Stochastic processes on trees: Brownian motion and beyond

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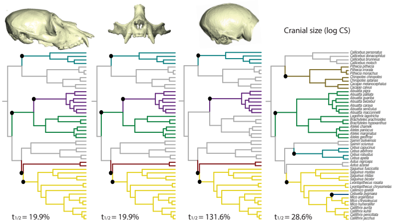
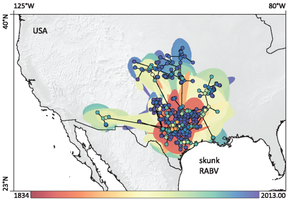
December 2021

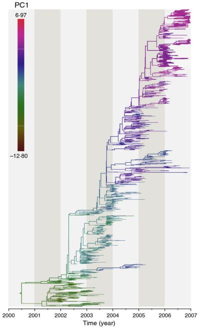
Phylogenetic Comparative Methods



Aristide et al. (2018)



Dellicour et al. (2017)



Vrancken et al. (2015)

- Various time scales: Myr – decade.
- Various traits: morpho, geo, viral.

Question: Trait dynamics for an evolving organism ?

Outline

Today

- Models of trait evolution.
- The phylogenetic regression.
- Application: HIV virulence heritability.

Tomorow

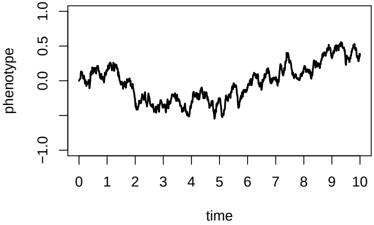
- Multivariate and heterogeneous models.
- Bayesian inference.
- Application: phylogeography.

Models of trait evolution

1. Brownian Motion
2. Ornstein-Uhlenbeck
3. Gaussian Models
4. General Diffusion Models

Outline

Brownian Motion

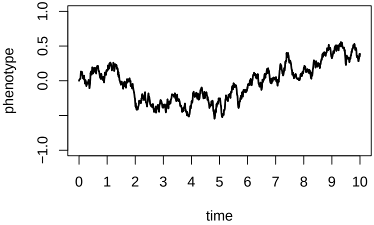


$$X_0 = \mu; \qquad \mathrm{d}\, X_t = \sigma\, \mathrm{d}\, B_t$$

Brownian Motion:

- Continuous time process.

Brownian Motion

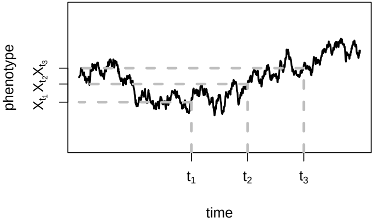


$$X_0 = \mu; \qquad \mathrm{d}\, X_t = \sigma \,\mathrm{d}\, B_t$$

Brownian Motion:

- Continuous time process.
- Continuous trajectory (almost surely)

Brownian Motion

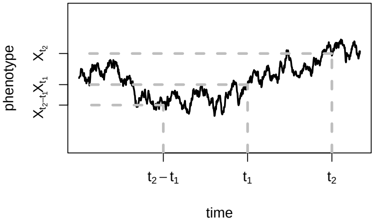


$$X_0 = \mu; \qquad \mathrm{d}\,X_t = \sigma\,\mathrm{d}\,B_t$$

Brownian Motion:

- Continuous time process.
- Continuous trajectory (almost surely)
- Independent increments: $(X_{t_3} - X_{t_2})$ ind. $(X_{t_2} - X_{t_1})$

Brownian Motion



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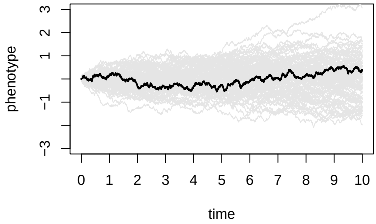
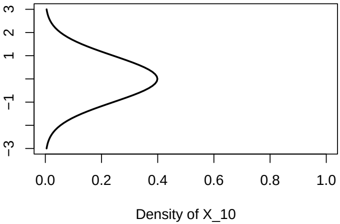
Brownian Motion





Brownian Motion:

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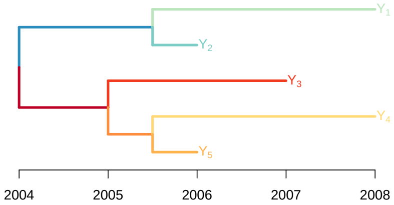
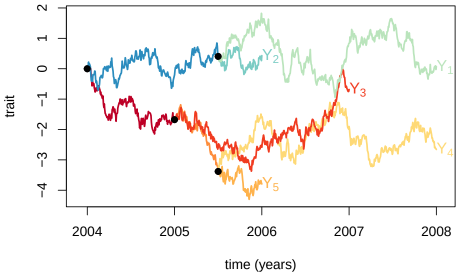
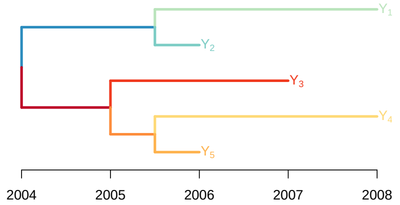
- Stationary increments: $(X_{t_2} - X_{t_1}) \sim X_{t_2 - t_1} - X_0$
- Gaussian: $X_t \sim \mathcal{N}(X_0, \sigma^2 t)$

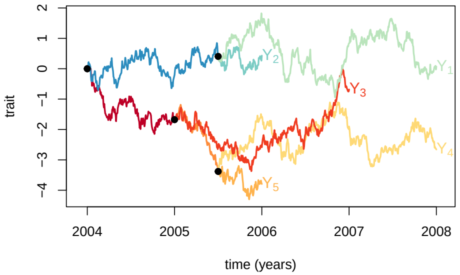
Brownian Motion on a Tree (Felsenstein, 1985)





Brownian Motion on a Tree (Felsenstein, 1985)





- The trait evolves like a BM in time

Brownian Motion on a Tree

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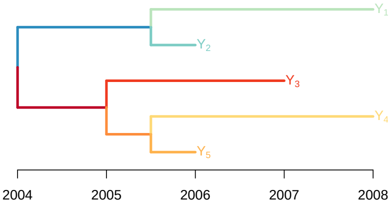

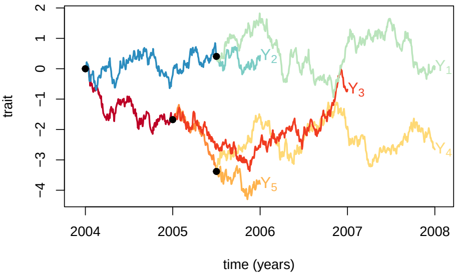

- The trait evolves like a BM in time
- Speciation → two independent processes

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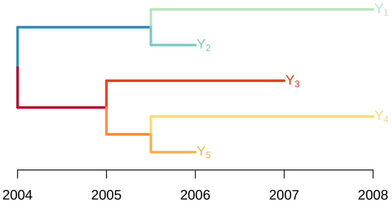

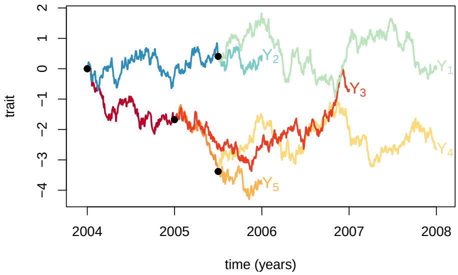

- The trait evolves like a BM in time
- Speciation → two independent processes
- Only tip values are measured

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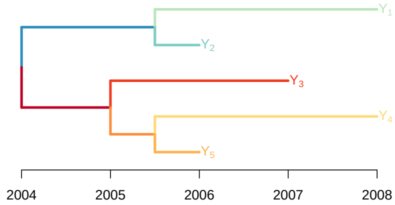

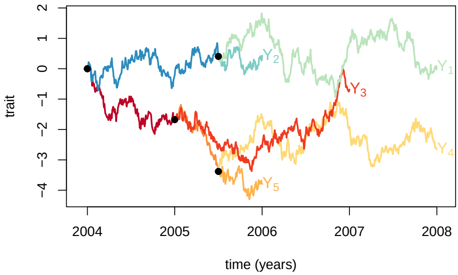

- SDE: $\mathrm{d}\,X_t = \sigma\,\mathrm{d}\,B_t$

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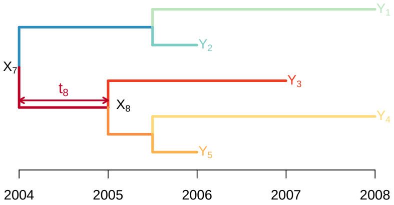

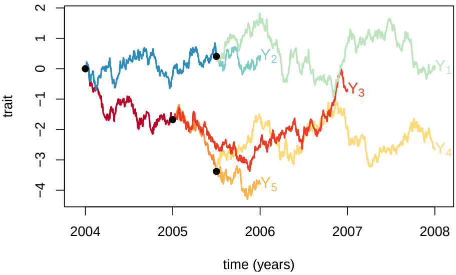

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- Heredity: $X_8 | X_7 \sim \mathcal{N}(X_7, \sigma^2 t_8)$

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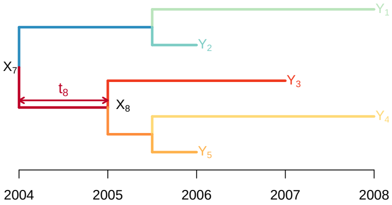

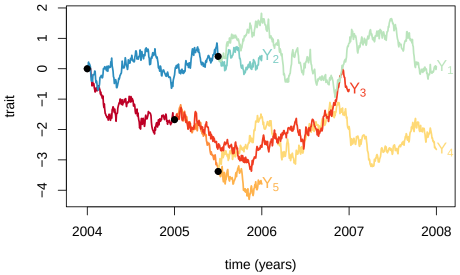

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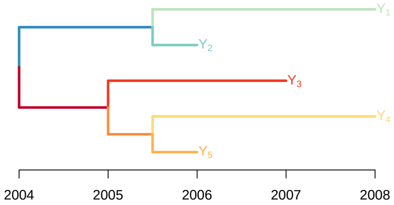
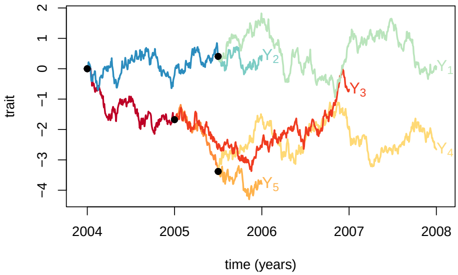
- Heredity: $X_8 | X_7 \sim \mathcal{N}(X_7, \sigma^2 t_8)$
- Root: $X_\rho = \mu$

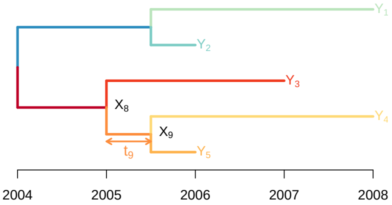
Variance Structure

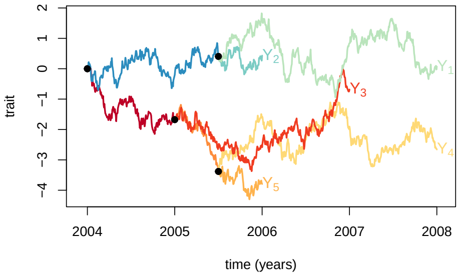




Structure: $X_i = X_{\mathrm{pa}(i)} + \sigma\sqrt{t_i} \times \epsilon_i$, with $\epsilon_i \sim \mathcal{N}(0,1)$ iid

Variance Structure

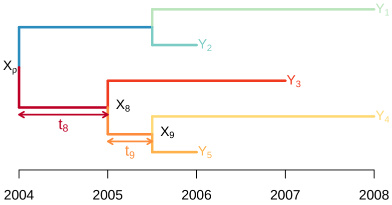


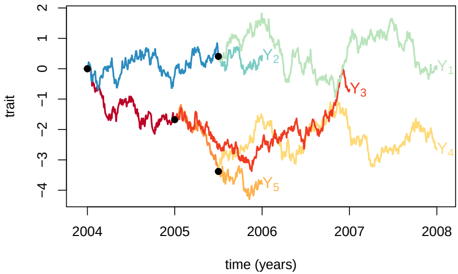


Structure: $X_i = X_{\mathrm{pa}(i)} + \sigma\sqrt{t_i} \times \epsilon_i$, with $\epsilon_i \sim \mathcal{N}(0,1)$ iid

$$\mathbb{V}\mathrm{ar}(X_9) = \mathbb{V}\mathrm{ar}(X_8) + \sigma^2 t_9$$

Variance Structure





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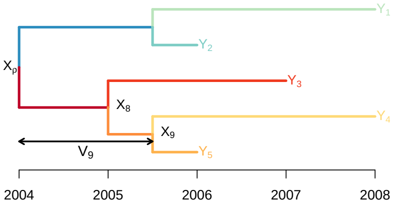
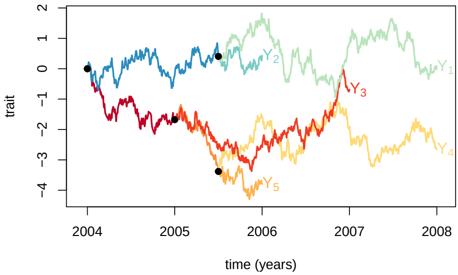
$$\begin{aligned}\mathbb{V}\mathrm{ar}(X_9) &= \mathbb{V}\mathrm{ar}(X_8) + \sigma^2 t_9 \\ &= \sigma^2 t_8 + \sigma^2 t_9\end{aligned}$$

Variance Structure





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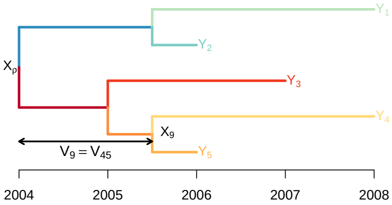
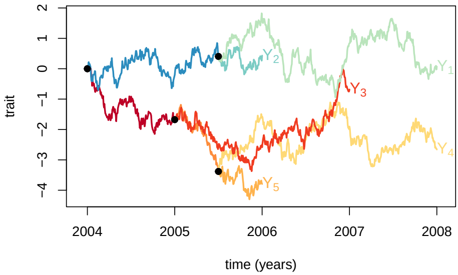


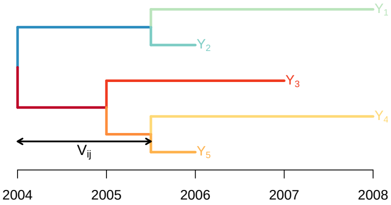


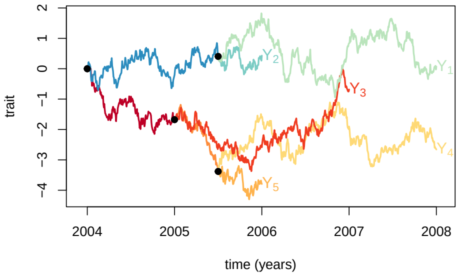
Structure: $X_i = X_{\mathrm{pa}(i)} + \sigma\sqrt{t_i} \times \epsilon_i$, with $\epsilon_i \sim \mathcal{N}(0,1)$ iid

$$\mathbb{V}\mathrm{ar}(X_9) = \sigma^2 V_9$$

$$\mathbb{C}\mathrm{ov}(Y_4, Y_5) = \mathbb{V}\mathrm{ar}(X_9) = \sigma^2 V_9 = \sigma^2 V_{45}$$

Variance Structure





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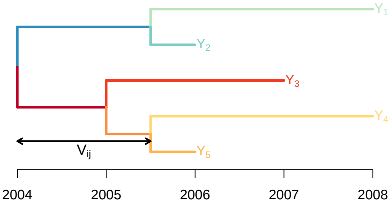
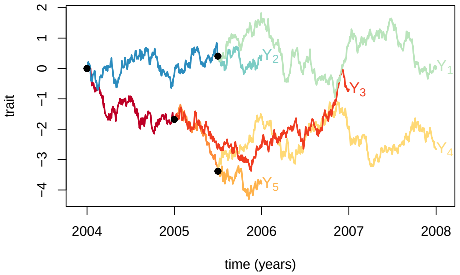
Covariances: $\mathbb{C}\text{ov}(Y_i, Y_j) = \sigma^2 V_{ij}$

Variance Structure





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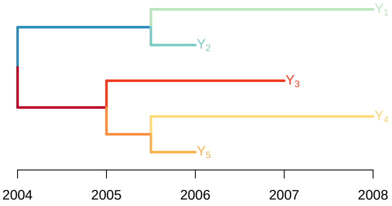
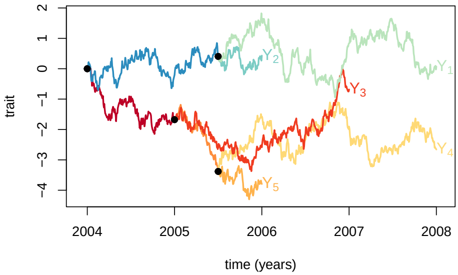
Distribution: $\mathbf{Y} \sim \mathcal{N}(\mu \mathbf{1}_n, \sigma^2 \mathbf{V})$ Gaussian Multivariate

Modelling





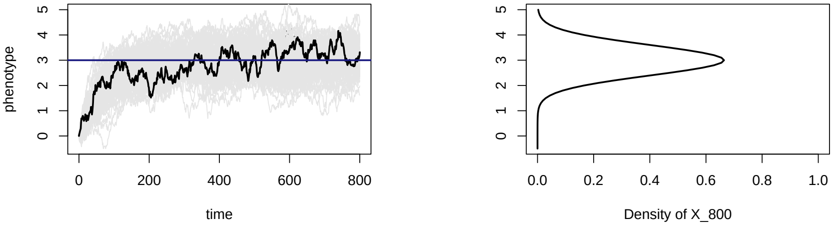
- Unbounded variance
- No direction

Outline

1. Brownian Motion
2. Ornstein-Uhlenbeck
    - Ornstein-Uhlenbeck
    - Variance
    - Modelling
3. Gaussian Models
4. General Diffusion Models

Ornstein-Uhlenbeck

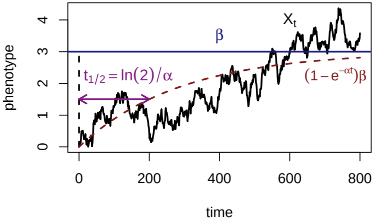
$$\mathrm{d}\, X_t = \alpha[\beta - X_t]\,\mathrm{d}\, t + \sigma\,\mathrm{d}\, B_t$$



Brownian with purpose:

- Gaussian: $X_t \sim \mathcal{N}(e^{-\alpha t}X_0 + (1-e^{-\alpha t})\beta,\ (1-e^{-2\alpha t})\frac{\sigma^2}{2\alpha})$
- Stationary state $\mathcal{N}(\beta, \frac{\sigma^2}{2\alpha})$
- Bounded variance.

Ornstein-Uhlenbeck



$$\mathrm{d}\,X_t = \alpha[\beta - X_t]\,\mathrm{d}\,t + \sigma\,\mathrm{d}\,B_t$$

Deterministic part:

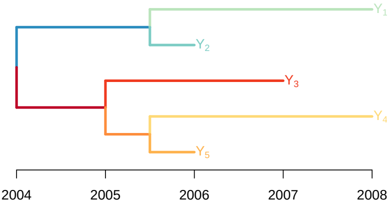
- β: primary optimum (mechanistically defined).
- $\ln(2)/\alpha$: phylogenetic half live.

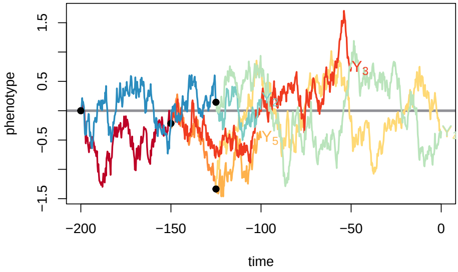
Stochastic part:

- X_t: trait value (actual optimum).
- $\sigma dB(t)$: Brownian fluctuations.

OU on a Tree

(Hansen, 1997)





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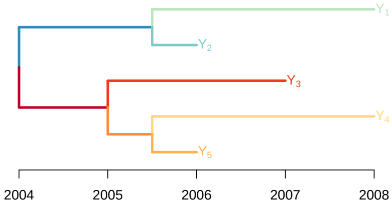

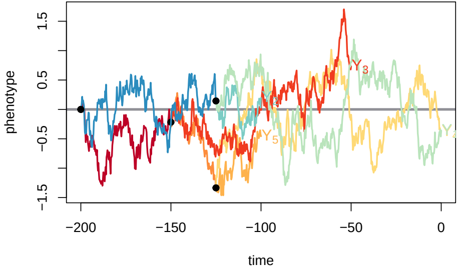

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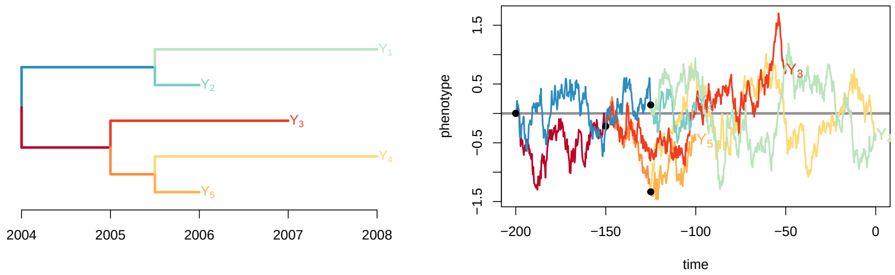

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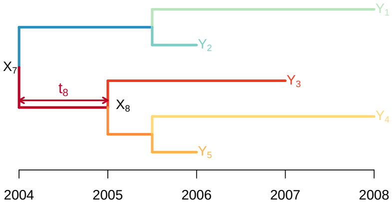

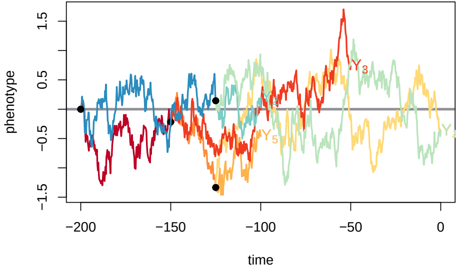

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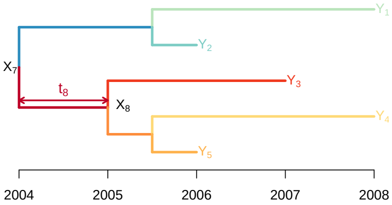

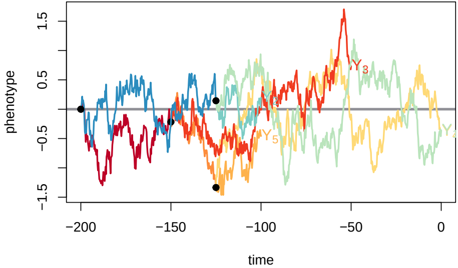

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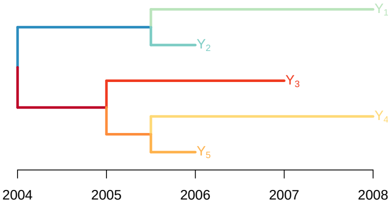
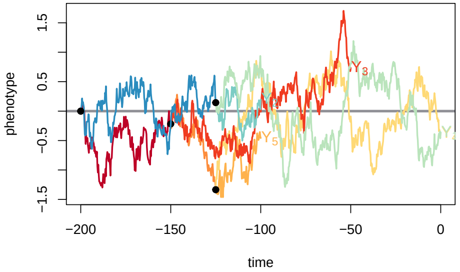
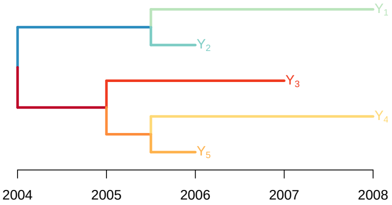
- Root: $X_\rho = \mu = \beta$

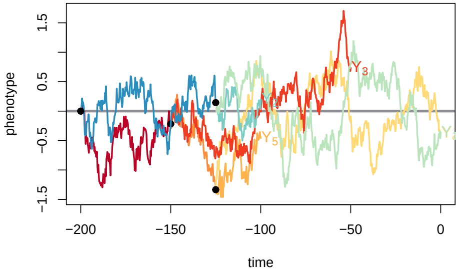
Distribution of an OU





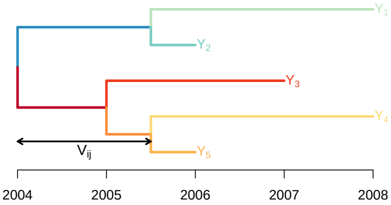
Distribution of an OU

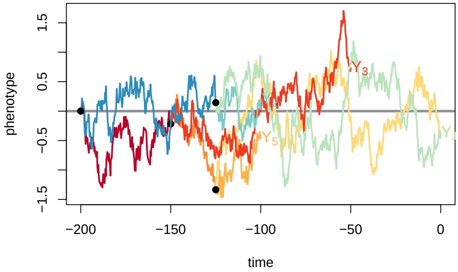




Structure: $X_i = e^{-\alpha t_i} X_{\mathrm{pa}(i)} + (1 - e^{-\alpha t_i})\beta + \sqrt{(1 - e^{-2\alpha t_i})\frac{\sigma^2}{2\alpha}} \times \epsilon_i$
with $\epsilon_i \sim \mathcal{N}(0,1)$ iid.

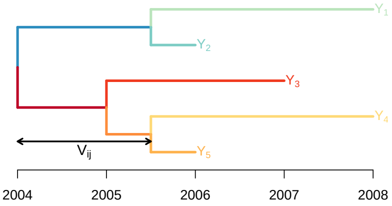
Distribution of an OU

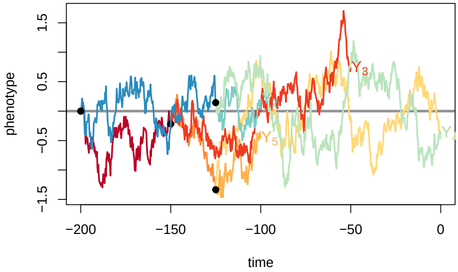




Covariances: $\mathbb{C}\mathrm{ov}\left[Y_i; Y_j\right] = \frac{\sigma^2}{2\alpha} e^{-\alpha(V_i+V_j)}(e^{2\alpha V_{ij}} - 1)$

Distribution of an OU





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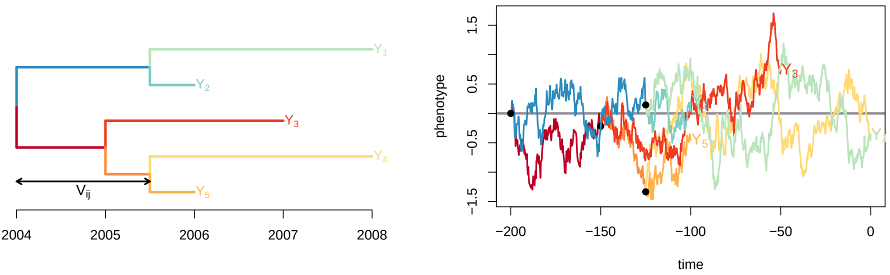
Distribution of an OU



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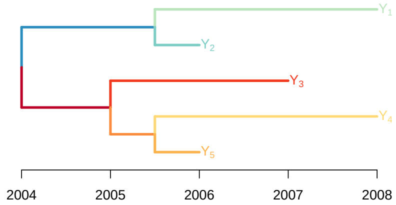
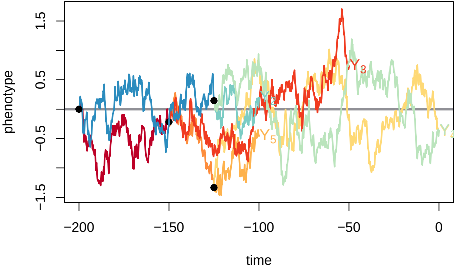
Distribution: $\mathbf{Y}$ still Gaussian Multivariate.

Modelling





- Bounded variance $\gamma^2 = \frac{\sigma^2}{2\alpha}$
- Stationary state
- Stabilizing selection

Non-Identifiability on an Ultrametric Tree

Ultrametric tree: $h = V_i$ for all tip i.

Expectation: All tips have the same expectation

$$\mathbb{E}\left[Y_i\right] = \mu e^{-\alpha h} + \beta(1 - e^{-\alpha h})$$

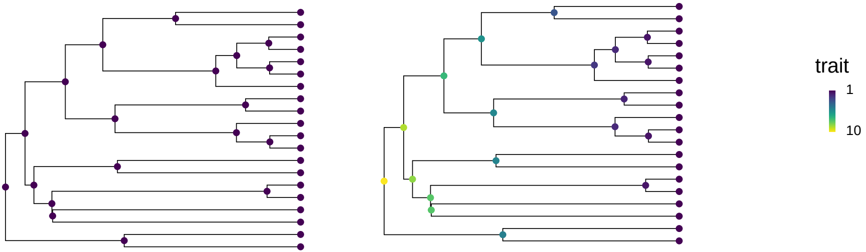
Non-Identifiability μ and β cannont be identified separatly.

Only $\lambda = \mu e^{-\alpha h} + \beta(1 - e^{-\alpha h})$ is identifiable.

Non-Identifiability on an Ultrametric Tree

- $\lambda = \mu = \beta = 1$
- Root in stationary state
- Tips expectation: 1.

Non-Identifiability on an Ultrametric Tree



- $\lambda = \mu = \beta = 1$
- Root in stationary state
- Tips expectation: 1.

- $\lambda = 1$, $\mu = 10$, $\beta = -2$
- Out of equilibrium.
- Tips expectation: 1.

Interpretation and time scale

Short Time Scale: Quantitative genetics (Lande, 1976)

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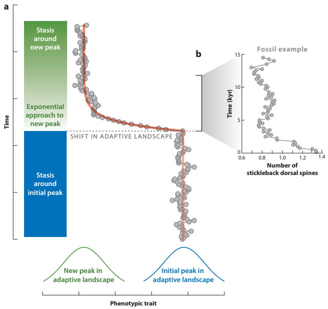
- BM: limit of a genetic aditive random drift on a flat landscape
- OU: on an adaptation landscape with one peak
- *Gasterosteidae*: trait optimum change in ∼1000 years



Hunt and Rabosky (2014)

Interpretation and time scale

Long Time Scale: Random fluctuations (Felsenstein, 2004)

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- Adaptation is almost instantaneous
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- OU: secondary optimum itself goes to a ”primary optimum”
- Empirical, no theoretical justification.
- ”Paradox of stasis” (Hansen and Houle, 2004)

Outline

1. Brownian Motion
2. Ornstein-Uhlenbeck
3. Gaussian Models
    - Accelerating / Decelerating Model
    - General Gaussian Model
    - Intra-species Variations
4. General Diffusion Models

Accelerating / Decelerating Model (Blomberg et al., 2003)

AC/DC: Exponentially increasing / decreasing variance

$$dX_t = \sigma_0 e^{rt/2} dB_t$$

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Variance:

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Variance:

$$\mathbb{C}\text{ov}(Y_i, Y_j) = \sigma_0^2 \frac{e^{rV_{ij}} - 1}{r}$$

Note: Equivalent to a single peak OU in some cases.

General Model

BM, OU: Instance of a general Gaussian propagation model.

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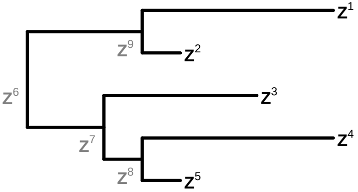

$$\mathbf{Z}^r \sim \mathcal{N}(\boldsymbol{\mu}, \boldsymbol{\Gamma}) \qquad \text{root}$$

$$\mathbf{Z}^j \,\Big|\, \mathbf{Z}^{\mathrm{pa}(j)} \sim \mathcal{N}\left(\mathbf{q}_j \mathbf{Z}^{\mathrm{pa}(j)} + \mathbf{r}_j,\ \boldsymbol{\Sigma}_j\right) \qquad \text{nodes}$$

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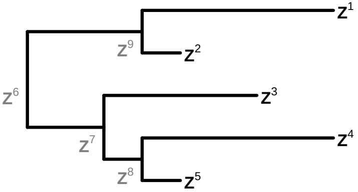

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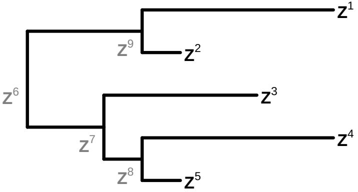

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Drift, shifts, Integrated OU...

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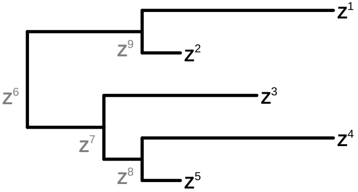

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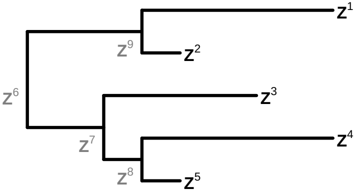
Drift, shifts, Integrated OU...

Easy computations (Kalman filter)

Intra-species variations Model



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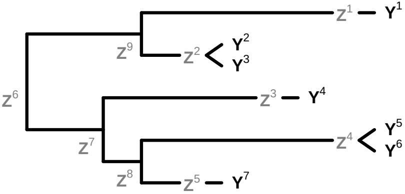

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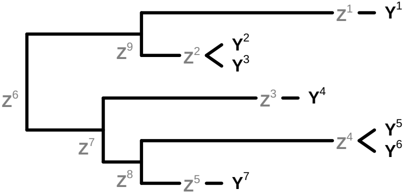
$$\mathbf{Y}^i \mid \mathbf{Z}^{\mathrm{pa}(i)} \sim \mathcal{N}\left(\mathbf{Z}^{\mathrm{pa}(i)}, \mathbf{S}_i\right) \qquad \text{obs}$$

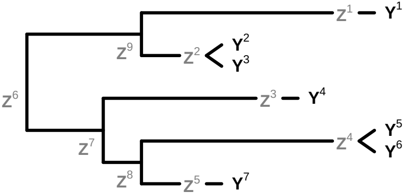
Intra-species variations Model



$$\begin{aligned} \mathbf{Z}^r &\sim \mathcal{N}(\boldsymbol{\mu}, \boldsymbol{\Gamma}) && \text{root} \\ \mathbf{Z}^j \,\Big|\, \mathbf{Z}^{\mathrm{pa}(j)} &\sim \mathcal{N}\left(\mathbf{q}_j \mathbf{Z}^{\mathrm{pa}(j)} + \mathbf{r}_j,\ \boldsymbol{\Sigma}_j\right) && \text{nodes} \\ \mathbf{Y}^i \,\Big|\, \mathbf{Z}^{\mathrm{pa}(i)} &\sim \mathcal{N}\left(\mathbf{Z}^{\mathrm{pa}(i)}, \mathbf{S}_i\right) && \text{obs} \end{aligned}$$

Measurement Errors, Non phylogenetic variations, intra-species variations, ...

Intra-species variations Model



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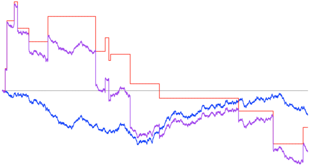
Measurement Errors, Non phylogenetic variations, intra-species variations, ...

"Heritability": $h^2 = \dfrac{V(\mathbf{Z}_{tips})}{V(\mathbf{Y})}$

Outline

1. Brownian Motion
2. Ornstein-Uhlenbeck
3. Gaussian Models
4. General Diffusion Models
    - Lévy processes
    - General diffusions

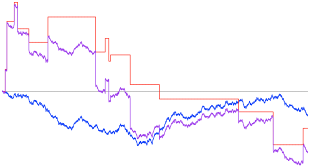
Lévy processes



Lévy processes

- Continuous time process.

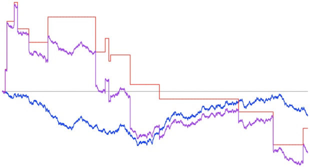
Lévy processes



Lévy processes

- Continuous time process.
- Independent increments: $(X_{t_3} - X_{t_2})$ ind. $(X_{t_2} - X_{t_1})$

Lévy processes



Lévy processes

- Continuous time process.
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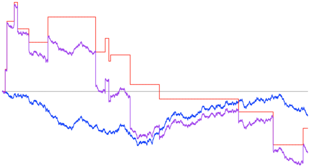
Lévy processes



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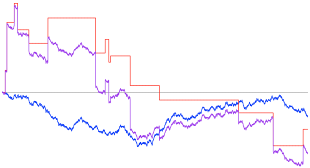
- Càdlàg trajectory (almost surely)

Lévy processes



- BM is a Lévy process

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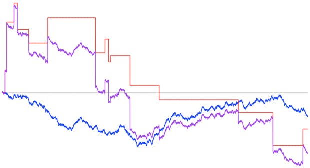

- BM is a Lévy process
- OU is not a Lévy process

Lévy processes

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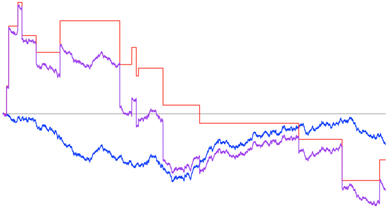
- Càdlàg trajectory (almost surely)

Lévy processes

(Landis et al., 2013; Duchen et al., 2017)



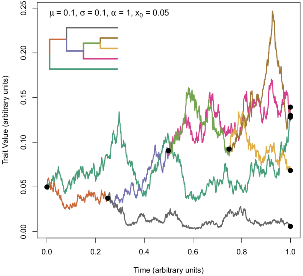
Lévy-Ito decomposition: $X = B + J$

- B and J are independent
- B is a BM with rate σ^2, $B(0) = \mu$
- J compound Poisson process, rate λ, jumps $\sim \mathcal{N}(0, s_1^2)$

$$\mathbb{E}(X_i) = \mu \quad \text{and} \quad \mathbb{C}\text{ov}(X_i, X_j) = V_{ij}(\sigma^2 + \lambda s_1^2)$$

General diffusions

(Blomberg et al., 2020)



$$dX_t = b(X_t, t)dt + \sigma(X_t, t)dB_t$$

Brownian motion is a poor model, and so is Ornstein-Uhlenbeck, but just as democracy is the worst method of organizing a society "except for all the other", so these two models are all we've really got that is tractable. Critics will be admitted to the event, but only if they carry with them another tractable model. J. Felsenstein, 2008.

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Thank you for listening

Institut Montpelliérain Alexander Grothendieck

Appendices