

# Dynamical Modeling of Abundance Data in Ecology

Guillaume Franchi

ENSAI, Bruz

14 February 2022

# Outlines

## I. Abundance Data

## II. General framework

## III. Data transformation

## IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

# Outlines

## I. Abundance Data

## II. General framework

## III. Data transformation

## IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

## Definition

## Definition

The **standard abundance** of a species is the total number of individuals of this species.

## Definition

The **standard abundance** of a species is the total number of individuals of this species.

The **relative abundance** of a species in an ecosystem is the proportion of individuals of the species among all individuals from all species.

## Example

## Example

Consider the extremely childish example where we are located in the savanna, and our ecosystem is composed as follow.



## Example

Consider the extremely childish example where we are located in the savanna, and our ecosystem is composed as follow.

Lions	Zebras	Buffalos	Hyenas	Total
12	36	48	24	120
10 %	30%	40%	20%	100%

## Example

Consider the extremely childish example where we are located in the savanna, and our ecosystem is composed as follow.

Lions	Zebras	Buffalos	Hyenas	Total
12	36	48	24	120
10 %	30%	40%	20%	100%

The vector  $(12, 36, 48, 24)$  is the standard abundance of our ecosystem, while the vector  $(0.1, 0.3, 0.4, 0.2)$  is the relative abundance.

## Remark

## Remark

Relative abundance data are therefore compositional data, i.e. taking values in the simplex:

$$\mathcal{S}_{d-1} = \left\{ (y_1, \dots, y_d) \in ]0; 1[^d \mid \sum_{i=1}^d y_i = 1 \right\}.$$

# Outlines

I. Abundance Data

II. General framework

III. Data transformation

IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

In all that follows, we will focus on relative abundance.

In all that follows, we will focus on relative abundance.

The abundance of a species can be explained by several exogenous variables:

In all that follows, we will focus on relative abundance.

The abundance of a species can be explained by several exogenous variables:

- climatic variables;



In all that follows, we will focus on relative abundance.

The abundance of a species can be explained by several exogenous variables:

- climatic variables;
- pollution

In all that follows, we will focus on relative abundance.

The abundance of a species can be explained by several exogenous variables:

- climatic variables;
- pollution

⇒ leads to regression problems for compositional data.

The abundance of one species is also affected by the abundance of other species.

The abundance of one species is also affected by the abundance of other species.

One can immediately guess that the abundance of species in a given ecosystem is a dynamic process, varying along the time.

We will propose time series models for abundance data, in order to explain the dynamic of abundance.

We will propose time series models for abundance data, in order to explain the dynamic of abundance.

We will not consider in our models the impact of exogenous variables on the abundance, but only the impact of species between them.

We will propose time series models for abundance data, in order to explain the dynamic of abundance.

We will not consider in our models the impact of exogenous variables on the abundance, but only the impact of species between them.

In all that follows, we will study the relative abundance along time  $t \in \mathbb{Z}$  of  $d \geq 2$  studies in a given ecosystem, modeled by a sequence  $Y^{(t)} = \left( Y_1^{(t)}, \dots, Y_d^{(t)} \right)$  of random variables, valued in  $\mathcal{S}_{d-1}$ .

We will assume that we have in our possession a sample  $(y^{(t)})_{0 \leq t \leq N} \in \mathcal{S}_{d-1}^N$  of this abundance, where  $y^{(t)}$  is a realization of the random variable  $Y^{(t)}$ .



We will assume that we have in our possession a sample  $(y^{(t)})_{0 \leq t \leq N} \in \mathcal{S}_{d-1}^N$  of this abundance, where  $y^{(t)}$  is a realization of the random variable  $Y^{(t)}$ .

### Example *Scandinavian birds*

We will assume that we have in our possession a sample  $(y^{(t)})_{0 \leq t \leq N} \in \mathcal{S}_{d-1}^N$  of this abundance, where  $y^{(t)}$  is a realization of the random variable  $Y^{(t)}$ .

### Example *Scandinavian birds*

Consider an ecosystem composed by three alpine birds species: «Anthus pratensis», «Calcarius lapponicus» and «Oenanthe oenanthe».

We will assume that we have in our possession a sample  $(y^{(t)})_{0 \leq t \leq N} \in \mathcal{S}_{d-1}^N$  of this abundance, where  $y^{(t)}$  is a realization of the random variable  $Y^{(t)}$ .

### Example *Scandinavian birds*

Consider an ecosystem composed by three alpine birds species: «Anthus pratensis», «Calcarius lapponicus» and «Oenanthe oenanthe». The relative abundance of this ecosystem has been registered from 1964 to 2001:

We will assume that we have in our possession a sample  $(y^{(t)})_{0 \leq t \leq N} \in \mathcal{S}_{d-1}^N$  of this abundance, where  $y^{(t)}$  is a realization of the random variable  $Y^{(t)}$ .

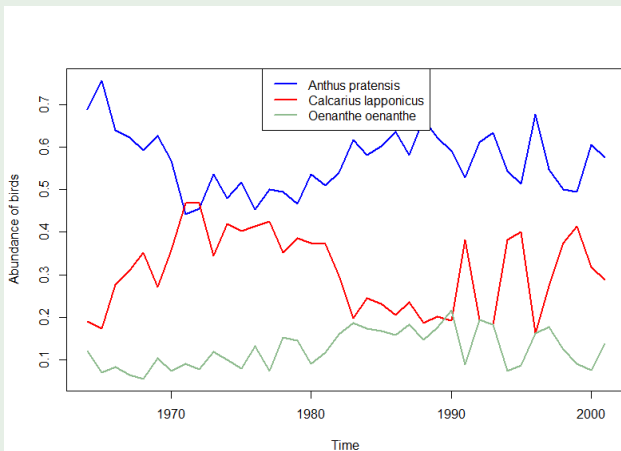
### Example *Scandinavian birds*

Consider an ecosystem composed by three alpine birds species: «Anthus pratensis», «Calcarius lapponicus» and «Oenanthe oenanthe». The relative abundance of this ecosystem has been registered from 1964 to 2001:

YEAR	Anthus	Calcarius	Oenanthe
1964	0.69	0.19	0.12
1965	0.76	0.17	0.07
1966	0.64	0.28	0.08
1967	0.62	0.31	0.07

## Example

A graphical representation of the time series is presented below.



# Outlines

I. Abundance Data

II. General framework

III. Data transformation

IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

As in the static case, the idea is to use a one-to-one mapping:

$$\begin{aligned} \text{alr} : \mathcal{S}_{d-1} &\longrightarrow \mathbb{R}^{d-1} \\ y = (y_1, \dots, y_d) &\longmapsto z = \left( \log \left( \frac{y_1}{y_d} \right), \dots, \log \left( \frac{y_{d-1}}{y_d} \right) \right). \end{aligned}$$

As in the static case, the idea is to use a one-to-one mapping:

$$\begin{aligned} \text{alr} : \mathcal{S}_{d-1} &\longrightarrow \mathbb{R}^{d-1} \\ y = (y_1, \dots, y_d) &\longmapsto z = \left( \log \left( \frac{y_1}{y_d} \right), \dots, \log \left( \frac{y_{d-1}}{y_d} \right) \right). \end{aligned}$$

We thus transform our abundance time series  $(Y^{(t)})_t$  valued in the simplex into a time series  $(Z^{(t)})_t$  valued in  $\mathbb{R}^{d-1}$  with:

$$\forall t \in \mathbb{Z}, Z^{(t)} = \text{alr} \left( Y^{(t)} \right).$$



Once we have obtained a fitted time series  $\left(\widehat{Z^{(t)}}\right)_t$  on the transformed scale, it is possible to get a fitted time series  $\left(\widehat{Y^{(t)}}\right)_t$  on the original scale with:

$$\forall t \in \mathbb{Z}, \widehat{Y^{(t)}} = alr^{-1} \left( \widehat{Z^{(t)}} \right).$$

Once we have obtained a fitted time series  $(\widehat{Z^{(t)}})_t$  on the transformed scale, it is possible to get a fitted time series  $(\widehat{Y^{(t)}})_t$  on the original scale with:

$$\forall t \in \mathbb{Z}, \widehat{Y^{(t)}} = alr^{-1}(\widehat{Z^{(t)}}).$$

### Remark

Once we have obtained a fitted time series  $\left(\widehat{Z^{(t)}}\right)_t$  on the transformed scale, it is possible to get a fitted time series  $\left(\widehat{Y^{(t)}}\right)_t$  on the original scale with:

$$\forall t \in \mathbb{Z}, \widehat{Y^{(t)}} = alr^{-1}\left(\widehat{Z^{(t)}}\right).$$

### Remark

Let us recall that we have:

$$alr^{-1} : \mathcal{S}_{d-1} \longrightarrow \mathbb{R}^{d-1}$$

$$z = (z_1, \dots, z_{d-1}) \longmapsto \left( \frac{\exp(z_1)}{1 + \sum_{j=1}^{d-1} \exp(z_j)} \right)_{1 \leq i \leq d}.$$

One of the easiest model for the time series ( $Z^{(t)}$ ) is the **VAR**( $p$ ) model:

One of the easiest model for the time series  $(Z^{(t)})$  is the **VAR**( $p$ ) model:

$$\forall t \in \mathbb{Z}, Z^{(t)} = c + \sum_{i=1}^p \phi_i \cdot Z^{(t-i)} + \varepsilon_t$$

where  $\phi_1, \dots, \phi_p$  are  $(d-1) \times (d-1)$  matrices,  $c \in \mathbb{R}^{d-1}$  and  $(\varepsilon_t)_{t \in \mathbb{Z}}$  is a gaussian white noise in  $\mathbb{R}^{d-1}$ .

## Proposition

## Proposition

For  $z \in \mathbb{C}$ , let us denote  $\phi(z)$  the complex matrix given by:

$$\phi(z) = I_{d-1} - \sum_{j=1}^p z^j \phi_j.$$

## Proposition

For  $z \in \mathbb{C}$ , let us denote  $\phi(z)$  the complex matrix given by:

$$\phi(z) = I_{d-1} - \sum_{j=1}^p z^j \phi_j.$$

If all the solutions of the equation:

$$\det(\phi(z)) = 0$$

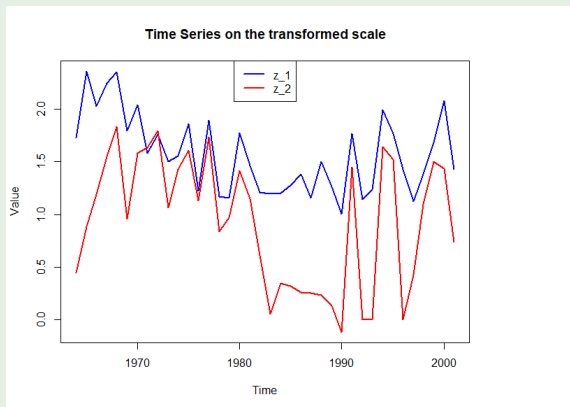
have an absolute value strictly larger than 1, then there exists a unique stationary process satisfying equation.



## Example *Scandinavian Birds*

## Example *Scandinavian Birds*

Applying the *alr* transformation to the time series of Scandinavian birds, we obtain the time series given below.

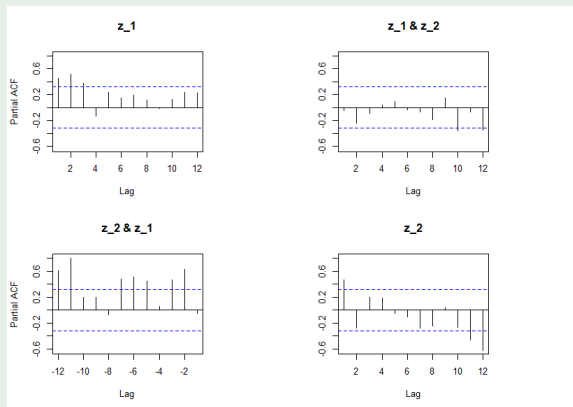


## Example

A visual inspection of the partial autocorrelograms leads us to use a VAR(3) model for the time series  $(Z^{(t)})_t$ .

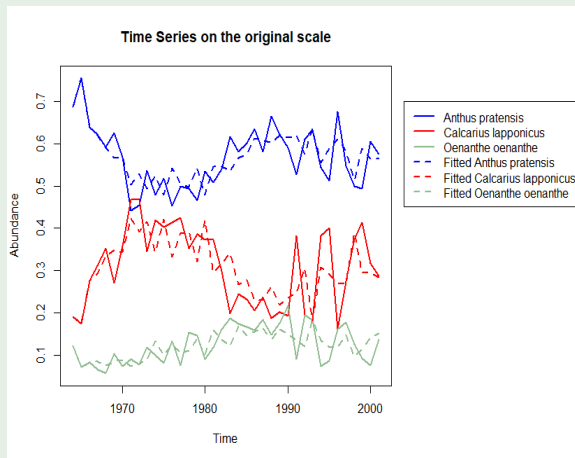
## Example

A visual inspection of the partial autocorrelograms leads us to use a VAR(3) model for the time series  $(Z^{(t)})_t$ .



## Example

Finally, a backtransformation of those fitted values gives us fitted values on the original scale.



# Outlines

## I. Abundance Data

## II. General framework

## III. Data transformation

## IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

Some basic ideas of the Dirichlet regression for compositional data:

Some basic ideas of the Dirichlet regression for compositional data:

The response variable  $Y$  follows the Dirichlet distribution of mean  $\mu = (\mu_1, \dots, \mu_d)$  and dispersion parameter  $\phi$  with for all  $1 \leq i \leq d - 1$ :

$$\mu_i = \frac{\exp(\beta^{(i)} \cdot X)}{1 + \sum_{j=1}^{d-1} \exp(\beta^{(j)} \cdot X)}$$

where  $X$  is the vector of explanatory variables.



Taking into account the dynamic of the process leads to consider naturally the past values of the process as explanatory variables themselves.

Taking into account the dynamic of the process leads to consider naturally the past values of the process as explanatory variables themselves.

We thus suggest that for all  $t \in \mathbb{Z}$ ,  $Y^{(t)}$  follows the Dirichlet distribution with mean  $\mu_t = (\mu_{t,1}, \dots, \mu_{t,d})$  satisfying:

Taking into account the dynamic of the process leads to consider naturally the past values of the process as explanatory variables themselves.

We thus suggest that for all  $t \in \mathbb{Z}$ ,  $Y^{(t)}$  follows the Dirichlet distribution with mean  $\mu_t = (\mu_{t,1}, \dots, \mu_{t,d})$  satisfying:

$$\forall 1 \leq i \leq d-1, \mu_{t,i} = \frac{\exp(\beta^{(i)} \cdot Y^{(t-1)})}{1 + \sum_{j=1}^{d-1} \exp(\beta^{(j)} \cdot Y^{(t-1)})}$$

and constant dispersion parameter  $\phi$ .

## Remark

Observe that we only took the previous value  $Y^{(t-1)}$  as covariate. It is of course possible to take several lag-values  $Y^{(t-2)}, Y^{(t-3)}, \dots$  in this expression.

# Outlines

## I. Abundance Data

## II. General framework

## III. Data transformation

## IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

## Definition *Transition Kernel*

### Definition *Transition Kernel*

Let us consider  $(E, \mathcal{E})$  and  $(F, \mathcal{F})$  two measurable spaces.

### Definition *Transition Kernel*

Let us consider  $(E, \mathcal{E})$  and  $(F, \mathcal{F})$  two measurable spaces.  
An application  $K : E \times \mathcal{F} \rightarrow [0; 1]$  is a **transition kernel** on  $E \times \mathcal{F}$  if:



### Definition *Transition Kernel*

Let us consider  $(E, \mathcal{E})$  and  $(F, \mathcal{F})$  two measurable spaces.  
An application  $K : E \times \mathcal{F} \rightarrow [0; 1]$  is a **transition kernel** on  $E \times \mathcal{F}$  if:

- for all  $x \in E$  the application  $K(x, \cdot)$  is a probability measure;

### Definition *Transition Kernel*

Let us consider  $(E, \mathcal{E})$  and  $(F, \mathcal{F})$  two measurable spaces.  
An application  $K : E \times \mathcal{F} \rightarrow [0; 1]$  is a **transition kernel** on  $E \times \mathcal{F}$  if:

- for all  $x \in E$  the application  $K(x, \cdot)$  is a probability measure;
- for all  $B \in \mathcal{F}$ , the application  $K(\cdot, B)$  is  $\mathcal{E}$ -measurable.

## Definition *Markov chain*

### Definition *Markov chain*

Consider a stochastic process  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in a measurable space  $(E, \mathcal{E})$ , and denote for all  $t \in \mathbb{Z}$ :

### Definition *Markov chain*

Consider a stochastic process  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in a measurable space  $(E, \mathcal{E})$ , and denote for all  $t \in \mathbb{Z}$ :

$$\mathcal{F}_t^- = \sigma \left( Y^{(t-1)}, Y^{(t-2)}, \dots \right)$$

and:

### Definition *Markov chain*

Consider a stochastic process  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in a measurable space  $(E, \mathcal{E})$ , and denote for all  $t \in \mathbb{Z}$ :

$$\mathcal{F}_t^- = \sigma \left( Y^{(t-1)}, Y^{(t-2)}, \dots \right)$$

and:

$$\mathcal{F}_t = \sigma \left( Y^{(t)} \right).$$

The process  $Y^{(t)}$  is a **Markov chain** if for any measurable bounded function  $f: E \rightarrow \mathbb{R}$ :

$$\mathbb{E} \left( f \left( Y^{(t)} \right) \mid \mathcal{F}_{t-1}^- \right) = \mathbb{E} \left( f \left( Y^{(t)} \right) \mid \mathcal{F}_{t-1} \right).$$

## Remark

## Remark

Intuitively, this means that knowing the entire history of the process does not bring more information than knowing the last value.



## Definition

## Definition

Let  $K$  be a transition kernel on  $E \times \mathcal{E}$ .

## Definition

Let  $K$  be a transition kernel on  $E \times \mathcal{E}$ .

A Markov chain  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in  $(E, \mathcal{E})$  has transition kernel  $K$  if for all  $t \in \mathbb{Z}$  and all  $A \in \mathcal{E}$ :

$$\mathbb{P}\left(Y^{(t)} \in A \mid Y_{t-1} = y_{t-1}\right) = K(y_{t-1}, A).$$

## Definition

Let  $K$  be a transition kernel on  $E \times \mathcal{E}$ .

A Markov chain  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in  $(E, \mathcal{E})$  has transition kernel  $K$  if for all  $t \in \mathbb{Z}$  and all  $A \in \mathcal{E}$ :

$$\mathbb{P}\left(Y^{(t)} \in A \mid Y_{t-1} = y_{t-1}\right) = K(y_{t-1}, A).$$

In this case, the chain is said to be homogeneous.

# Outlines

## I. Abundance Data

## II. General framework

## III. Data transformation

## IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

## Definition

## Definition

Consider a strongly stationary process  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in a measurable space  $(E, \mathcal{E})$ , of law  $\mathbb{P}_Y$ .

## Definition

Consider a strongly stationary process  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in a measurable space  $(E, \mathcal{E})$ , of law  $\mathbb{P}_Y$ .

Let us define the shift operator  $\sigma : E^{\mathbb{Z}} \rightarrow E^{\mathbb{Z}}$  by  
$$\tau \left( (y_t)_{t \in \mathbb{Z}} \right) = (y_{t+1})_{t \in \mathbb{Z}}.$$



## Definition

Consider a strongly stationary process  $(Y^{(t)})_{t \in \mathbb{Z}}$  valued in a measurable space  $(E, \mathcal{E})$ , of law  $\mathbb{P}_Y$ .

Let us define the shift operator  $\sigma : E^{\mathbb{Z}} \rightarrow E^{\mathbb{Z}}$  by  
 $\tau((y_t)_{t \in \mathbb{Z}}) = (y_{t+1})_{t \in \mathbb{Z}}$ .

The process  $(Y^{(t)})_{t \in \mathbb{Z}}$  is **ergodic** if for all  $\tau$ -invariant event  $A \subset E^{\mathbb{Z}}$ :

$$\mathbb{P}_Y(A) = 0 \text{ or } 1.$$

## Remark

## Remark

The importance of ergodicity is that it allows to establish a strong law of large numbers.

## Remark

The importance of ergodicity is that it allows to establish a strong law of large numbers.

If  $(Y_t)_{t \in \mathbb{Z}}$  is an ergodic process, for any measurable function  $f: E^{\mathbb{Z}} \rightarrow \mathbb{R}$  such that  $\mathbb{E}(|f(Y)|) < +\infty$  we have:

$$\frac{1}{n} \sum_{k=1}^n f \circ \tau^k \rightarrow \mathbb{E}(f(Y)) \quad \mathbb{P}_Y - a.s.$$

## Remark

The importance of ergodicity is that it allows to establish a strong law of large numbers.

If  $(Y_t)_{t \in \mathbb{Z}}$  is an ergodic process, for any measurable function  $f: E^{\mathbb{Z}} \rightarrow \mathbb{R}$  such that  $\mathbb{E}(|f(Y)|) < +\infty$  we have:

$$\frac{1}{n} \sum_{k=1}^n f \circ \tau^k \longrightarrow \mathbb{E}(f(Y)) \quad \mathbb{P}_Y - a.s.$$

In particular, for any function  $g: E \rightarrow \mathbb{R}$  such that  $\mathbb{E}(|g(Y_0)|) < +\infty$ :

$$\frac{1}{n} \sum_{k=1}^n g(Y_k) \longrightarrow \mathbb{E}(g(Y_0)) \quad a.s.$$

## Definition

## Definition

Let  $K$  be a transition kernel on a measurable space  $(E, \mathcal{E})$ .

## Definition

Let  $K$  be a transition kernel on a measurable space  $(E, \mathcal{E})$ . A probability  $\pi$  on  $E$  is said to be  $K$ -**invariant** if:



## Definition

Let  $K$  be a transition kernel on a measurable space  $(E, \mathcal{E})$ . A probability  $\pi$  on  $E$  is said to be  **$K$ -invariant** if:

$$\pi \cdot K = \pi$$

## Definition

Let  $K$  be a transition kernel on a measurable space  $(E, \mathcal{E})$ . A probability  $\pi$  on  $E$  is said to be  **$K$ -invariant** if:

$$\pi \cdot K = \pi$$

where:

$$\pi \cdot K(A) = \int K(y, A)\pi(dy)$$

## Theorem

## Theorem

If a transition kernel  $K$  admits a unique invariant measure  $\pi$ , then there exists a unique strongly stationary Markov chain  $(Y^{(t)})_t$  with transition kernel  $K$ , and it is ergodic.

# Outlines

## I. Abundance Data

## II. General framework

## III. Data transformation

## IV. The «Stay in the simplex approach»

- Some properties about Markov Chains
- Some properties about ergodicity
- Back to the model

We thus decide to model our abundance times series  $(Y^{(t)})_{t \in \mathbb{Z}}$  as a Markov chain with Dirichlet transition kernel  $K$  with mean  $\mu$  and unknown dispersion parameter  $\phi$  with:

$$\mu_i = \frac{\exp(\beta^{(i)} \cdot y)}{1 + \sum_{j=1}^{d-1} \exp(\beta^{(j)} \cdot y)}.$$

It can be shown that our kernel  $K$  satisfies the Doeblin's condition:

It can be shown that our kernel  $K$  satisfies the Doeblin's condition:

### Definition



It can be shown that our kernel  $K$  satisfies the Doeblin's condition:

### Definition

A transition kernel  $K$  defined on  $E \times \mathcal{E}$  satisfies the **Doeblin's condition** if there exists a constant  $\eta > 0$  and a probability measure  $\lambda$  on  $E$  such that:

$$\forall A \in \mathcal{E}, \forall y \in E, K(y, A) \geq \eta \cdot \lambda(A).$$

The following proposition is then crucial:

The following proposition is then crucial:

## Proposition

The following proposition is then crucial:

### Proposition

If  $K$  satisfies the Doeblin's condition, then it admits a unique invariant probability measure  $\pi$ .

The following proposition is then crucial:

### Proposition

If  $K$  satisfies the Doeblin's condition, then it admits a unique invariant probability measure  $\pi$ .

### Corollary

The following proposition is then crucial:

### Proposition

If  $K$  satisfies the Doeblin's condition, then it admits a unique invariant probability measure  $\pi$ .

### Corollary

There exists a unique strongly stationary Markov chain  $(Y^{(t)})_t$  with transition kernel  $K$ , and it is ergodic.

The model parameters  $\phi$  and  $\beta^{(1)}, \dots, \beta^{(d-1)}$  can be estimated by the maximum of conditional likelihood,

The model parameters  $\phi$  and  $\beta^{(1)}, \dots, \beta^{(d-1)}$  can be estimated by the maximum of conditional likelihood, and ergodicity is an essential point here, because it ensures the strong consistency of these estimates, as well as their asymptotic normality.



## Example *Scandinavian Birds*

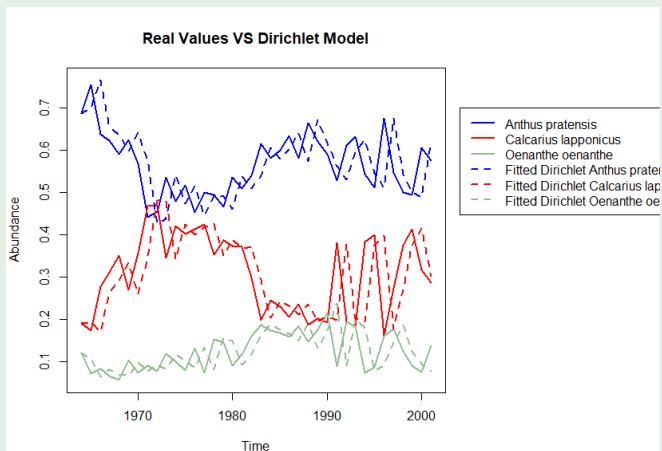
### Example *Scandinavian Birds*

If we try to apply our model to the Scandinavian Birds data, we obtain the following results:

	$\hat{\phi}$	$\beta_1^{(1)}$	$\beta_2^{(1)}$	$\beta_3^{(1)}$	$\beta_1^{(2)}$	$\beta_2^{(2)}$	$\beta_3^{(2)}$
Estimates	171.61	3.70	1.16	-7.20	1.10	3.91	-7.32

## Example

We present below the fitted values of abundance according to our model.

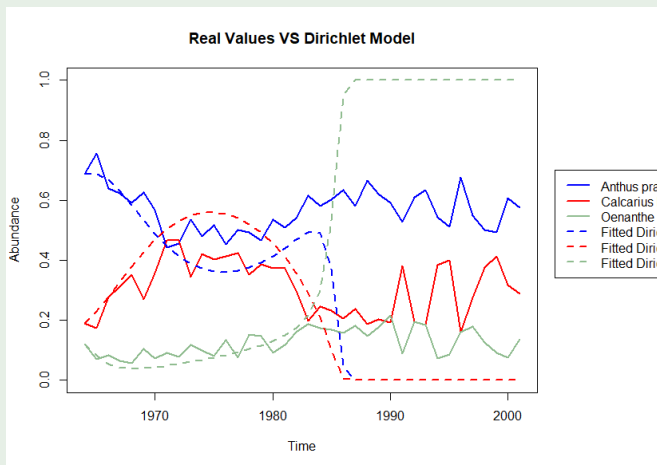


## Example

We present now the true prediction, i.e. we only rely on the first true abundance.

## Example

We present now the true prediction, i.e. we only rely on the first true abundance.



One final question of interest is the interpretation of the parameters  $\beta^{(i)}$ .

One final question of interest is the interpretation of the parameters  $\beta^{(i)}$ .

### Remark

One final question of interest is the interpretation of the parameters  $\beta^{(i)}$ .

### Remark

Take again our Scandinavian birds.



One final question of interest is the interpretation of the parameters  $\beta^{(i)}$ .

### Remark

Take again our Scandinavian birds.

Assume that between  $t$  and  $t + 1$ , the abundance is evolving according to the following equation:

One final question of interest is the interpretation of the parameters  $\beta^{(i)}$ .

### Remark

Take again our Scandinavian birds.

Assume that between  $t$  and  $t + 1$ , the abundance is evolving according to the following equation:

$$y^{(t+1)} = y^{(t)} + (c, -c, 0).$$

One final question of interest is the interpretation of the parameters  $\beta^{(i)}$ .

### Remark

Take again our Scandinavian birds.

Assume that between  $t$  and  $t + 1$ , the abundance is evolving according to the following equation:

$$y^{(t+1)} = y^{(t)} + (c, -c, 0).$$

Consider the **power balance** between the two species defined by:

$$\frac{\mu_{1,t}}{\mu_{2,t}}.$$

## Remark

This balance evolves according to:

$$\frac{\mu_{1,t+1}}{\mu_{2,t+1}} = \frac{\mu_{1,t}}{\mu_{2,t}}$$

## Remark

This balance evolves according to:

$$\frac{\frac{\mu_{1,t+1}}{\mu_{2,t+1}}}{\frac{\mu_{1,t}}{\mu_{2,t}}} = \exp \left( c \cdot (\beta_1^{(1)} + \beta_2^{(2)} - \beta_2^{(1)} - \beta_1^{(2)}) \right).$$