111/2041-210X.14259>.