# Estimating the pollen backward dispersion function using genetic markers 

## The backward dispersion function ?

- Forward dispersion function:
"where does the pollen go when flying from a father tree at 0 ?"
- Backward dispersion function:
"where does the pollen grain observed on the seed of a mother tree at 0 come from?


## Model

- trees $=$ stationary point process $X$
- genotypes of trees $=$ marks $M$
- genotype of seeds attached to trees $=$ marks $G$


## Assumptions

- genotypes are randomly independently distributed among trees
- the loci are independent
- the two alleles at a given locus are independent
- a seed receives an allele from the father, the other from the mother
- the allele received from a given parent (father or mother) is chosen randomly among the two alleles of the parent


## Data

- sample some trees and genotype them
- sample some seeds on these trees
locations of other trees unknown


## What do researcher in pollen dispersion do ?

$X$ Poisson

- $f(x-y)=$ probability density to find the father of a flower at $y$ at position $x$
- copaternity $Q(A, B)=$ probability that two flowers on trees at $A$ and $B$ have the same father
- adjust parameters by least square between $Q(A, B) / Q(A, A)$ and its estimator


## Computing $Q(A, B)$

| $Q(A, B)=\int_{x} f(x-A)$ | $f(x-B)$ | $\frac{1}{\lambda} d x$ |
| :---: | :---: | :---: |
| tree pollinating $A$ | tree pollinating $B$ | around $x$ |
| is at $x$ | falls within | there are $\lambda d x$ trees |
|  | the same region |  |

- self-pollination not taken into account
- dependance between the two pollination events is not taken into account
- Poisson necessary to drop $\lambda$ in $Q(A, B) / Q(A, A)$


## What do we want to estimate?

$1_{\{\text {pollinator of } A \text { is at } x\}}=1_{\{x \in X\}} 1_{\{x \text { pollinates } A\}}$

- $p($ the pollinator of $A$ is at $x)=\lambda h(x ; A) r(x-A), x \neq A$
- $p($ the pollinator of $A$ is at $x)=h(x ; A), \quad x=A$
- $\lambda$ intensity of $X$
- $r(u), u \in \mathrm{R}$ pair correlation function
- $h(y ; 0)$ probability that a tree at $y$ pollinates 0

$$
==>f(x)=1_{\{x \neq 0\}} \lambda h(x ; 0) r(x), \quad F(0)=h(0 ; 0)
$$

## Looking at the copaternity

$1_{\{\text {pollinator of } A \text { is at } x\}} 1_{\{\text {pollinator of } B \text { is at } x\}}=$ $1_{\{x \in X\}}{ }^{1}\{x$ pollinates $A\}{ }^{1}{ }^{1} x$ pollinates $\left.B\right\}$

- $p($ the pollinator of $A$ and $B$ is at $x)=\lambda h^{(2)}(x ; A, B) r(x ; A, B)$, $x \neq A, x \neq B$,
- $p($ the pollinator of $A$ is at $x)=h^{(2)}(x ; A, B)$,
$x=A$ or $x=B$

$$
\begin{aligned}
h^{(2)}(x ; A, B) & =\mathrm{E}\left(1_{\{x \text { pollinates } A\}} 1_{\{x \text { pollinates } B\}} \mid x \in X\right) \\
& \neq \mathrm{E}\left(1_{\{x \text { pollinates } A\}} \mid x \in X\right) \mathrm{E}\left(1_{\{x \text { pollinates } B\}} \mid x \in X\right) \\
& =h(x ; A) h(x ; B)
\end{aligned}
$$

- $\lambda r(x ; A, B)$ intensity of the Palm measure with respect to $A$ and $B$.

$$
Q(A, B)=2 h^{(2)}(x ; A, B)+\lambda \int_{x} h^{(2)}(x ; A, B) r(x ; A, B) d x
$$

## Conclusion

- No self-pollination taken into account
- what is estimated is not what is wanted


## Estimating $f(x)$

Assumptions

- $X$ stationary isotropic point process
- marks $M$ are independent
- No self-pollination
- $\lambda$ and $r(x)$ classically
- estimate $h(x ; 0)$ through observations of the genotypes of $x, 0$ and seeds on 0


## Non parametric estimation

- $\left(m_{1}, m_{2}\right)$ the alleles of the tree at 0
- $\left(k_{1}, k_{2}\right)$ the alleles of the tree at $B$
- $\left(g_{1}, g_{2}\right)$ the alleles of a seed on the tree at $O$
- $\alpha_{g}$ the allele frequency of $g$ in the tree population
- $F=$ \{the father gives the first allele $\}$
- $C=\left\{O\right.$ carries $\left(m_{1}, m_{2}\right), B$ carries ... $\}$
$P\left(g_{1} \mid C \cap F\right)=\frac{1}{2} h(x)\left(1_{\left\{g_{1}=k_{1}\right\}}+1_{\left\{g_{1}=k_{2}\right\}}\right)+(1-h(x)) \alpha_{g_{1}}$.

$$
\begin{equation*}
P\left(\left(g_{1}, g_{2}\right) \mid C\right)=a_{1} \alpha_{g_{1}} h(x)+a_{2} \alpha_{g_{2}} h(x)+b h(x)+c_{1} \alpha_{g_{1}}+c_{2} \alpha_{g_{2}} \tag{1}
\end{equation*}
$$ with

$$
\begin{aligned}
a_{1}= & -\frac{1}{4}\left(1_{\left\{g_{2}=m_{1}\right\}}+1_{\left\{g_{2}=m_{2}\right\}}\right) \\
a_{2}= & -\frac{1}{4}\left(1_{\left\{g_{1}=m_{1}\right\}}+1_{\left\{g_{1}=m_{2}\right\}}\right) \\
b= & \frac{1}{8}\left(1_{\left\{g_{1}=k_{1}\right\}}+1_{\left\{g_{1}=k_{2}\right\}}\right)\left(1_{\left\{g_{2}=m_{1}\right\}}+1_{\left\{g_{2}=m_{2}\right\}}\right) \\
& +\frac{1}{8}\left(1_{\left\{g_{2}=k_{1}\right\}}+1_{\left\{g_{2}=k_{2}\right\}}\right)\left(1_{\left\{g_{1}=m_{1}\right\}}+1_{\left\{g_{1}=m_{2}\right\}}\right) \\
c_{1}= & \frac{1}{4}\left(1_{\left\{g_{2}=m_{1}\right\}}+1_{\left\{g_{2}=m_{2}\right\}}\right)=-a_{1} \\
c_{2}= & \frac{1}{4}\left(1_{\left\{g_{1}=m_{1}\right\}}+1_{\left\{g_{1}=m_{2}\right\}}\right)=-a_{2}
\end{aligned}
$$

$$
\hat{h}(x)=\frac{\sum_{i} \sum_{k} \sum_{g_{1}} \sum_{g_{2}} K_{u}\left(x-\left|x_{i}-y_{i}\right|\right) U_{i}\left(g_{1}, g_{2}\right)}{2 G^{2} \sum_{i} \sum_{k} K_{u}\left(x-\left|x_{i}-y_{i}\right|\right)}
$$

with

$$
\begin{aligned}
U_{i}\left(g_{1}, g_{2}\right)= & \frac{\hat{P}^{(A, i, k)}\left(g_{1}, g_{2}\right)-c_{1}^{(A, i, k)} \alpha_{g_{1}}-c_{2}^{(A, i, k)} \alpha_{g_{2}}}{a_{1}^{(A, B, i, k)} \alpha_{g_{1}}+a_{2}^{(A, B, i, k)} \alpha_{g_{2}}+b^{(A, B, i, k)}} \\
& +\frac{\hat{P}^{(B, i, k)}\left(g_{1}, g_{2}\right)-c_{1}^{(B, i, k)} \alpha_{g_{1}}-c_{2}^{(B, i, k)} \alpha_{g_{2}}}{a_{1}^{(B, A, i, k)} \alpha_{g_{1}}+a_{2}^{(B, A, i, k)} \alpha_{g_{2}}+b^{(B, A, i, k)}}
\end{aligned}
$$


$\lambda=0.25$
$\alpha=(0.1,0.1,0.4,0.4)$
father $=$ nearest tree
$15 \times 15$ couples

## Parametric estimation

$$
P\left(\left(g_{1}^{(A, i, k)}, g_{2}^{(A, i ; k)}\right) \mid C_{A, B, i}\right)=P_{2, i, k} h_{\theta}\left(d\left(A_{i}, B_{i}\right)\right)+P_{2, i, k}\left(1-h_{\theta}\left(d\left(A_{i}, B_{i}\right)\right)\right)
$$

$B$ is not the father

$$
\begin{aligned}
& P_{1, i, k}=\left(\frac{1}{2}\right)^{L} \prod_{l \leq L}\left\{\alpha_{g_{2, l}^{(A, i, k)}}\left(1_{g_{1, l}^{(A, i, k)}=m_{1, l}^{(A, i)}}+1_{g_{1, l}^{(A, i, k)}=m_{2, l}^{(A, i)}}\right)\right. \\
&+\left.\alpha_{g_{1, l}^{(A, i, k)}}\left(1_{g_{2, l}^{(A, i, k)}=m_{1, l}^{(A, i)}}+1_{g_{2, l}^{(A, i, k)}=m_{2, l}^{(A, i)}}\right)\right\}
\end{aligned}
$$

$B$ is the father

$$
P_{2, i, k}=\left(\frac{1}{2}\right)^{L} \prod_{l \leq L}
$$

$$
\left\{\left(1_{g_{1, l}^{(A, i, k)}=m_{1, l}^{(A, i)}}+1_{g_{1, l}^{(A, i, k)}=m_{2, l}^{(A, i)}}\right)\left(1_{g_{2, l}^{(A, i, k)}=m_{1, l}^{(B, i)}}+1_{g_{2, l}^{(A, i, k)}=m_{2, l}^{(B, i)}}\right)\right.
$$

$$
\left.+\left(1_{g_{1, l}^{(A, i, k)}=m_{1, l}^{(B, i)}}+1_{g_{1, l}^{(A, i, k)}=m_{2, l}^{(B, i)}}\right)\left(1_{g_{2, l}^{(A, i, k)}=m_{1, l}^{(A, i)}}+1_{g_{2, l}^{(A, i, k)}=m_{2, l}^{(A, i)}}\right)\right\}
$$

## Conclusion

- parametric and non-parametric estimations can be performed
- no need to use second order statistics
- interest in confronting this estimation with one based on second order stat?
- convergence... strong mixing
- confidence intervals block-bootstrap


## self-pollination

$i(x)=P($ the tree at 0 is the father of its flower $\mid x \neq 0)$ $\epsilon(x)=P($ the father of the flower at $0 \notin\{0, x\})$

$$
1=h(x)+i(x)+\epsilon(x)
$$

$$
P\left(\left(g_{1}, g_{2}\right) \mid C\right)=a h(h)+b i(x)+c
$$

- $h(x)$ and $i(x)$ estimated in the same way
- self-pollination estimated as $1-\lambda \int_{x} h(x) r(x) d x$
- $i(x)$ can be used to choose the self-pollination model


## genetic dependance of trees

- no self-pollination
- $\lambda r_{x}(y)$ intensity of the Palm measure with respect to 0 and $x$.
- $h_{x}(y)$ the probability that a tree a $y$ pollinates a given seed at 0 knowing that trees are present at 0 ant $x$,
- $P_{x}\left(\left(l_{1}(y), l_{2}(y)\right) \mid C\right)$ the probability that the tree at $y$ carries genotype $\left(l_{1}(y), l_{2}(y)\right)$ knowing the genotypes of the trees at 0 and $x$.

$$
\begin{aligned}
& P\left(g_{1} \mid C \cap F\right)=\frac{h(x)}{2}\left(1_{\left\{g_{1}=k_{1}\right\}}+1_{\left\{g_{1}=k_{2}\right\}}\right) \\
& +\lambda \int_{y} r_{x}(y) h_{x}(y) \sum_{l_{1}, l_{2}} P_{x}\left(\left(l_{1}(y), l_{2}(y)\right)=\left(l_{1}, l_{2}\right) \mid C\right) \frac{1}{2}\left(1\left\{g_{1}=l_{1}\right\}+1_{\left\{g_{2}=l_{2}\right\}}\right) d y
\end{aligned}
$$

## Conclusion(1)

- estimate effectively $f(x)$
- no need to impose Poisson assumption
- possible to estimate furthermore with self-pollination, spatial genetic dependance(?)
- focus on $h(x)$ instead of $f(x)$
- link between $i(x)$ (self-pollination knowing a tree at $x$ ) and self-pollination ?
- estimate $h_{x}(y)$ (opening toward classical forward dispersion function) knowing $h(x)$ ?


## Conclusion(2)

- use of Campbell theorems
- $0, A \in X$
- $1=P$ (flower at 0 pollinated)
$=1_{\{A \text { pollinates }\}}+\sum_{x \in X \backslash\{0, A\}} 1_{\{x \text { pollinates }\}}$
- Austerlitz and al focus on the second term and forget the first term
- we focus on the first term and consider the second one as noise $==>$ How to combine ?

