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Analysing spatial and temporal variability in diversity

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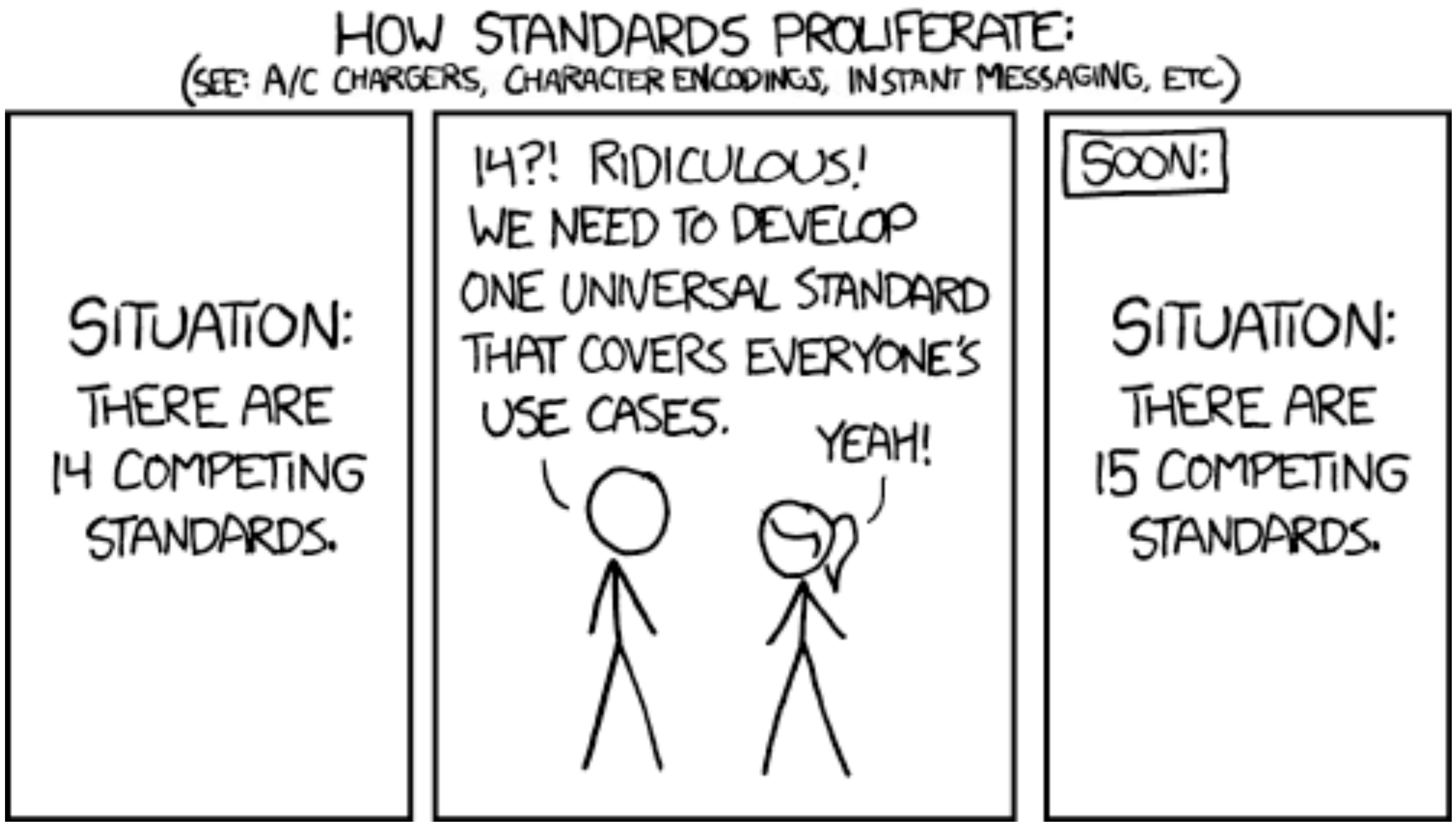
Diversity in diversity...



Overview

- Partitioning Diversity
  - Alpha, Beta and Gamma diversity
- Barro Colorado Island
  - Spatial Partitioning
  - Temporal Partitioning

Different kinds of diversity

- Diversity, even biodiversity, can mean lots of different things to different people
- Individual diversity measures can reflect many different aspects of this
- As a result measures can often disagree with one another about what is diverse
- This is often correct, but we need to understand what each measure is telling us and which measure (if any) answers the question we are interested in

Partitioning Diversity

- What do we mean when we talk about partitioning diversity?

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Partitioning Diversity

- Imagine we have divided up our ecosystem into N sub-communities
- We want to know:
  - How many distinct parts are there?
  - Which are the interesting ones?
  - Which should we conserve?

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Partitioning Diversity

- How do we divide up the "total" diversity into the diversity "within" the sub-communities, and the diversity "between" the sub-communities?
  - This is usually described as ***partitioning*** the ***gamma*** (global) diversity into ***alpha*** (average) and ***beta*** (between) components

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Partitioning Diversity

$\bar{p}_i$	$\left(\sum_{i=1}^{S} p_i^q\right)^{1/(q-1)}$	$\sqrt[q-1]{\sum_{i=1}^{S} p_i p_i^{q-1}}$	mean proportional species abundance; the weighted generalised mean with exponent $q-1$ of the p_i values
${}^q\lambda_\gamma$	$\sum_{i=1}^{S} p_i^q$	$\bar{p}_i^{q-1}$	basic sum of order q in relation to the γ-classification: the sum of p_i^q values over all species i, or mean proportional species abundance raised to the power $q-1$
${}^qD$	$1/\bar{p}_i$	${}^q\lambda^{1/(1-q)}$	true diversity of order q: the inverse of mean proportional abundances of the types of interest, or the numbers equivalent of ${}^q\lambda$
H'	$\log({}^1D)$	$\log(1/\bar{p}_i)$	Shannon entropy: the logarithm of true diversity of order 1, or the logarithm of the inverse of the geometric mean of the proportional abundances of the types of interest
γ'			the raw value of a species diversity index as calculated using the entire dataset, e.g. ${}^q\lambda_\gamma$ or $H'\gamma$
α'			the alpha component obtained when partitioning γ'
β'			the beta component obtained when partitioning γ'
${}^qD_\gamma$	$\gamma = 1/\bar{p}_i$	${}^q\lambda_\gamma^{1/(1-q)}$	true gamma diversity: total effective number of species in the dataset (measurement unit: effective species or sp_E)
$\bar{p}_{(i\|j)j}$	$\sqrt[q-1]{\sum_{i=1}^{S} p_{i\|j} p_{i\|j}^{q-1}}$		mean proportional species abundance within sampling unit j; the weighted generalised mean with exponent $q-1$ of the $p_{i\|j}$ values corresponding to sampling unit j
${}^qD_{\gamma j}$	$1/\bar{p}_{(i\|j)j}$	$\gamma_j = {}^q\lambda_{\gamma j}^{1/(1-q)}$	gamma diversity (= effective number of species) within sampling unit j (measurement unit: sp_E)
$\bar{p}_{(i\|j)\text{all}}$	$\sqrt[q-1]{\sum_{j=1}^{N}\sum_{i=1}^{S} p_{ij} p_{i\|j}^{q-1}}$		mean proportional species abundance in the dataset; the weighted generalised mean with exponent $q-1$ of all $p_{i\|j}$ values
α_t	${}^q\bar{D}_{\gamma j} = \bar{\gamma}_j$	$1/\bar{p}_{(i\|j)\text{all}}$	mean species diversity within sampling units: weighted generalised mean with exponent $1-q$ of the ${}^qD_{\gamma j}$ values with w_j used as weights (measurement unit: sp_E)
α_d	${}^qD_\alpha$	α_t/CU	true alpha diversity: effective number of species per virtual sampling unit of mean species diversity, or per compositional unit (measurement unit: sp_E/CU)
α_R	${}^qD_{\prime\gamma\omega'/\omega}$	${}^qD_{\prime\gamma\omega'}/{}^qD_\omega$	effective number of species abundance values per effective sampling unit (measurement unit: $sp_E SU_E/SU_E$)
β_{Md}	${}^qD_\beta = {}^qD_\gamma/{}^qD_\alpha$	γ/α_d	true beta diversity: number of compositional units in the dataset (measurement unit: CU)
β_{Mt}	${}^qD_{\gamma/\bar{\gamma}_j} = {}^qD_\gamma/{}^q\bar{D}_{\gamma j}$	γ/α_t	regional-to-local diversity ratio (measurement unit: sp_E/sp_E)
β_R	${}^qD_\gamma\ {}^qD_\omega/{}^qD_{\prime\gamma\omega'}$	γ/α_R	two-way diversity ratio (measurement unit: $sp_E SU_E/sp_E SU_E$)
β_{At}	${}^qD_\gamma - {}^q\bar{D}_{\gamma j}$	$\gamma - \alpha_t$	regional diversity excess; absolute effective species turnover (measurement unit: sp_E)
β_{Mt-1}	$\gamma/\alpha_t - 1$	$(\gamma - \alpha_t)/\alpha_t$	Whittaker's species turnover: effective species turnover expressed in multiples of the species diversity in a single compositional unit (measurement unit: sp_E/sp_E)
β_{Pt}	$1 - \alpha_t/\gamma$	$(\gamma - \alpha_t)/\gamma$	proportional species turnover: effective species turnover expressed as a proportion of total species diversity (measurement unit sp_E/sp_E)
H'_β	$H'_\gamma - H'_\alpha$	$\log({}^1\beta_{Md}) = \log(\gamma) - \log(\alpha_d)$	beta Shannon entropy (measurement unit: depends on the base of the logarithm)
$\bar{H}'_{\gamma-\gamma j}$	$H'_\gamma - \bar{H}'_{\gamma j}$	$\log({}^1\beta_{Mt}) = \log(\gamma) - \log(\alpha_t)$	regional Shannon entropy excess (measurement unit: depends on the base of the logarithm)
${}^2\bar{\lambda}_{\gamma j-\gamma}$	${}^2\bar{\lambda}_{\gamma j} - {}^2\lambda_\gamma$	$(\gamma - \alpha_t)/\gamma\alpha_t$	regional variance excess (measurement unit: sp_E/sp_E^2)

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Partitioning Diversity

- What do we mean when we talk about beta diversity?
  - Very broadly there are two definitions...

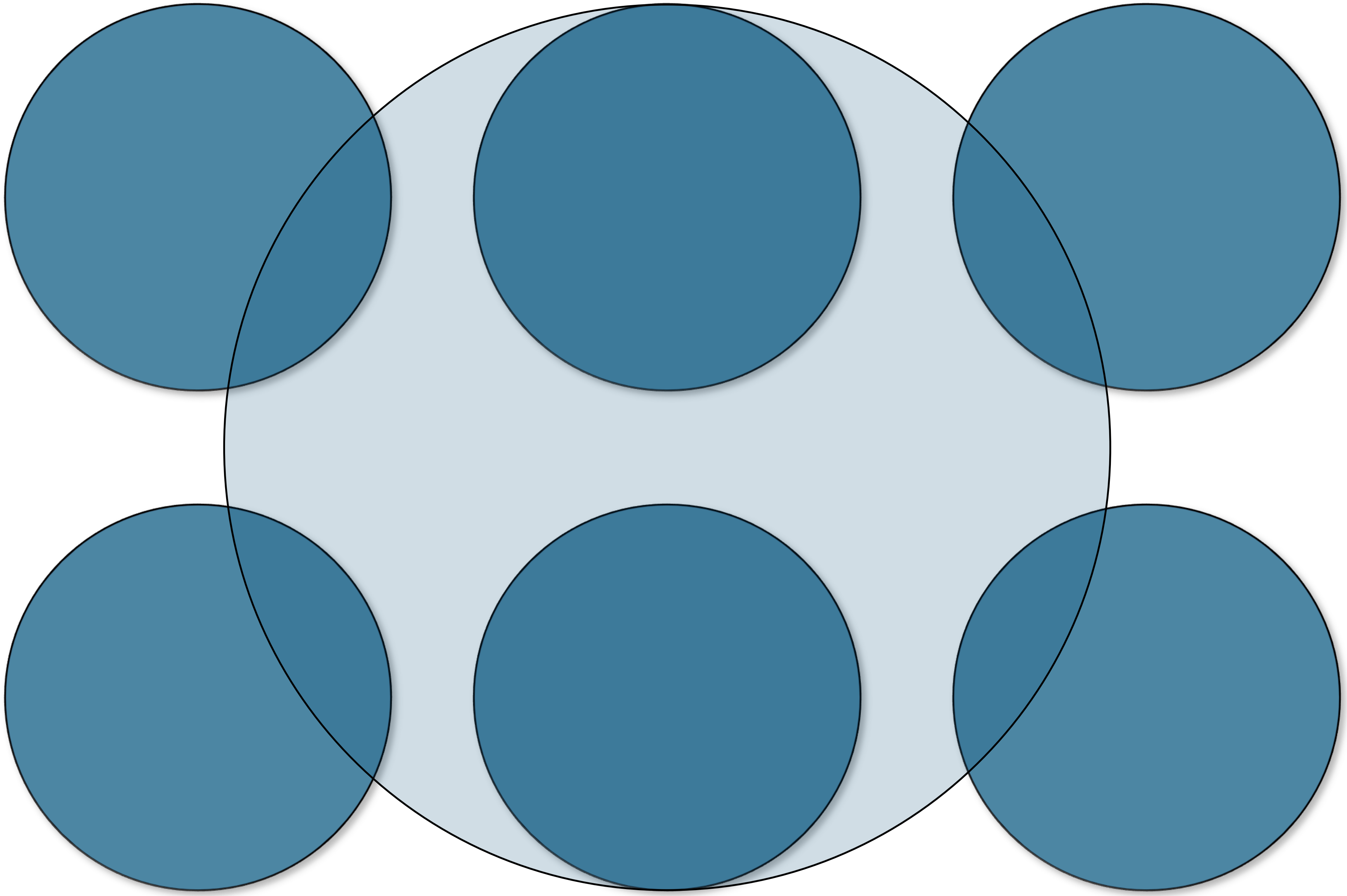
Partitioning Diversity

- What do we mean when we talk about beta diversity?
  1. Effective number of unique communities

Unique communities

ALPHA DIVERSITY: 100

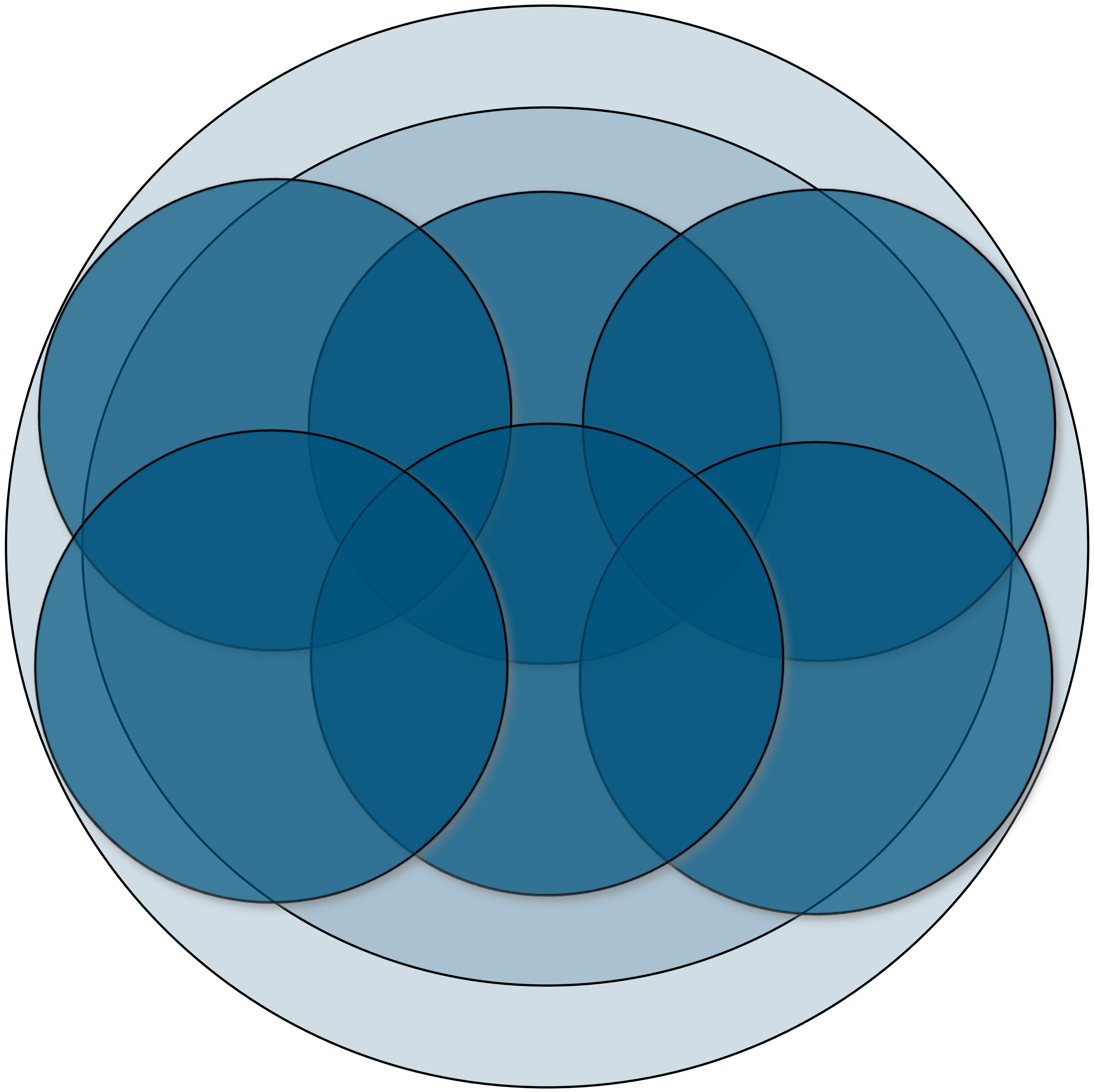
GAMMA DIVERSITY: 600



Unique communities

ALPHA DIVERSITY: 100

GAMMA DIVERSITY: 400



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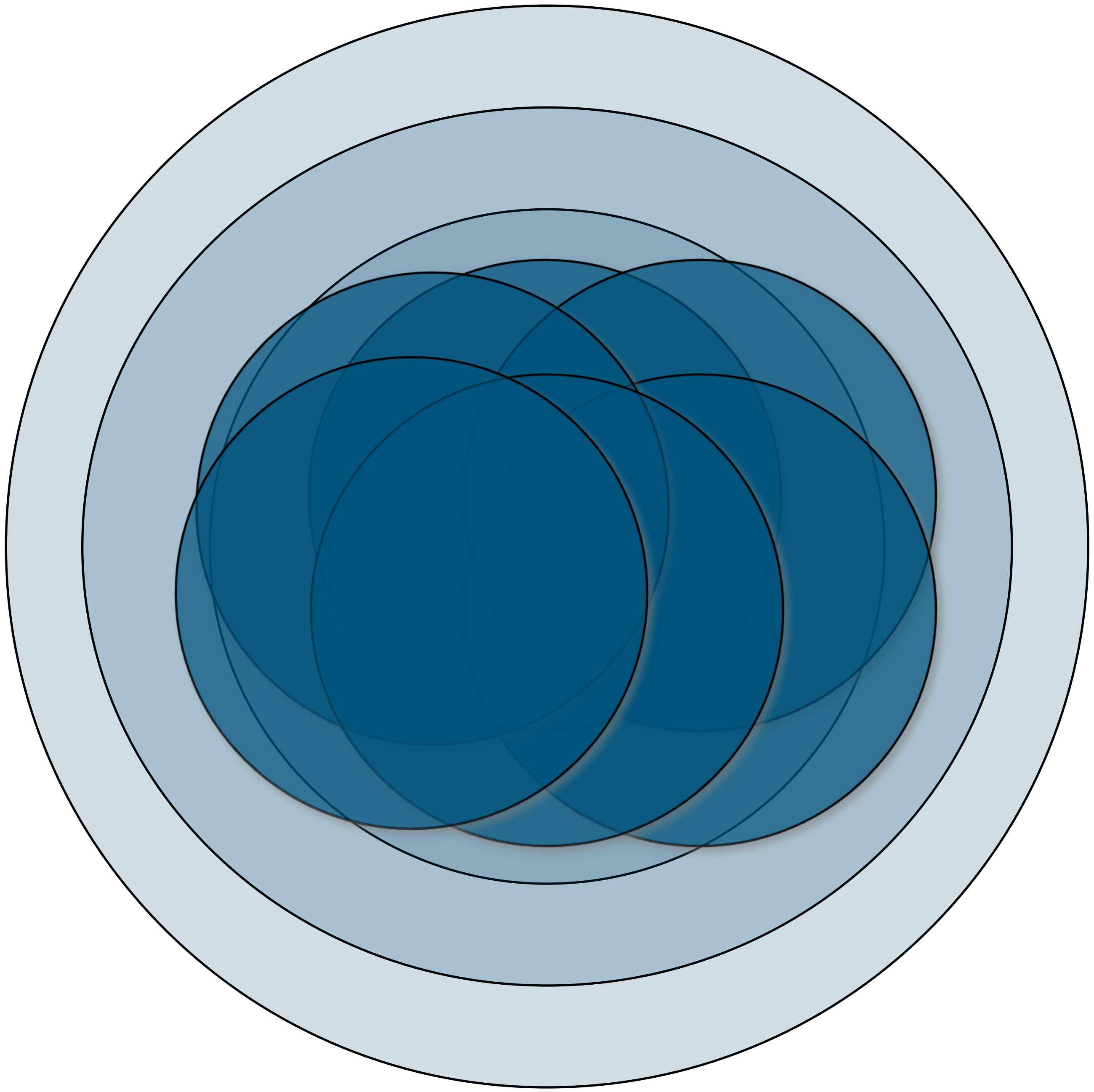
Unique communities

ALPHA DIVERSITY: 100

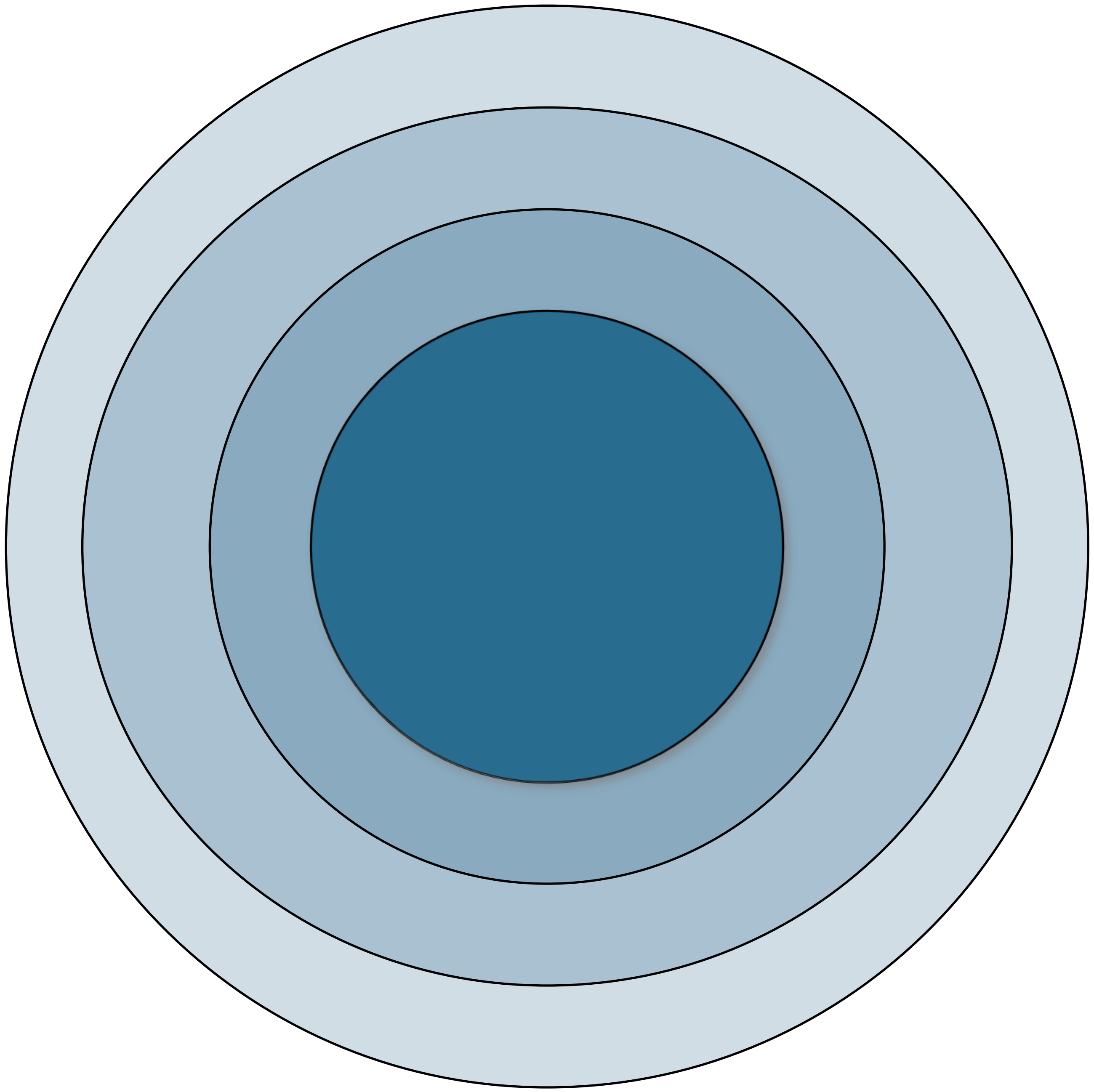
GAMMA DIVERSITY: 200



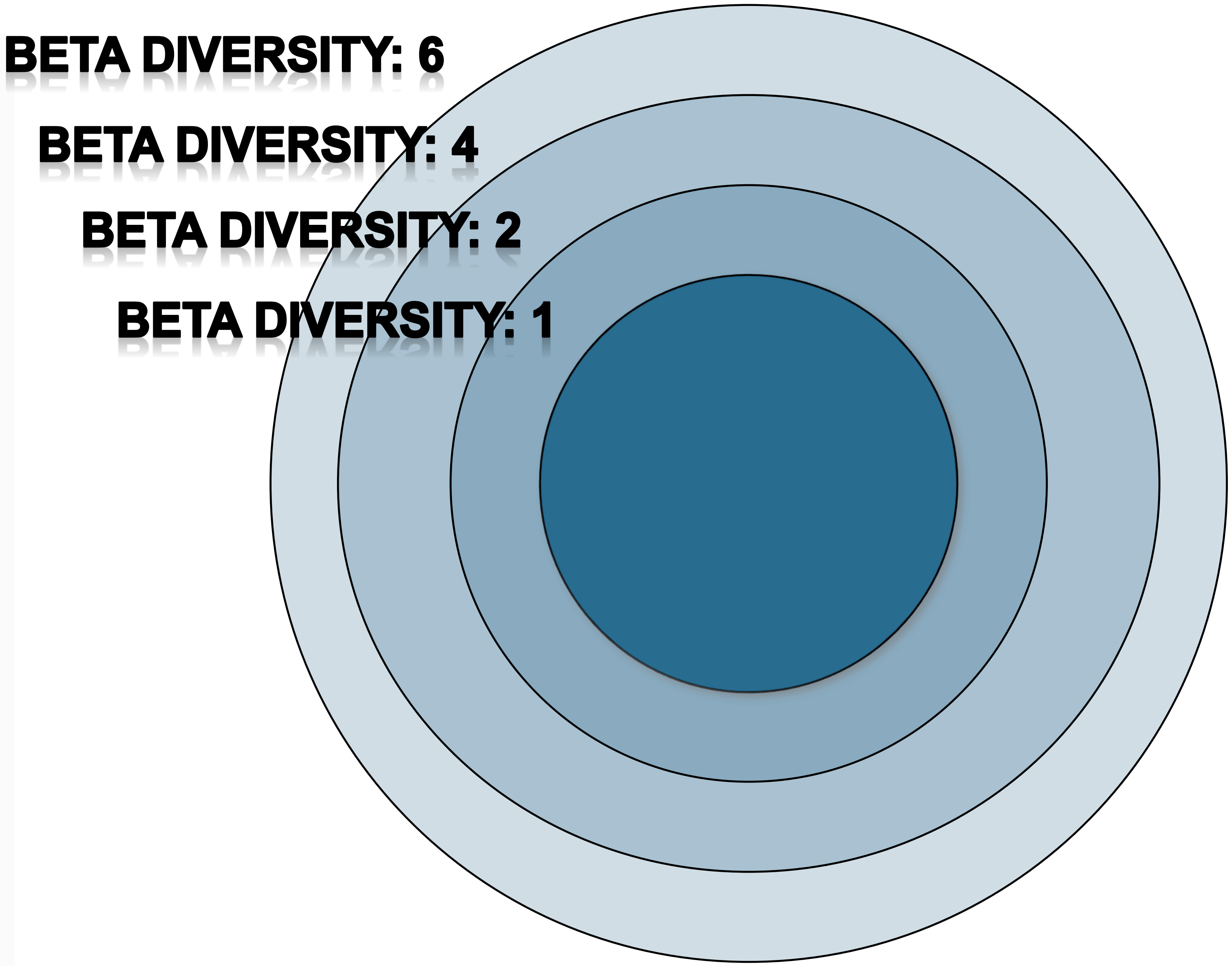
Unique communities

ALPHA DIVERSITY: 100

GAMMA DIVERSITY: 100



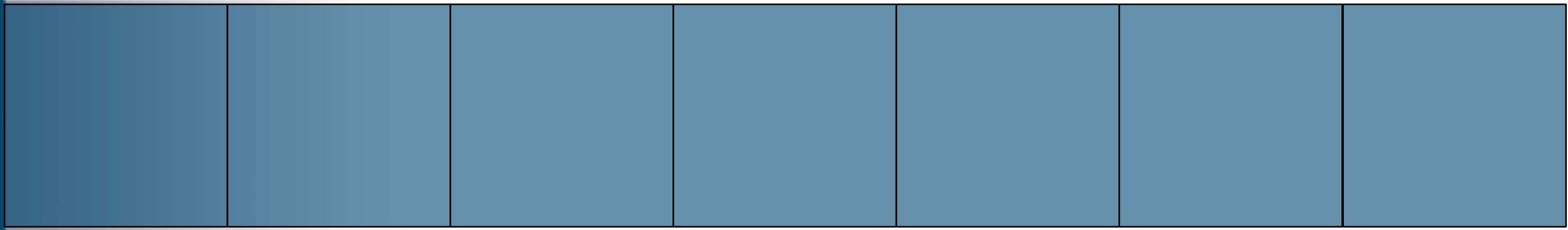
Unique communities



Partitioning Diversity

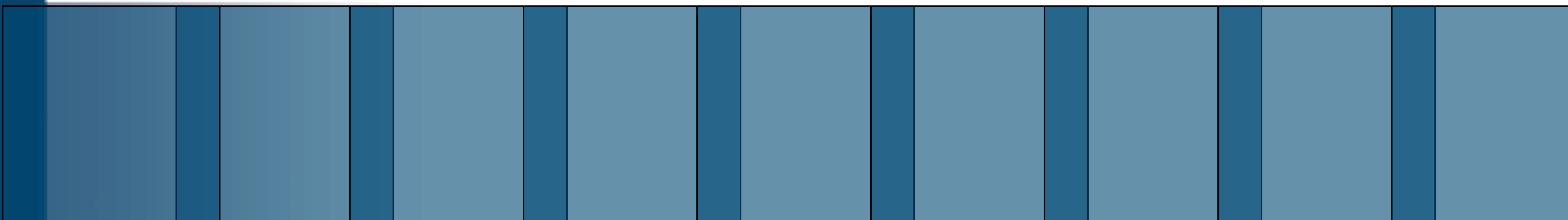
- What do we mean when we talk about beta diversity?
  1. Effective number of unique communities
  2. Turnover between communities

Partitioning Diversity



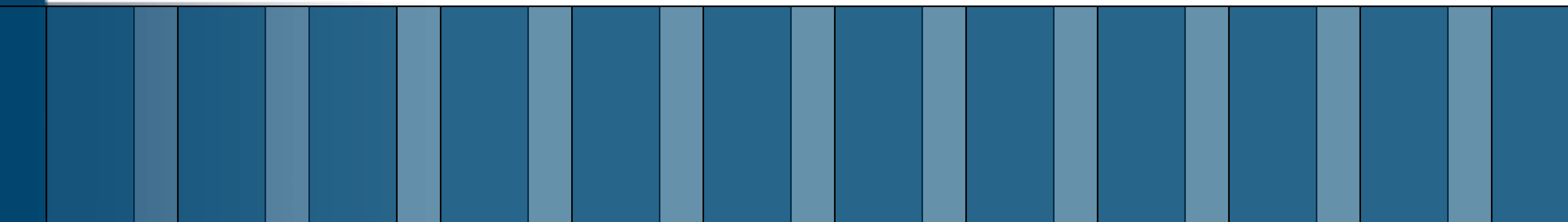
TURNOVER: 100%

Partitioning Diversity



TURNOVER: 80%

Partitioning Diversity



TURNOVER: 60%

Partitioning Diversity

TURNOVER: 40%

Partitioning Diversity

TURNOVER: 20%

Partitioning Diversity

- What do we mean when we talk about beta diversity?
  1. Effective number of unique communities
  2. Turnover between communities
- These turn out to be the same thing...

Diversity Profiles

The effective number of species:

- the number of species when all species are present at equal frequency
- the more uneven the distribution, the fewer species are "effectively" present

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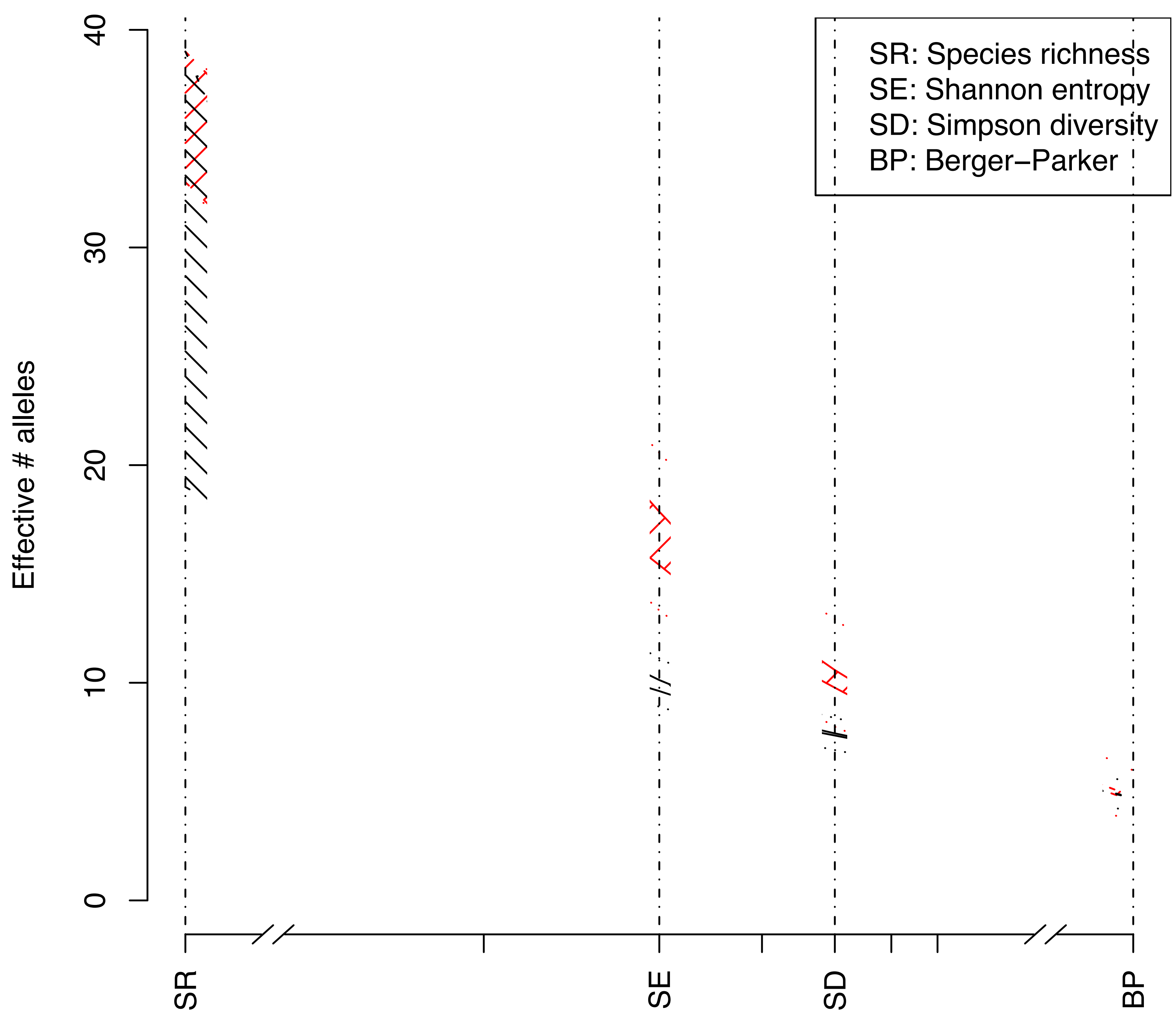
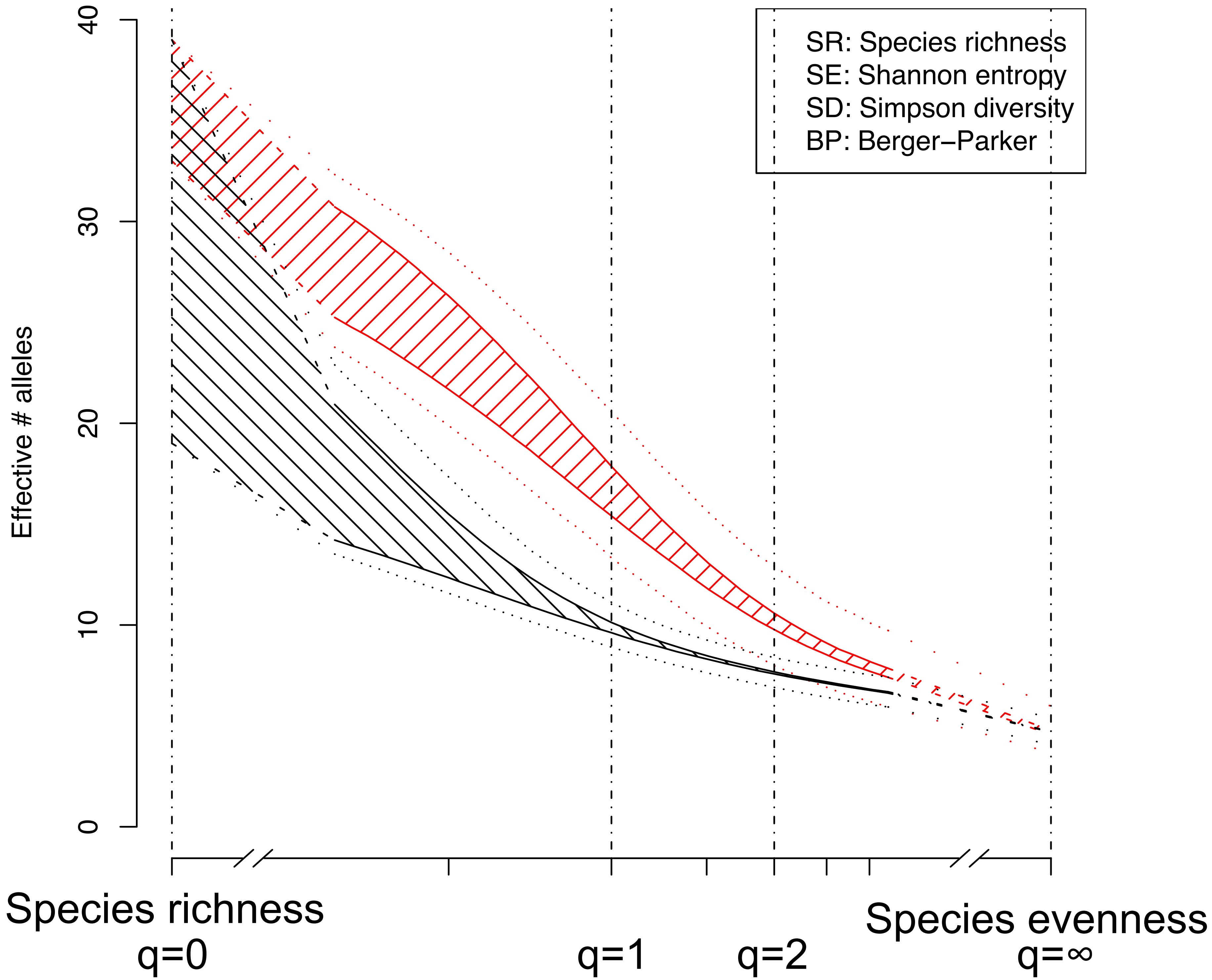
Diversity Profiles



Diversity Profiles



Diversity Profiles with Similarity

The effective number of species:

- the number of species when all species are present at equal frequency
- the more uneven the distribution, the fewer species are "effectively" present
- the more similar species are, the less "effectively present" each species is

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Diversity Profiles with Similarity

Name	Formula
Power mean of order r of $\boldsymbol{x}$ weighted by $\boldsymbol{w}$	$M_r(\boldsymbol{w},\boldsymbol{x}) = \begin{cases} \left[\sum_{i=1}^{S} w_i \times x_i^r\right]^{1/r} & r \neq 0 \\ \prod_{i=1}^{S} x_i^{w_i} & r = 0 \end{cases}$
Hill numbers	${}^qD(\boldsymbol{p}) = M_{q-1}(\boldsymbol{p},\boldsymbol{p})^{-1}$
Similarity-sensitive diversity	${}^qD^{\boldsymbol{Z}}(\boldsymbol{p}) = M_{q-1}(\boldsymbol{p},\boldsymbol{Z}\boldsymbol{p})^{-1}$ $[{}^qD(\boldsymbol{p}) = {}^qD^{\boldsymbol{I}}(\boldsymbol{p})]$

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Partitioning Diversity

- What's different?
  - We think in terms of individual sub-communities as much as the whole ecosystem
- Coming from that perspective allows us to answer specific questions:

ALPHA DIVERSITY – Which sub-communities are the most diverse?

BETA DIVERSITY – Which sub-communities are the most distinct?

GAMMA DIVERSITY – Which sub-communities contribute the most to overall diversity?

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Partitioning Diversity

Diversity measure	Sub-community diversity (d)	Ecosystem diversity (D)
Alpha diversity	$^q\alpha_j^{\mathbf{Z}}(\mathbf{P}_{.j}) = M_{q-1}(\widehat{\mathbf{P}}_{.j}, \mathbf{Z}\mathbf{P}_{.j})^{-1}$ $^q\hat{\alpha}_j^{\mathbf{Z}}(\mathbf{P}_{.j}) = {}^qD^{\mathbf{Z}}(\widehat{\mathbf{P}}_{.j})^* = w_j \times {}_\alpha^q d_j^{\mathbf{Z}}(\mathbf{P}_{.j})$	${}_\alpha^q D^{\mathbf{Z}}(\mathbf{P}) = M_{1-q}(\mathbf{w}, {}^q\alpha^{\mathbf{Z}}(\mathbf{P}_{.j})\vert_{j\in\{1\cdots N\}})$ ${}_\alpha^q \widehat{D}^{\mathbf{Z}}(\mathbf{P}) = M_{1-q}(\mathbf{w}, {}^q\hat{\alpha}^{\mathbf{Z}}(\mathbf{P}_{.j})\vert_{j\in\{1\cdots N\}})$
Beta diversity	$^q\beta_j^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p}) = M_{q-1}\left(\widehat{\mathbf{P}}_{.j}, \frac{\mathbf{Z}\mathbf{P}_{.j}}{\mathbf{Z}\mathbf{p}}\right)$ $^q\hat{\beta}_j^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p}) = M_{q-1}\left(\widehat{\mathbf{P}}_{.j}, \frac{\mathbf{Z}\widehat{\mathbf{P}}_{.j}}{\mathbf{Z}\mathbf{p}}\right) = \frac{^q\beta_j^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p})}{w_j}$	${}_\beta^q D^{\mathbf{Z}}(\mathbf{P}) = M_{1-q}(\mathbf{w}, {}^q\beta^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p})\vert_{j\in\{1\cdots N\}})$ ${}_\beta^q \widehat{D}^{\mathbf{Z}}(\mathbf{P}) = M_{1-q}(\mathbf{w}, {}^q\hat{\beta}^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p})\vert_{j\in\{1\cdots N\}})^\dagger$
Gamma diversity	$^q\gamma_j^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p}) = M_{q-1}(\widehat{\mathbf{P}}_{.j}, \mathbf{Z}\mathbf{p})^{-1} [= {}^q\hat{\gamma}_j^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p})]$	${}_\gamma^q D^{\mathbf{Z}}(\mathbf{P}) = M_{1-q}(\mathbf{w}, {}^q\gamma^{\mathbf{Z}}(\mathbf{P}_{.j}, \mathbf{p})\vert_{j\in\{1\cdots N\}})^\dagger$ $[{}_\gamma^q \widehat{D}^{\mathbf{Z}}(\mathbf{P}) = {}_\gamma^q D^{\mathbf{Z}}(\mathbf{P}) = {}^qD^{\mathbf{Z}}(\mathbf{p})^*]$

Sub-community diversity

$^{q}\alpha_{i}^{\mathbf{Z}}$ Patch diversity

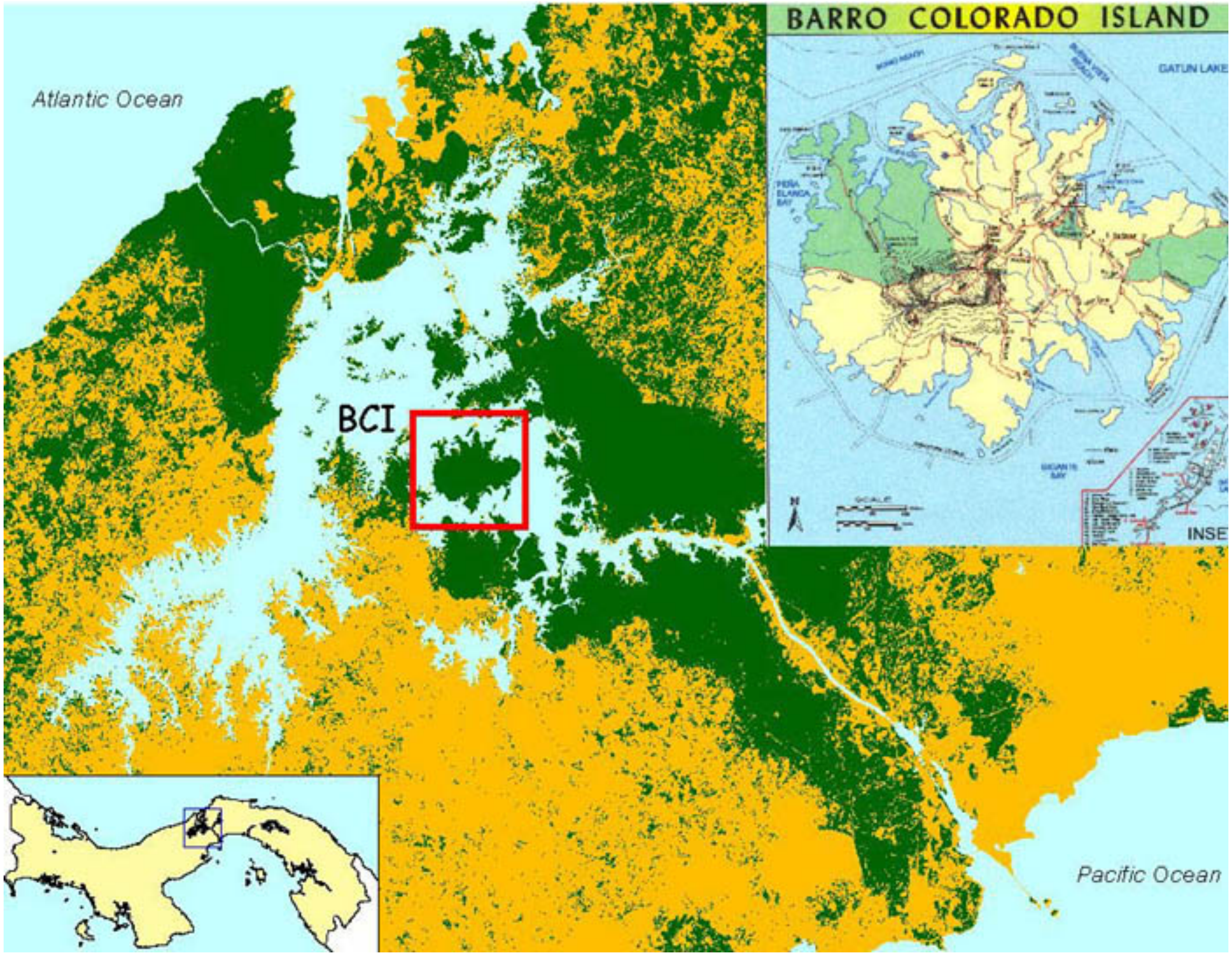
$^{q}\beta_{i}^{\mathbf{Z}}$ Distinctiveness from others

$^{q}\gamma_{i}^{\mathbf{Z}}$ Contribution to total diversity

Real World Example

Barro Colorado Island

Barro Colorado Island



Barro Colorado Island

- 50 ha plot in Panama
  - Every individual tree and sapling recorded
  - Species, Size, Location
  - 1981-2, 1985, 1990, 1995, 2000, 2005
  - Work done by Center for Tropical Forest Science and many others, funded by multiple sources

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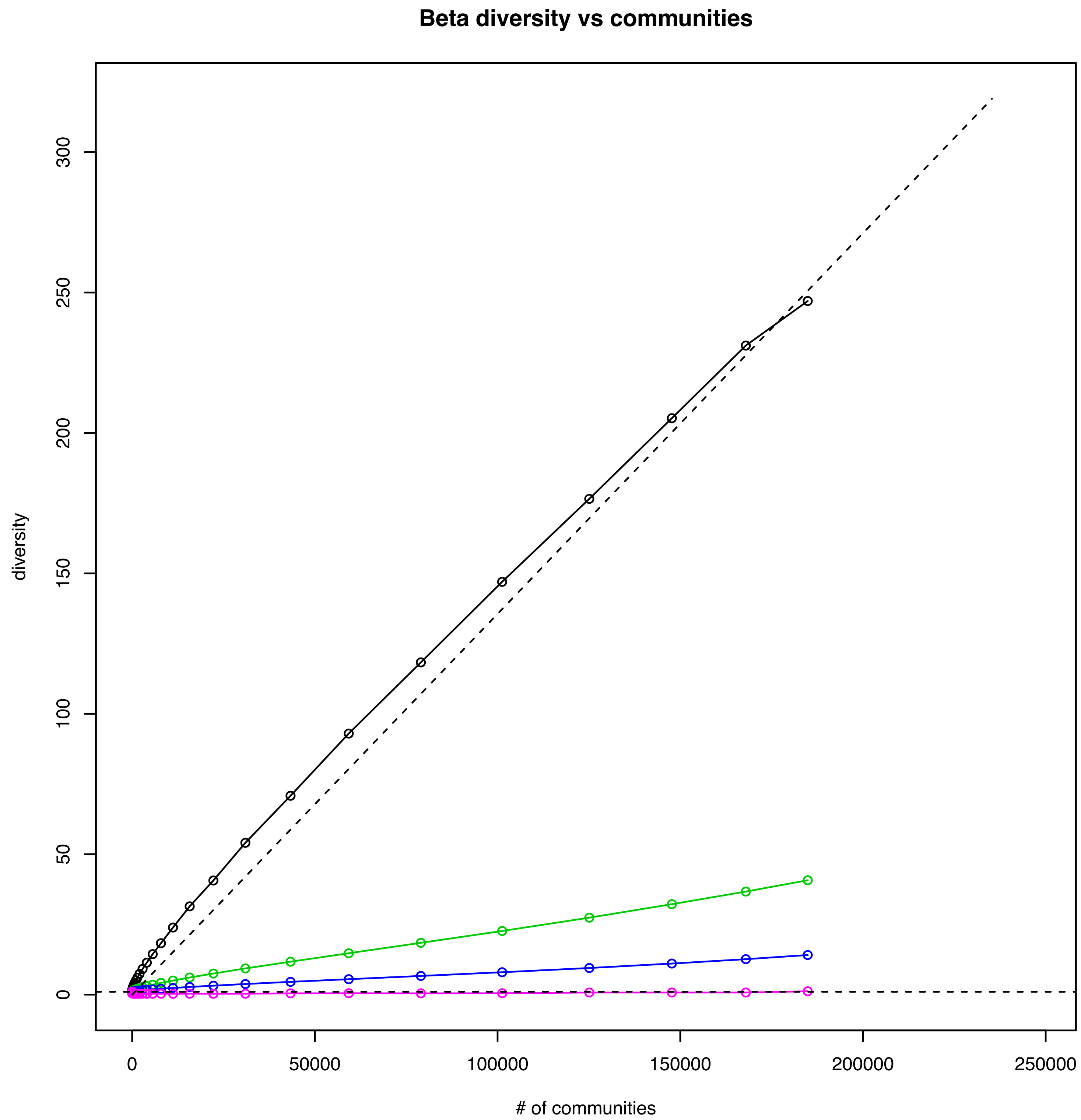
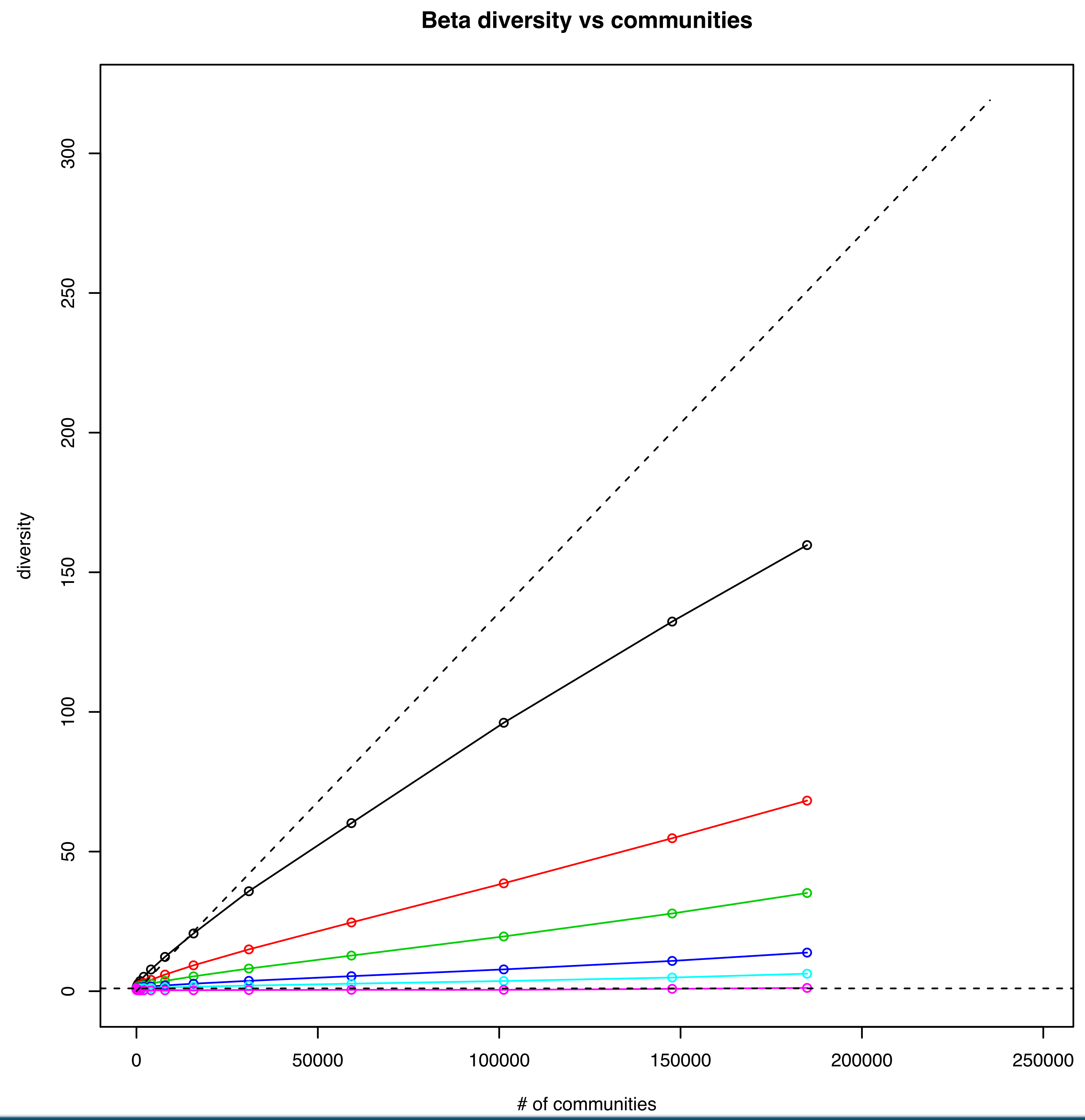
What can we tell from total beta diversity?



What can we tell from total beta diversity?



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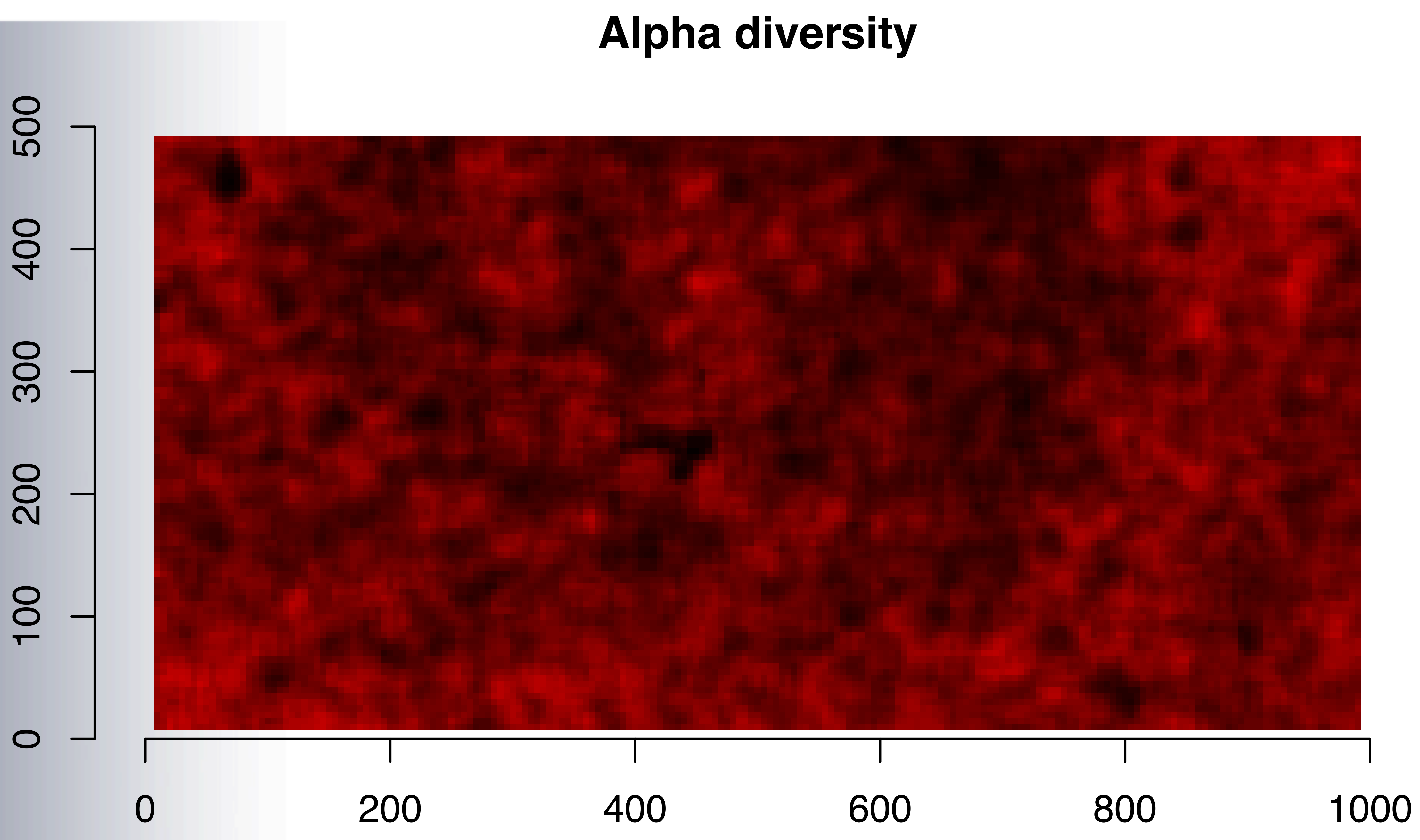
What can we tell from total beta diversity?

- Not much!
  - and total alpha and gamma diversity are similar...

How about individual alpha diversity?



What can we assess?

$^{q}\alpha_i^{\mathbf{Z}}$ Value in terms of patch diversity

$^{q}\beta_i^{\mathbf{Z}}$ Value in terms of distinctiveness

$^{q}\gamma_i^{\mathbf{Z}}$ Value in term of contribution to total diversity

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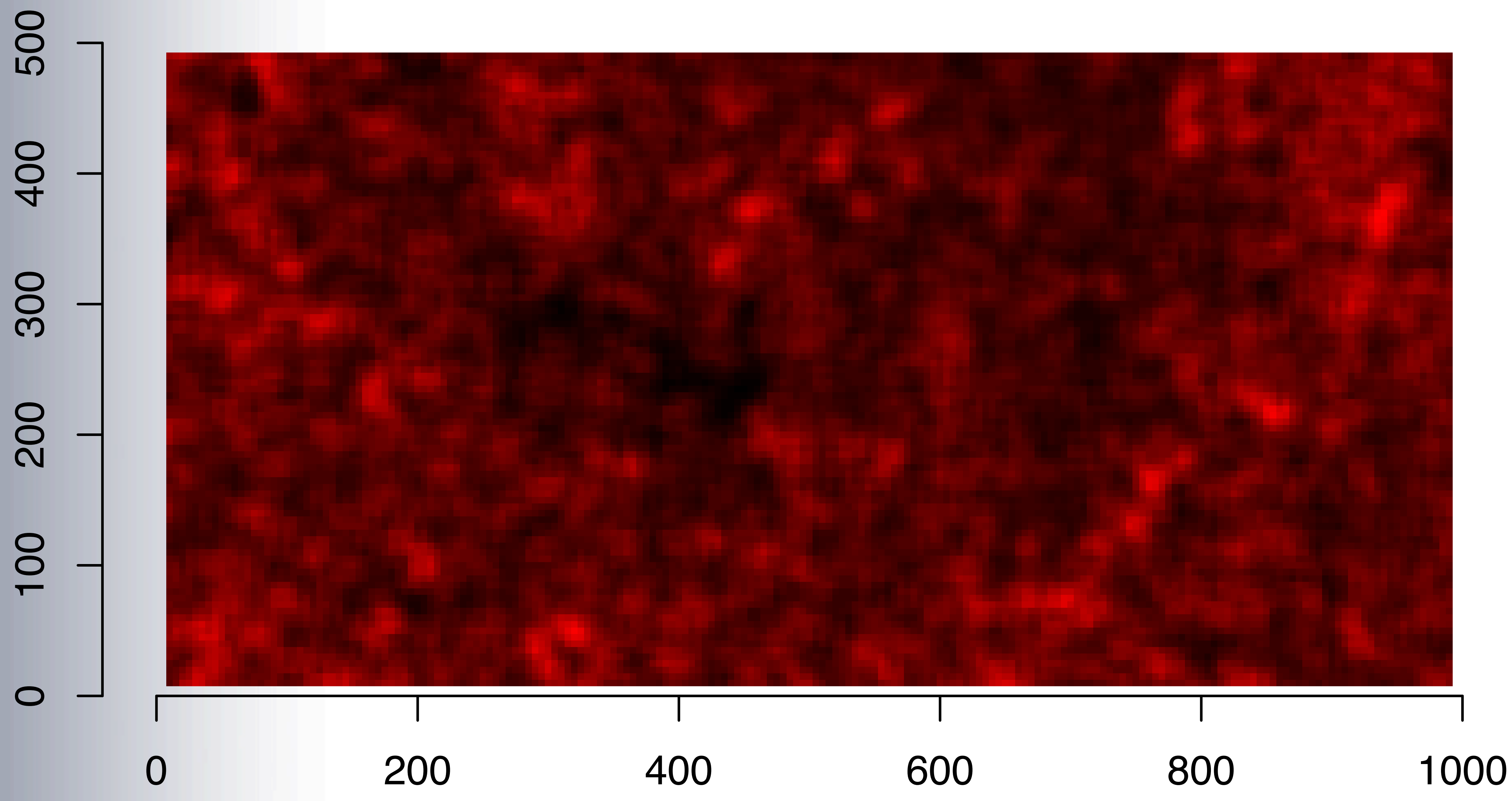
Value in terms of patch diversity



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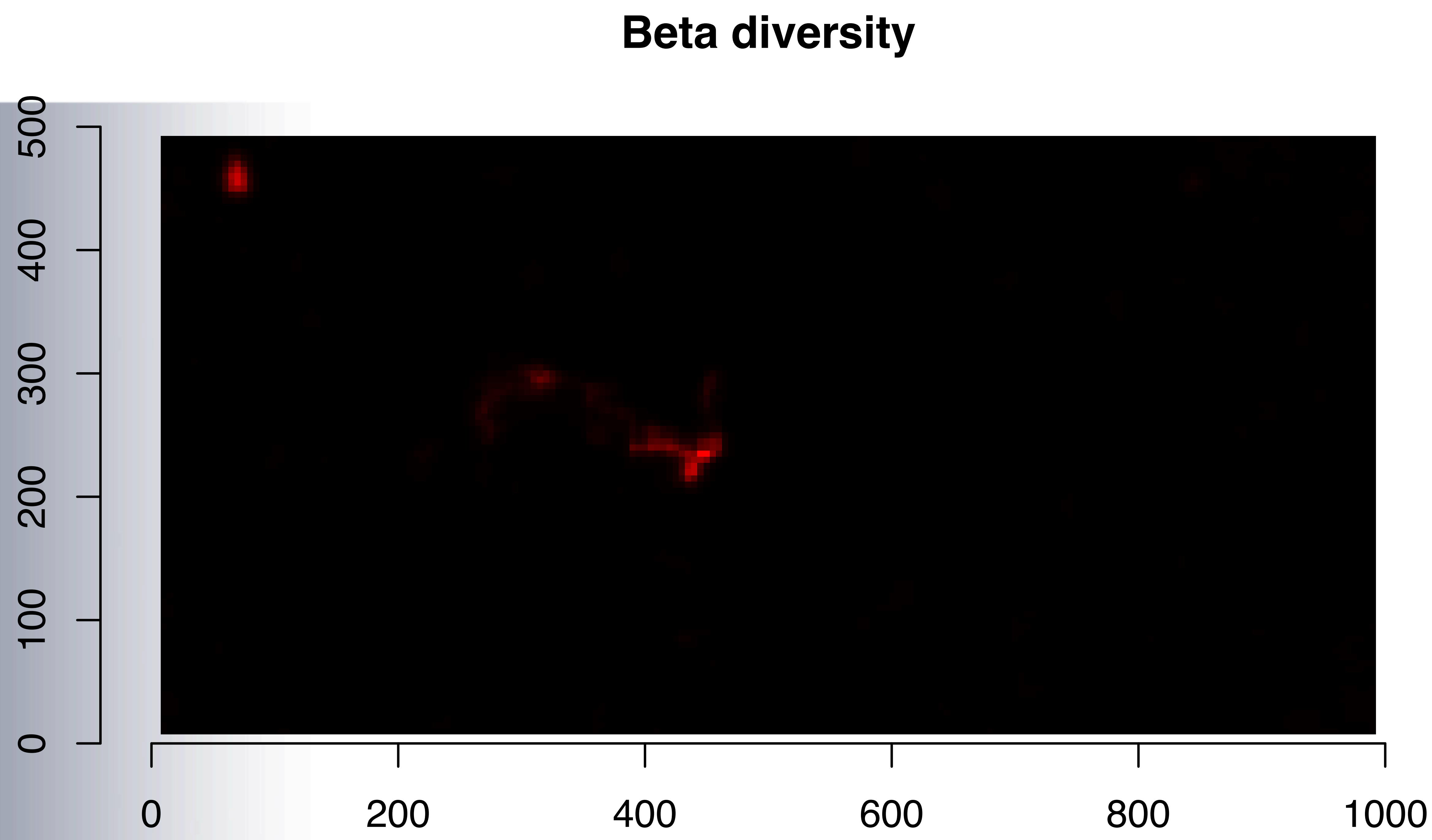
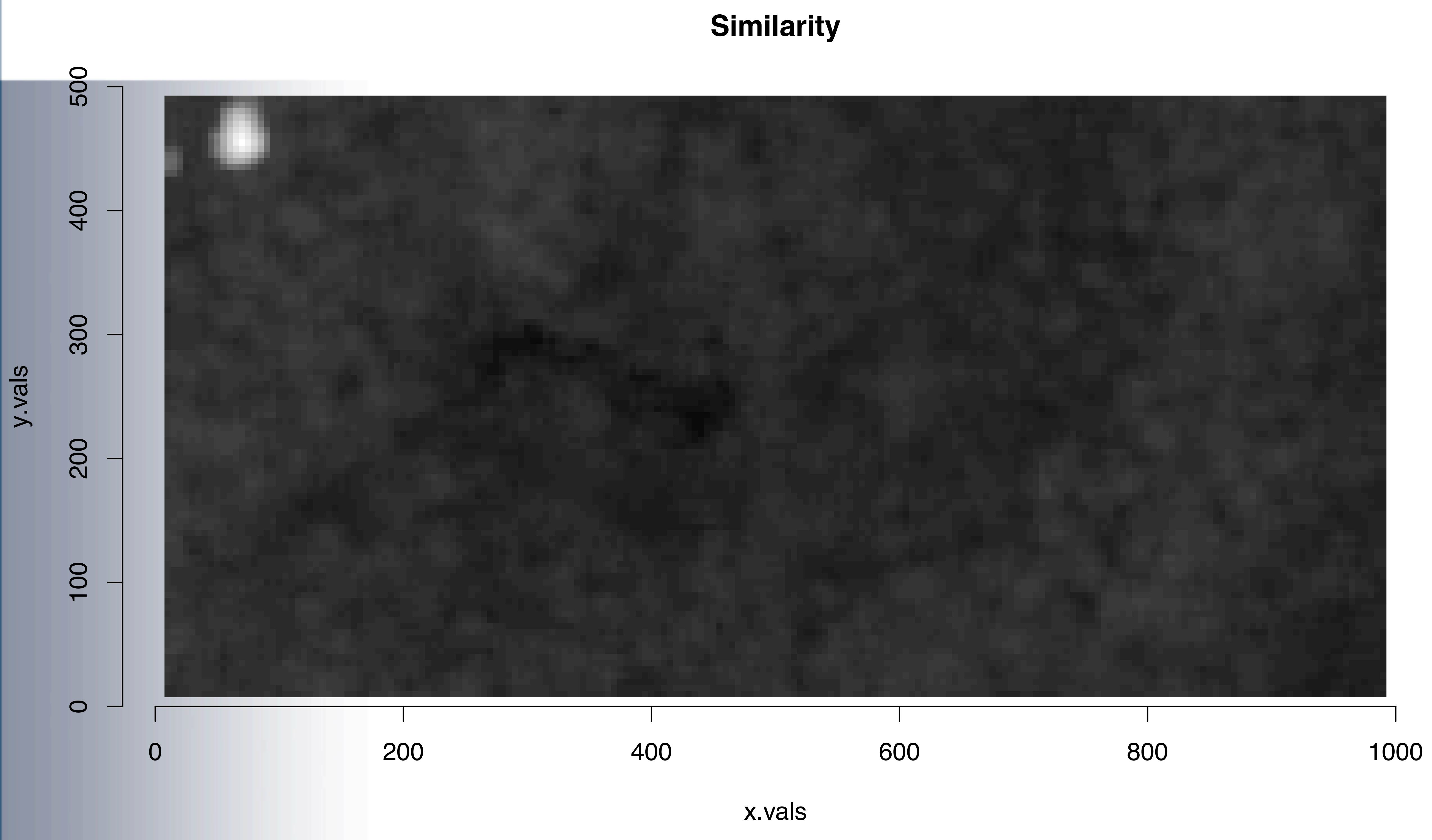
Value in terms of patch diversity

- We are beginning to see patterns here...
  - Picking out area with a lot of trees of high diversity
  - But not necessarily distinct from other areas, so selecting these, we may repeat ourselves with some species and miss others

Spatial Beta Diversity



What are these areas?



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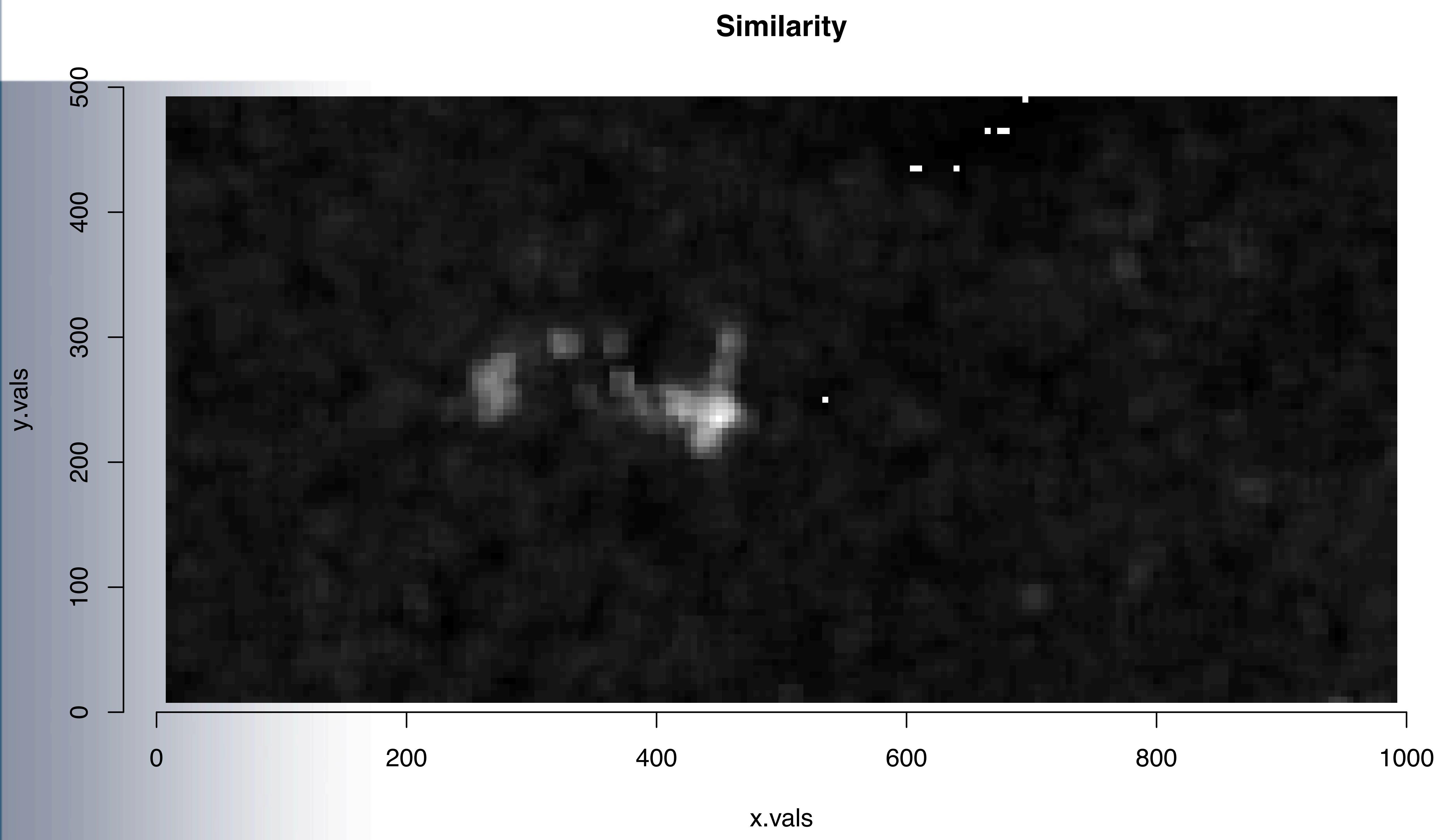

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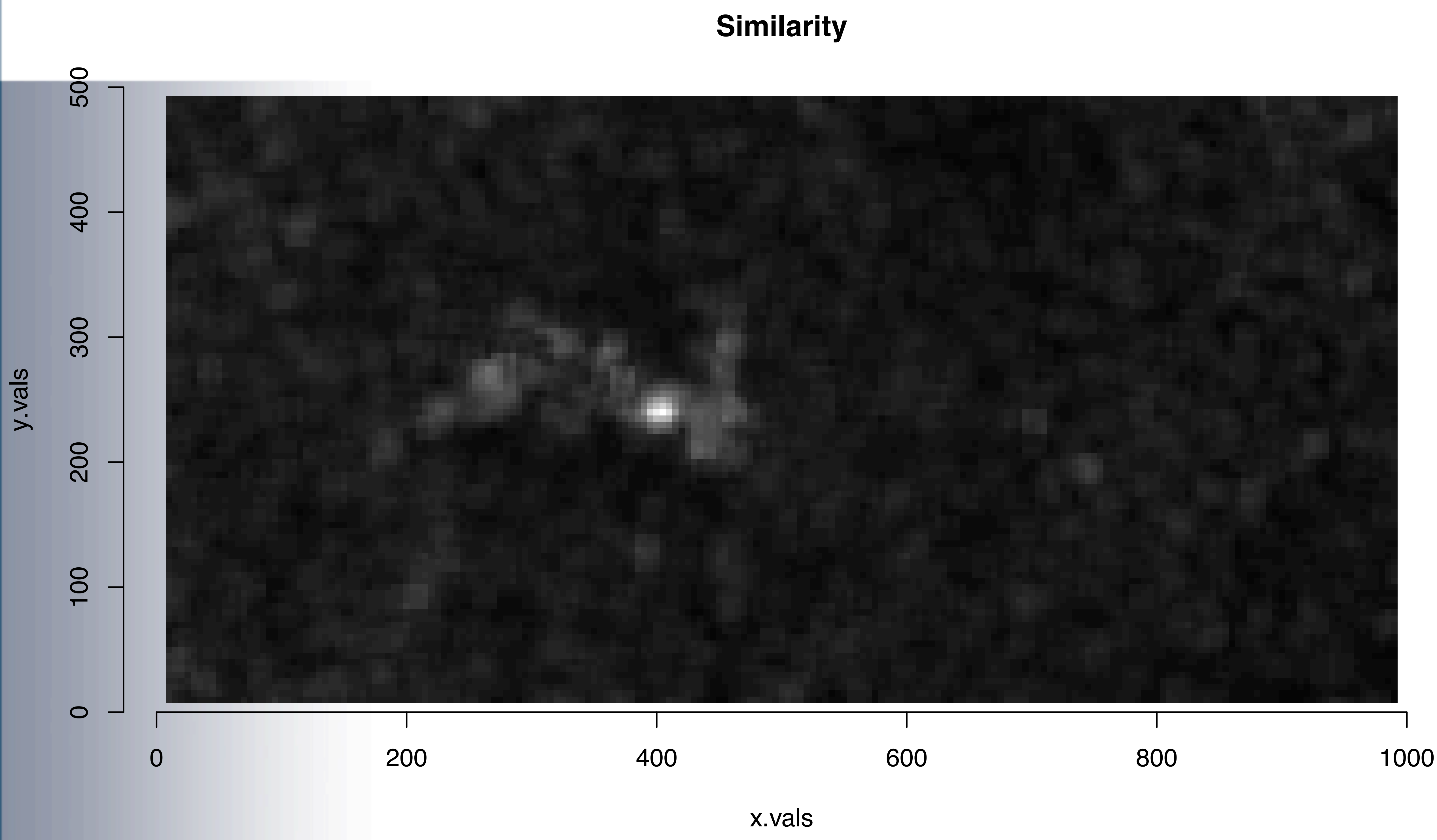

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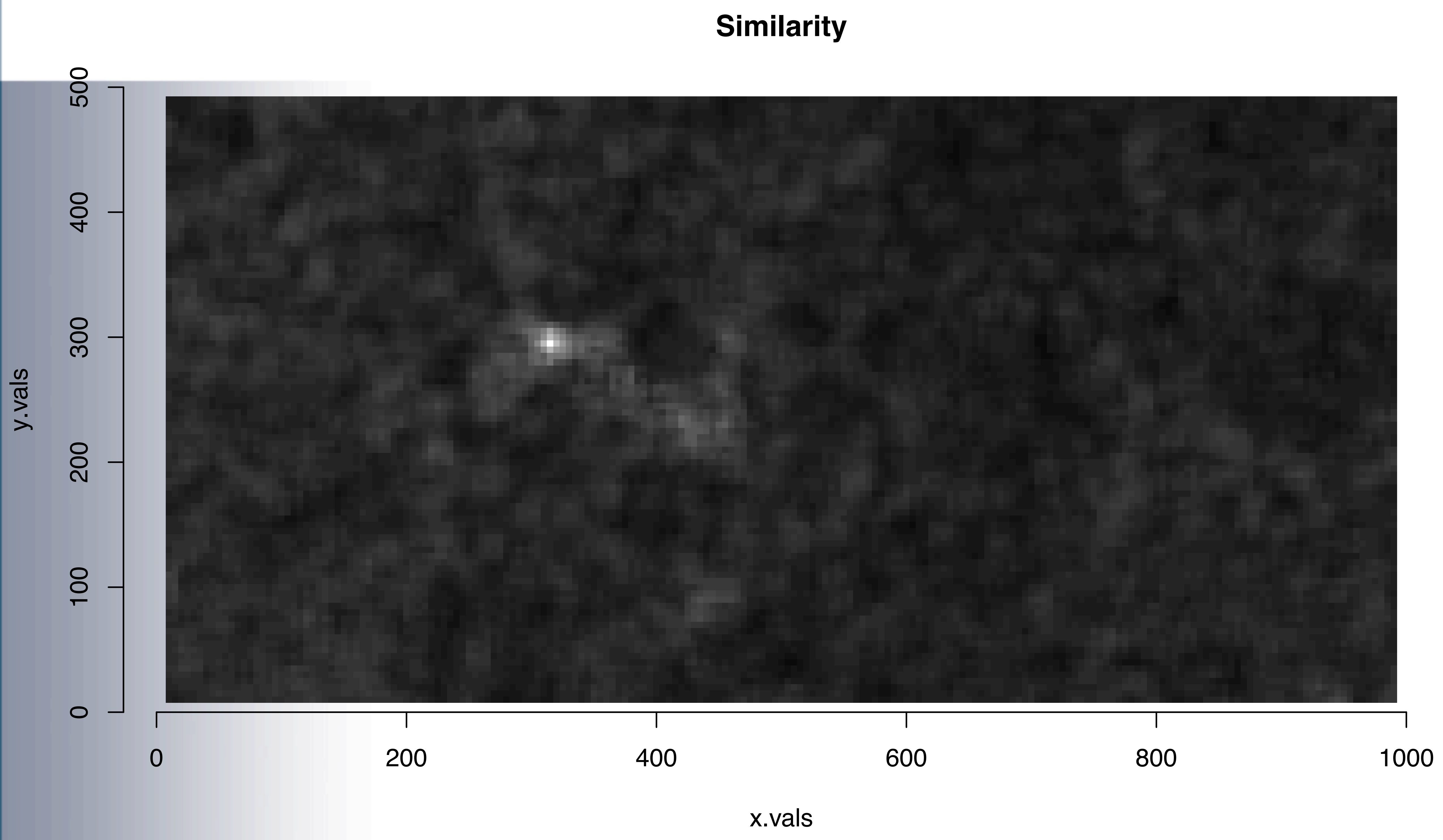
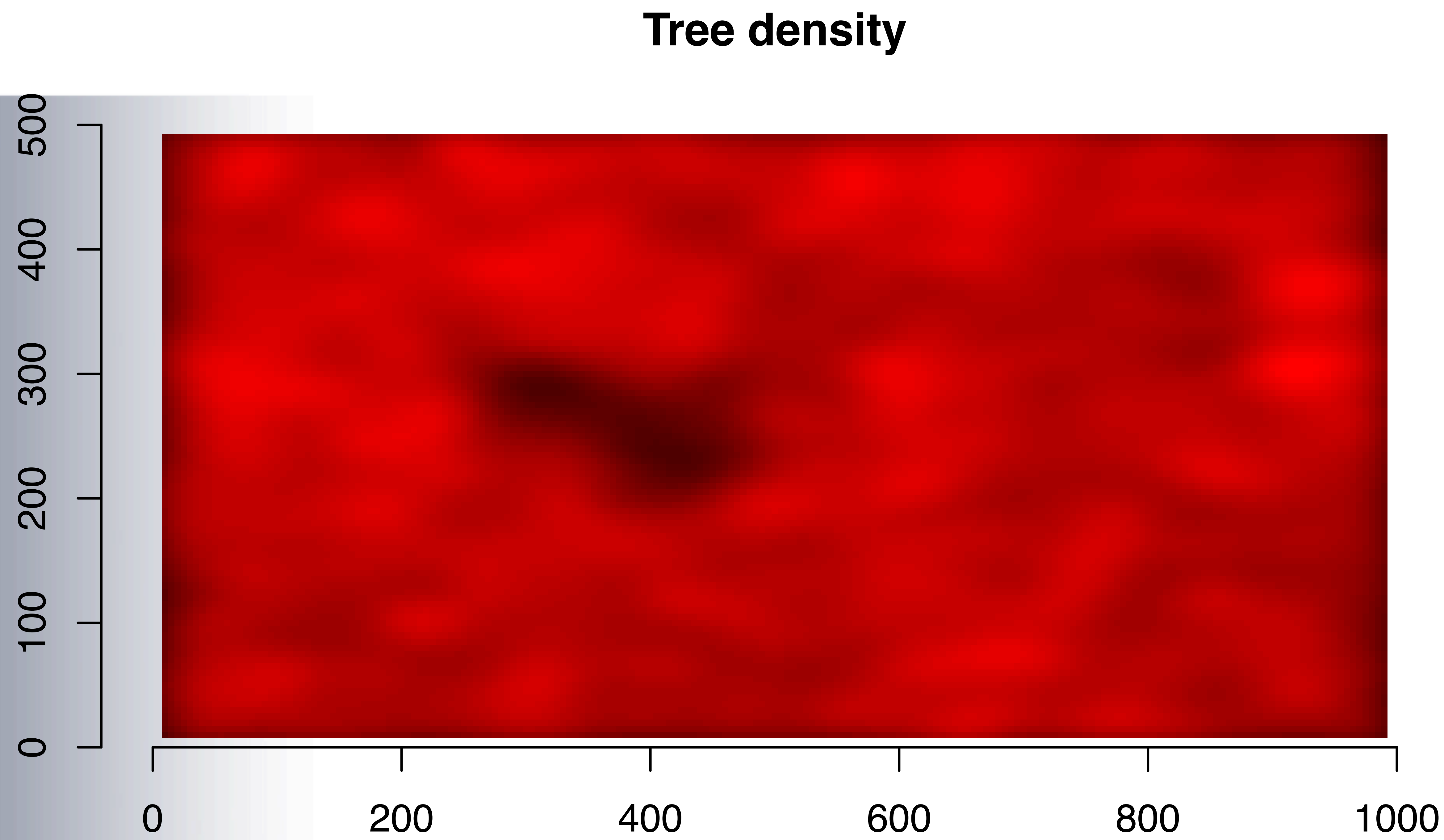
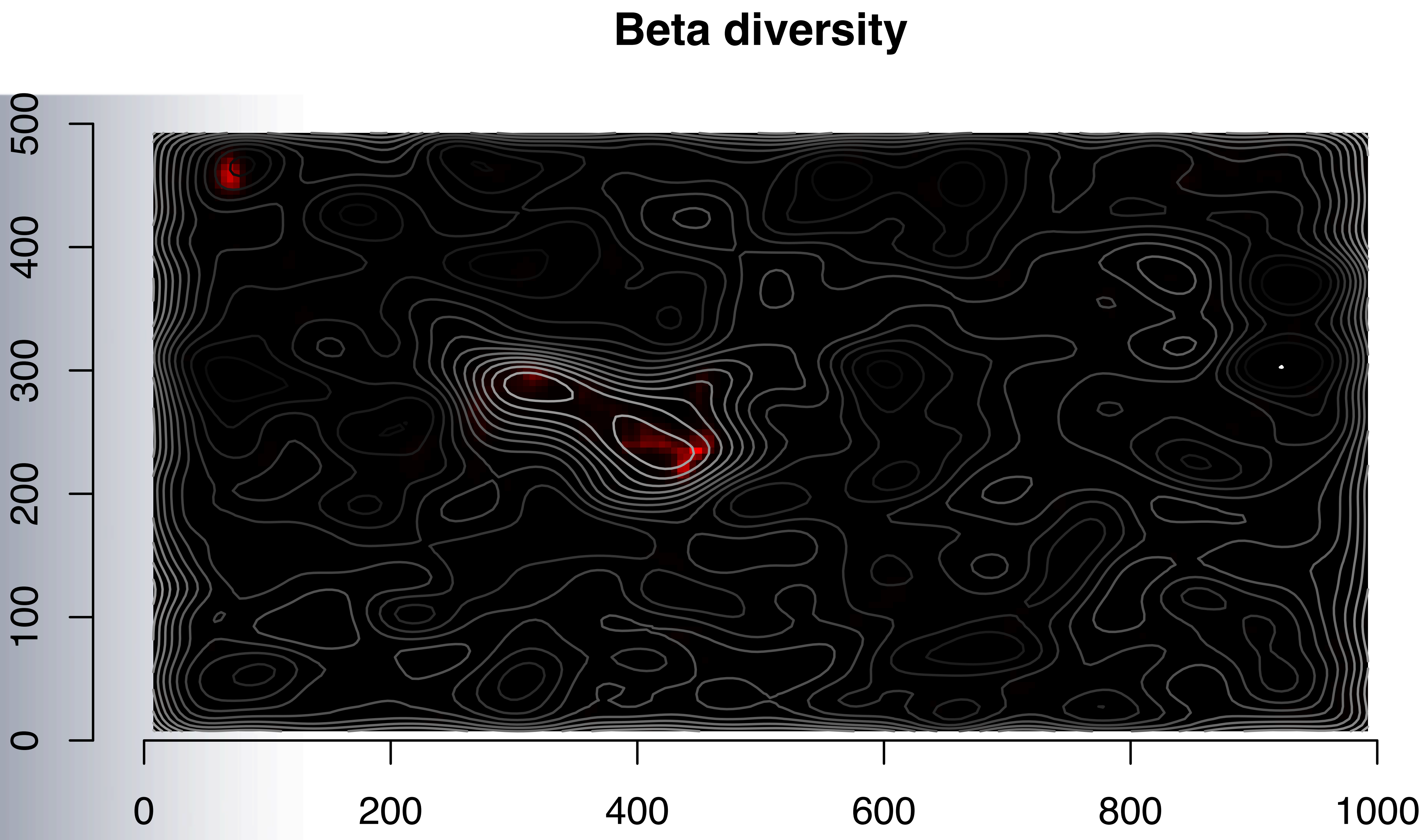
What are these areas?



What does Beta Diversity mean though?



What does Beta Diversity mean though?



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What does Beta Diversity mean though?

- Areas of high “distinctiveness”, but no regard for diversity or number of trees
- It identifies two areas, but one of them is largely devoid of trees...

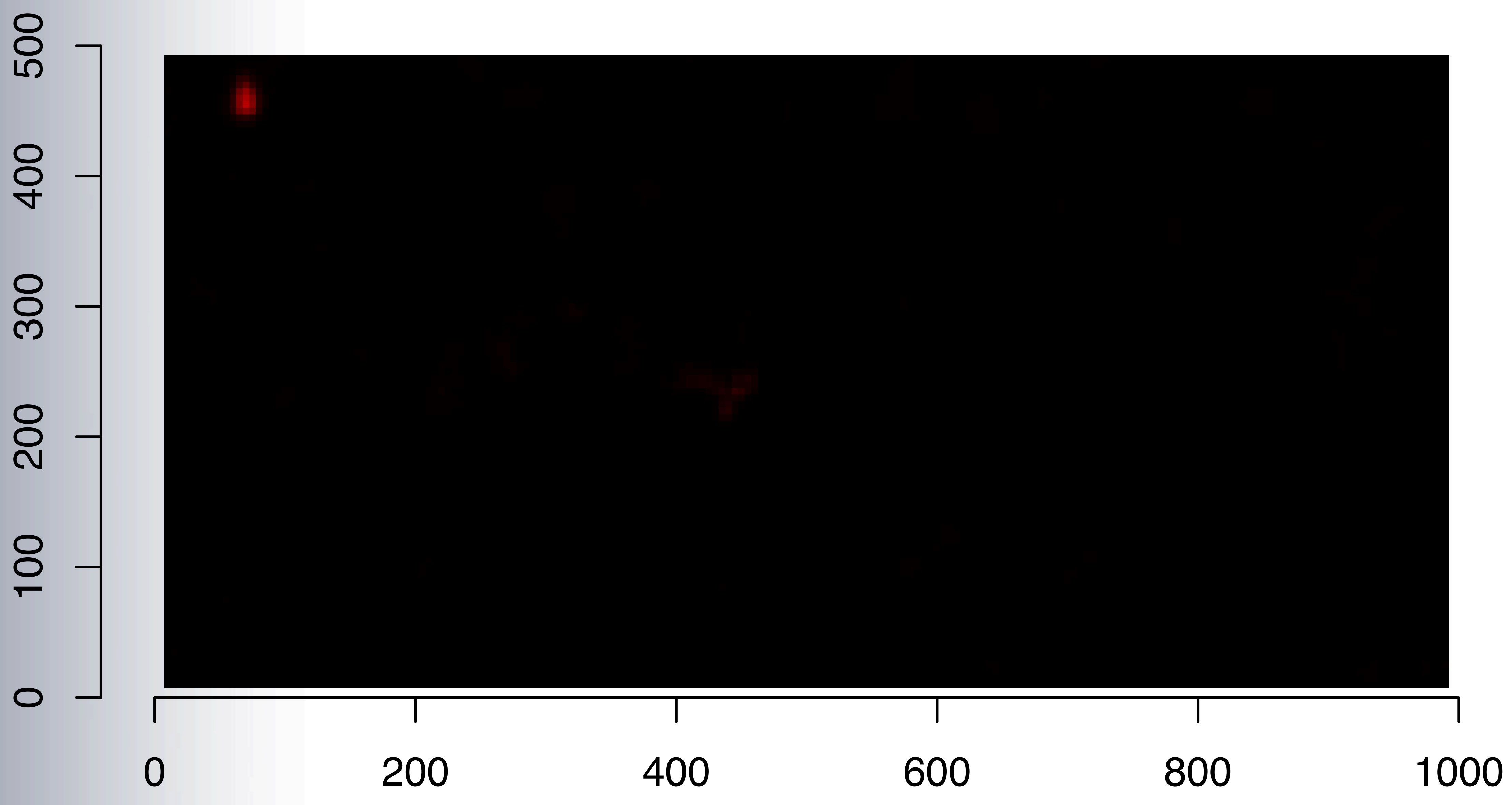
What can we assess?

${}^{q}\alpha_i^{\mathbf{Z}}$ Value in terms of patch diversity

${}^{q}\beta_i^{\mathbf{Z}}$ Value in terms of distinctiveness

${}^{q}\gamma_i^{\mathbf{Z}}$ Value in term of contribution to total diversity

Value in terms of distinctiveness



Value in terms of distinctiveness

- It identifies areas that contribute a lot to total beta diversity
- Specifically finds one area, the area with high individual beta diversity but which also has trees in it!

But is this what we want?

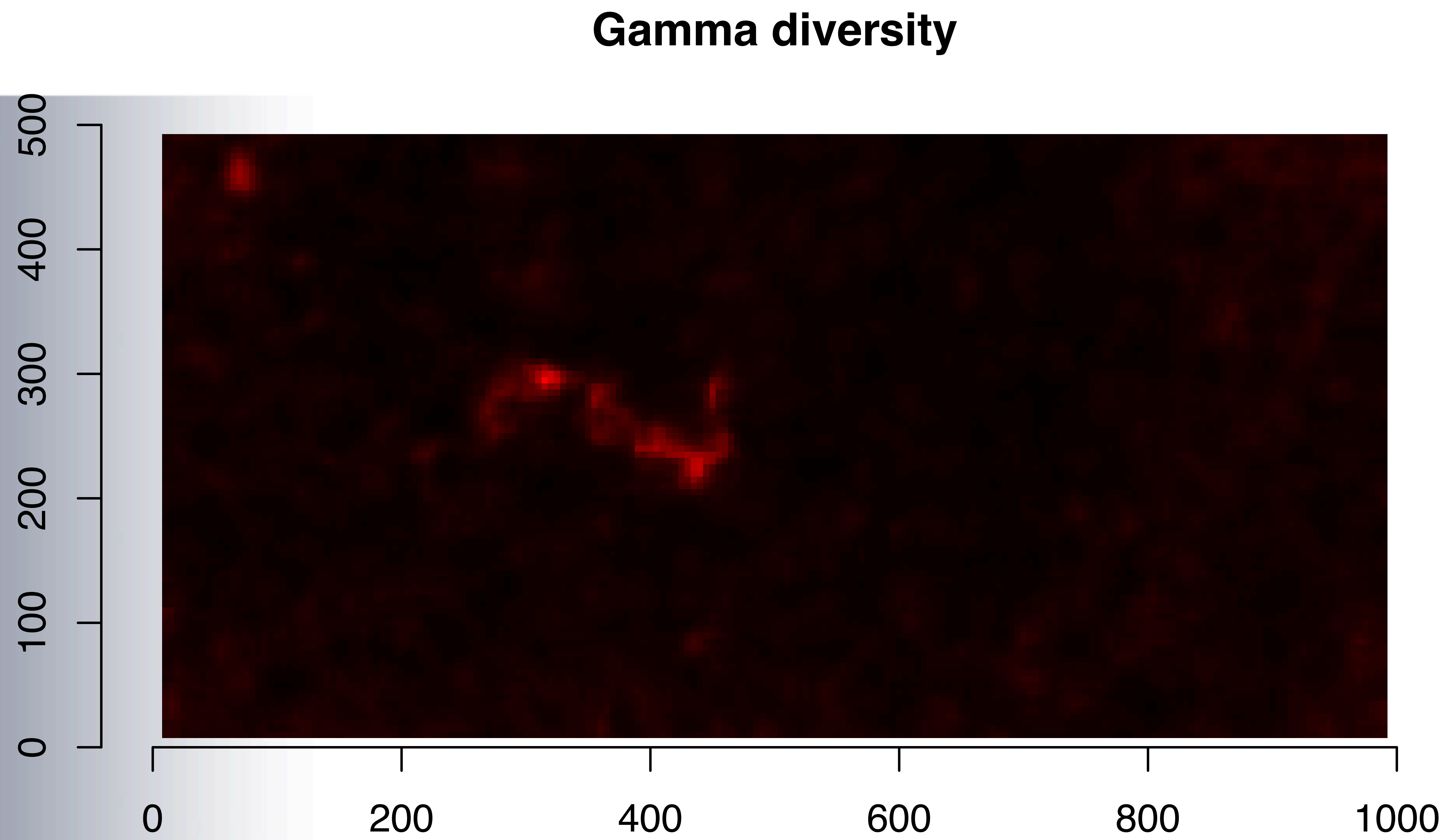
What can we assess?

$^{q}\alpha_i^{\mathbf{Z}}$ Value in terms of patch diversity

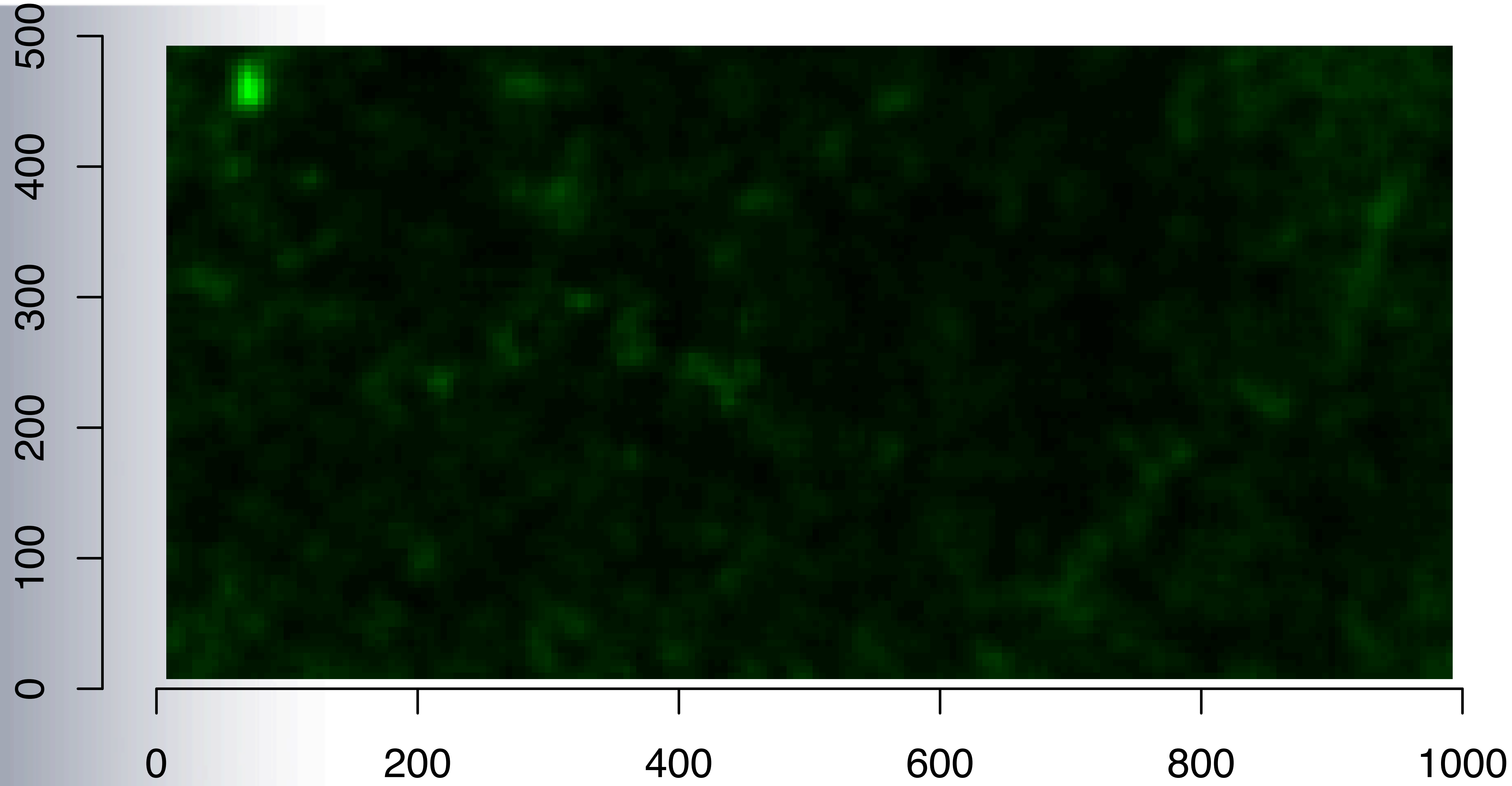
$^{q}\beta_i^{\mathbf{Z}}$ Value in terms of distinctiveness

$^{q}\gamma_i^{\mathbf{Z}}$ Value in term of contribution to total diversity

Spatial gamma diversity



Value in terms of contribution to total diversity



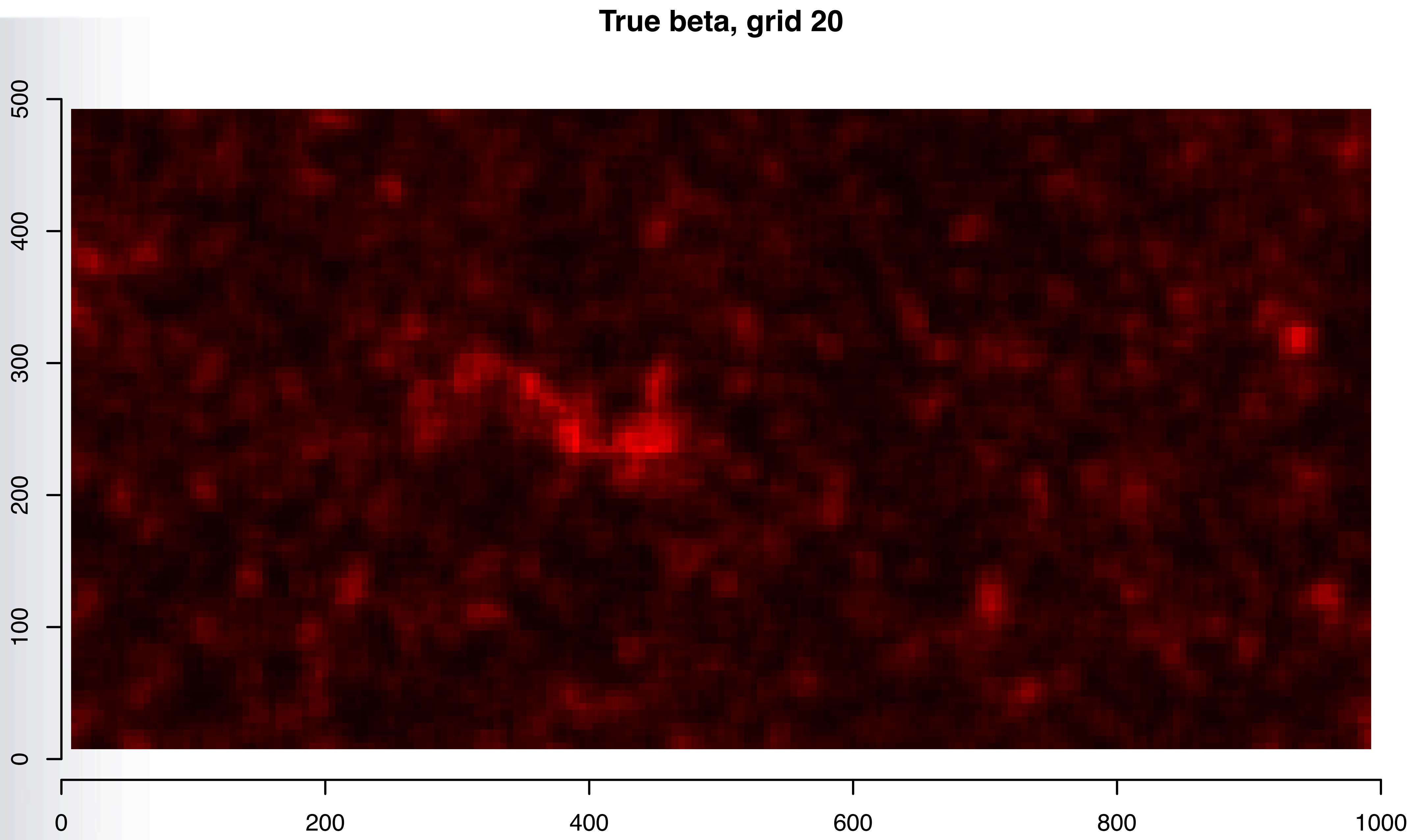
Value in terms of contribution to total diversity

- It identifies areas that contribute a lot to the total gamma diversity of the whole plot
- Which areas this encompasses varies depending on your meaning of diversity!

Temporal Beta Diversity

- Comparing a community at one timepoint to the “ecosystem” of that community measured at all timepoints

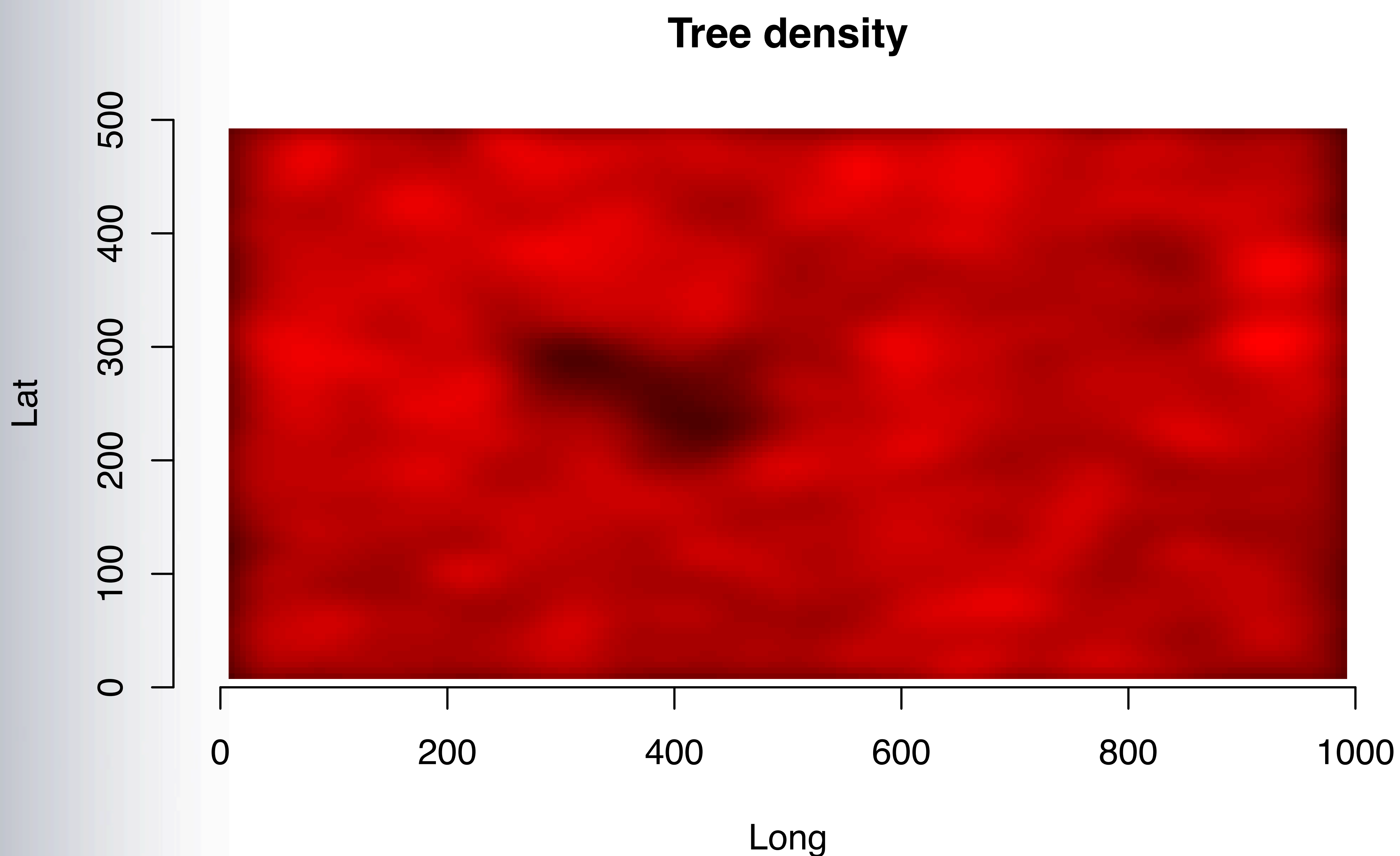
Temporal Beta Diversity



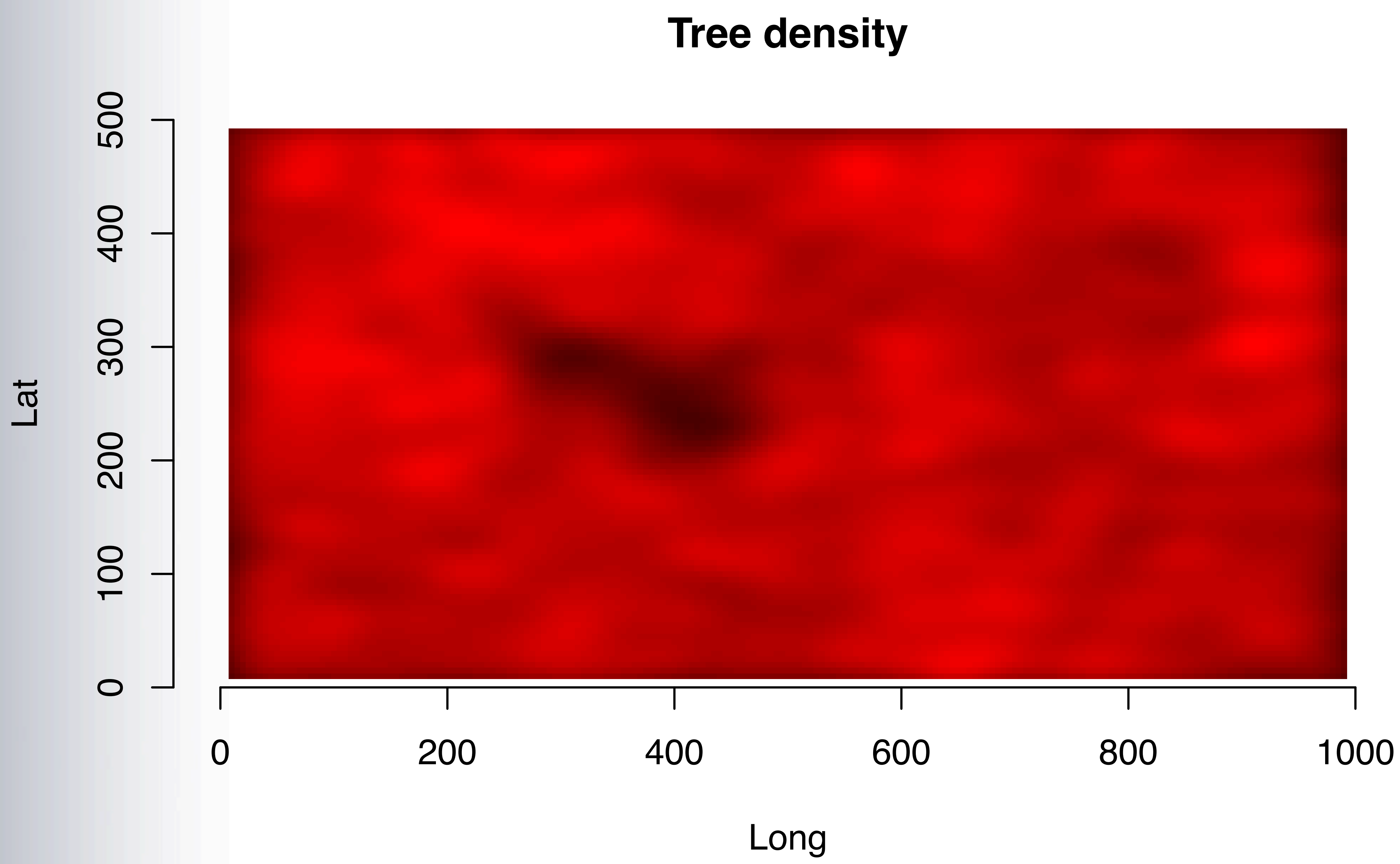
Temporal beta diversity

- One area has particularly high temporal beta diversity
  - and we've seen it before...

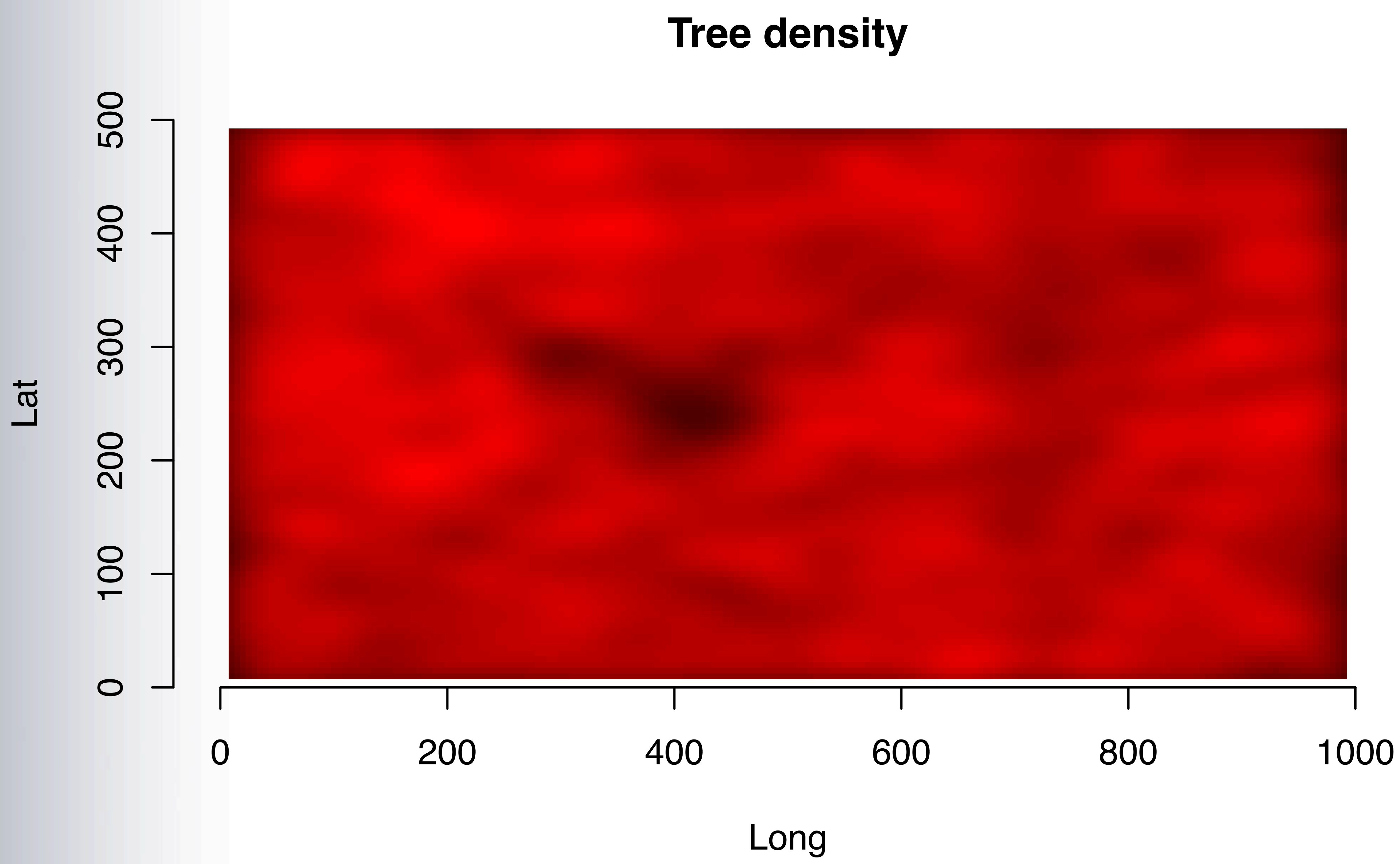
What's happening in this patch – 1981



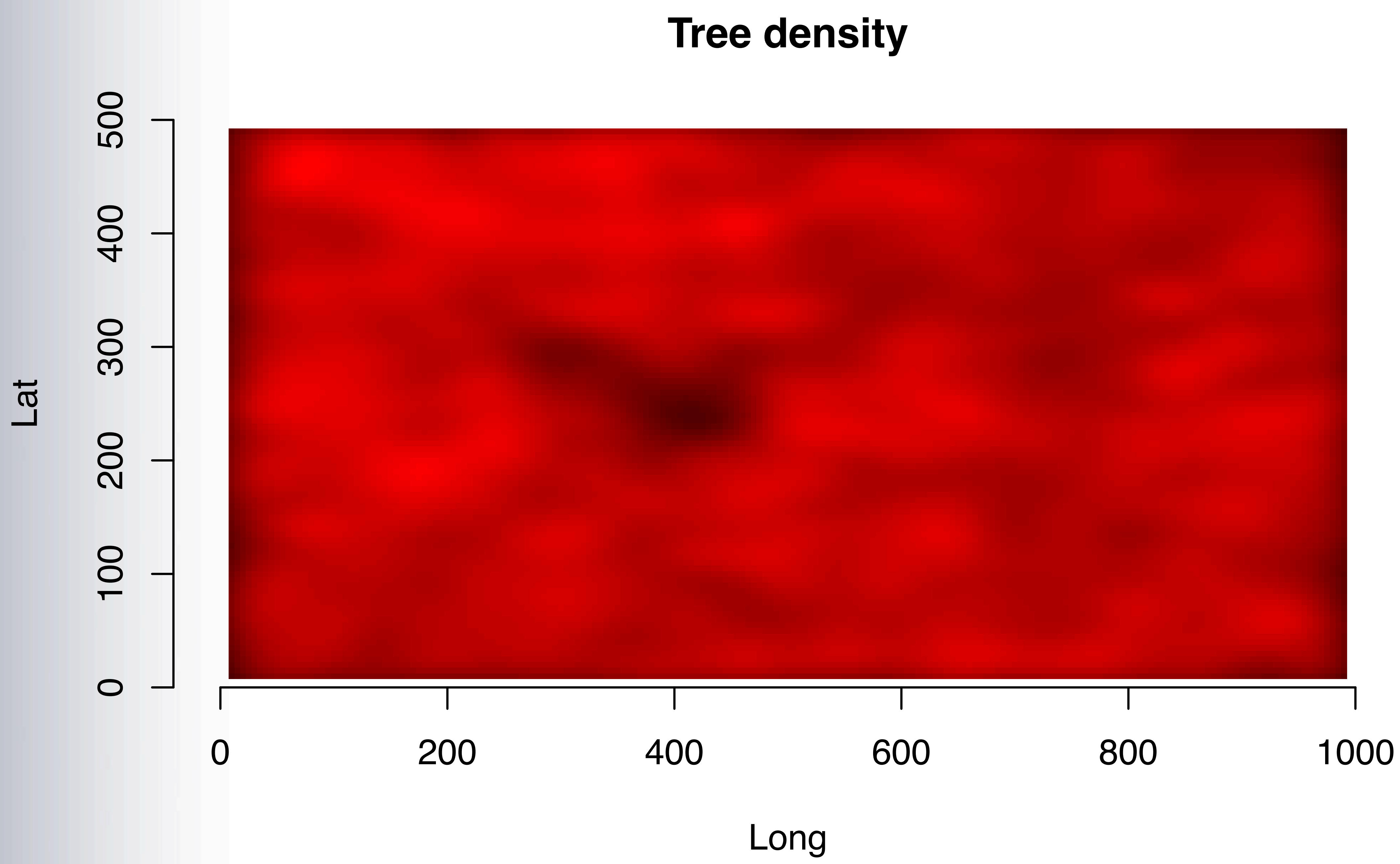
What's happening in this patch – 1985



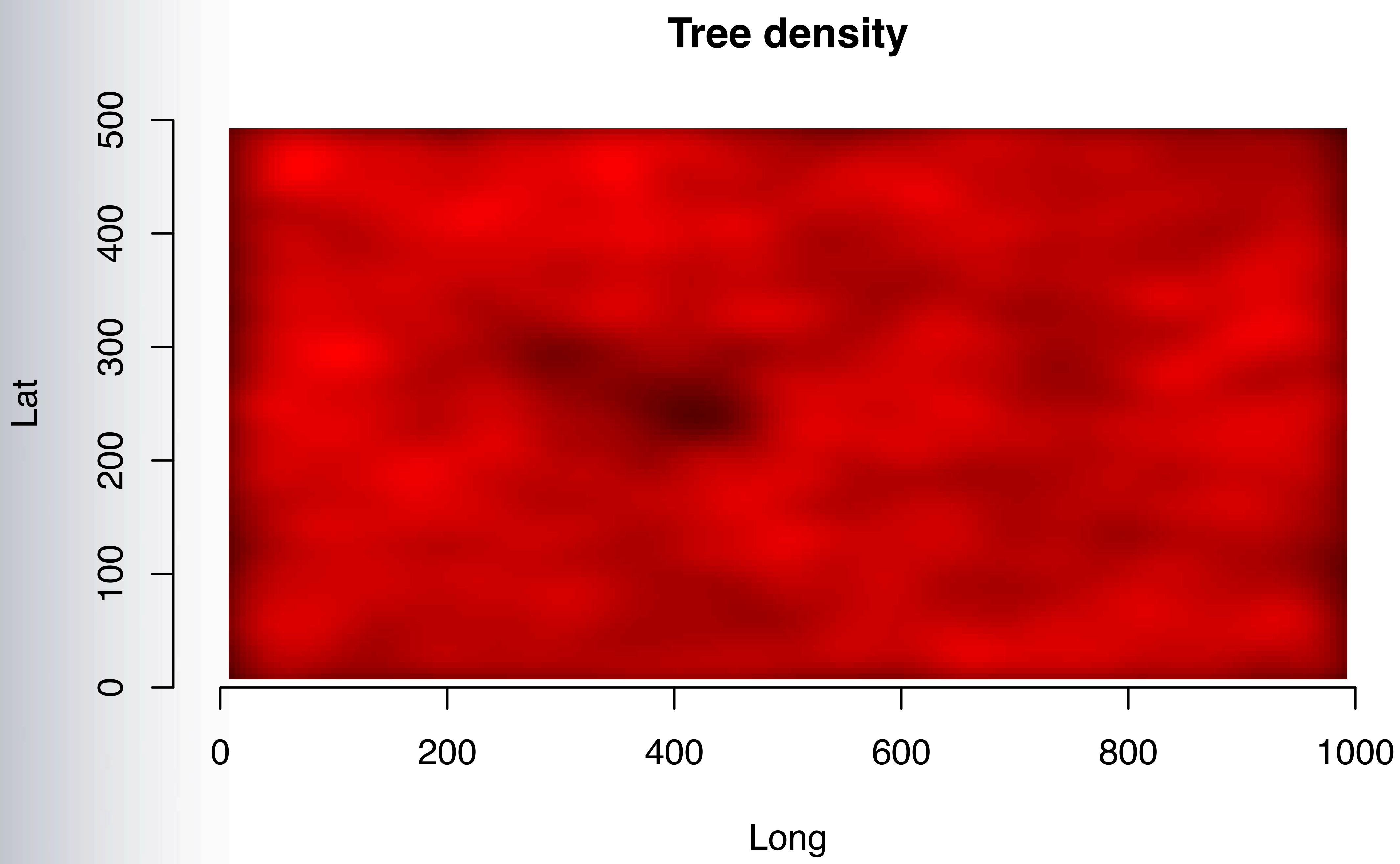
What's happening in this patch – 1990



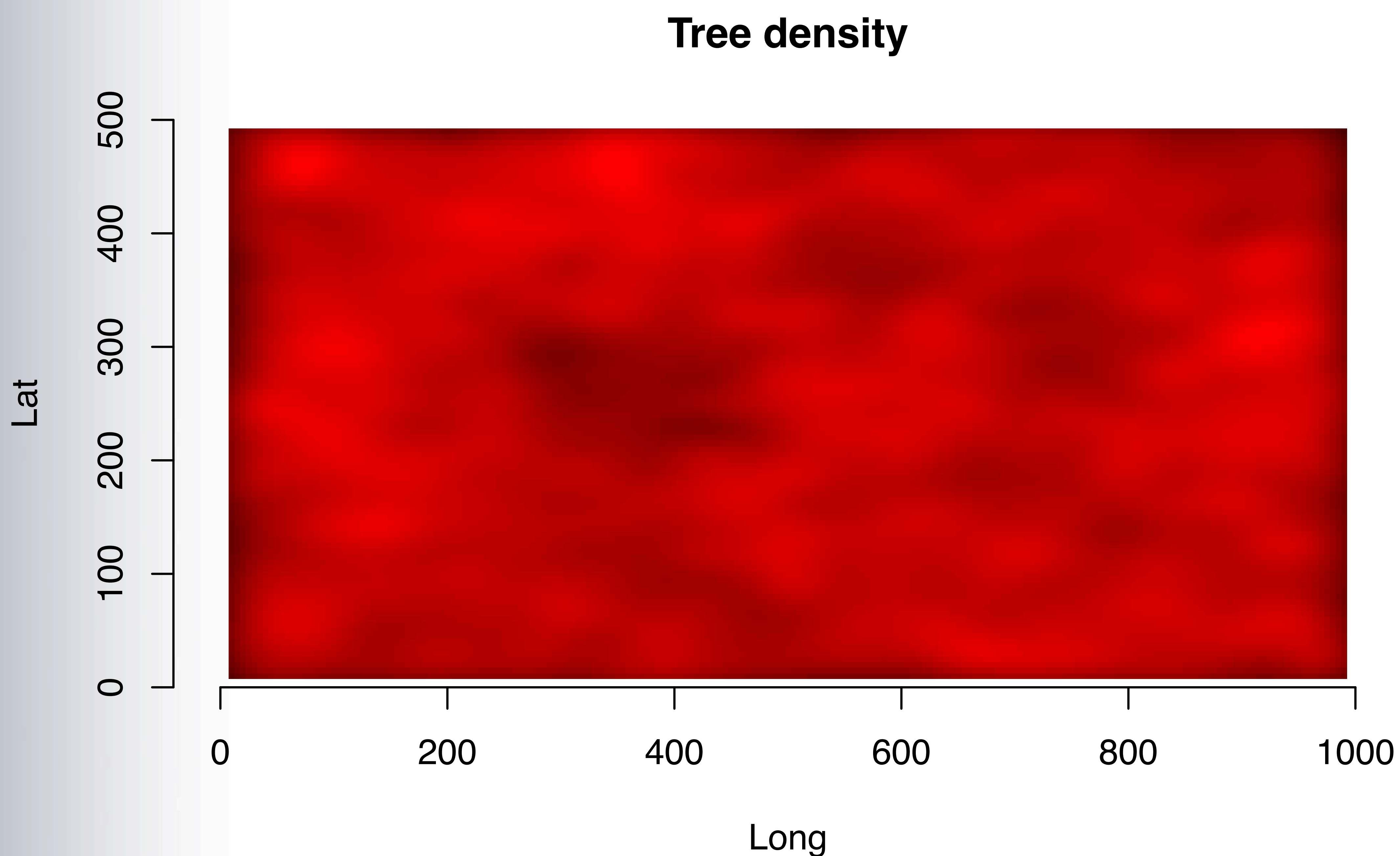
What's happening in this patch – 1995



What's happening in this patch – 2000



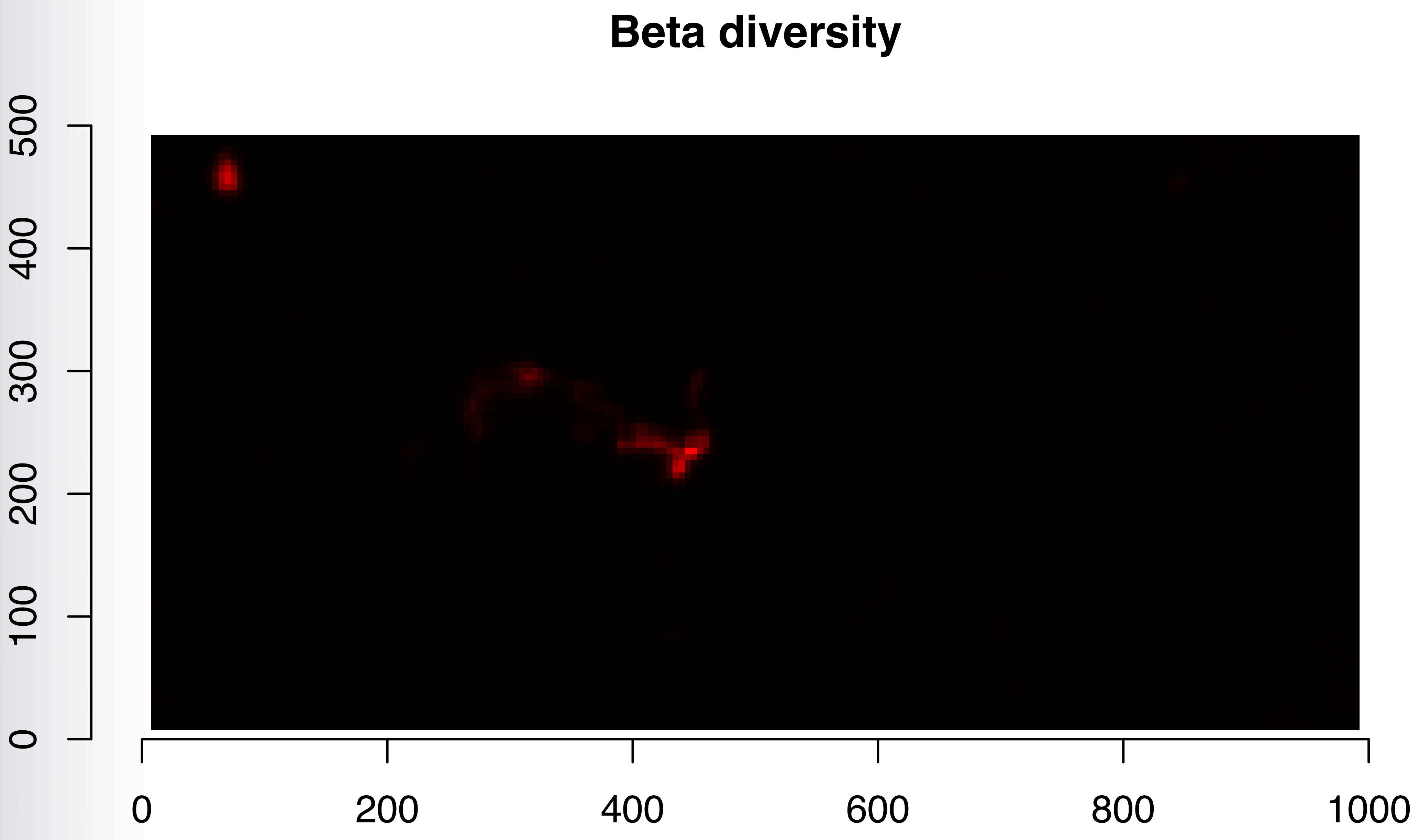
What's happening in this patch – 2005



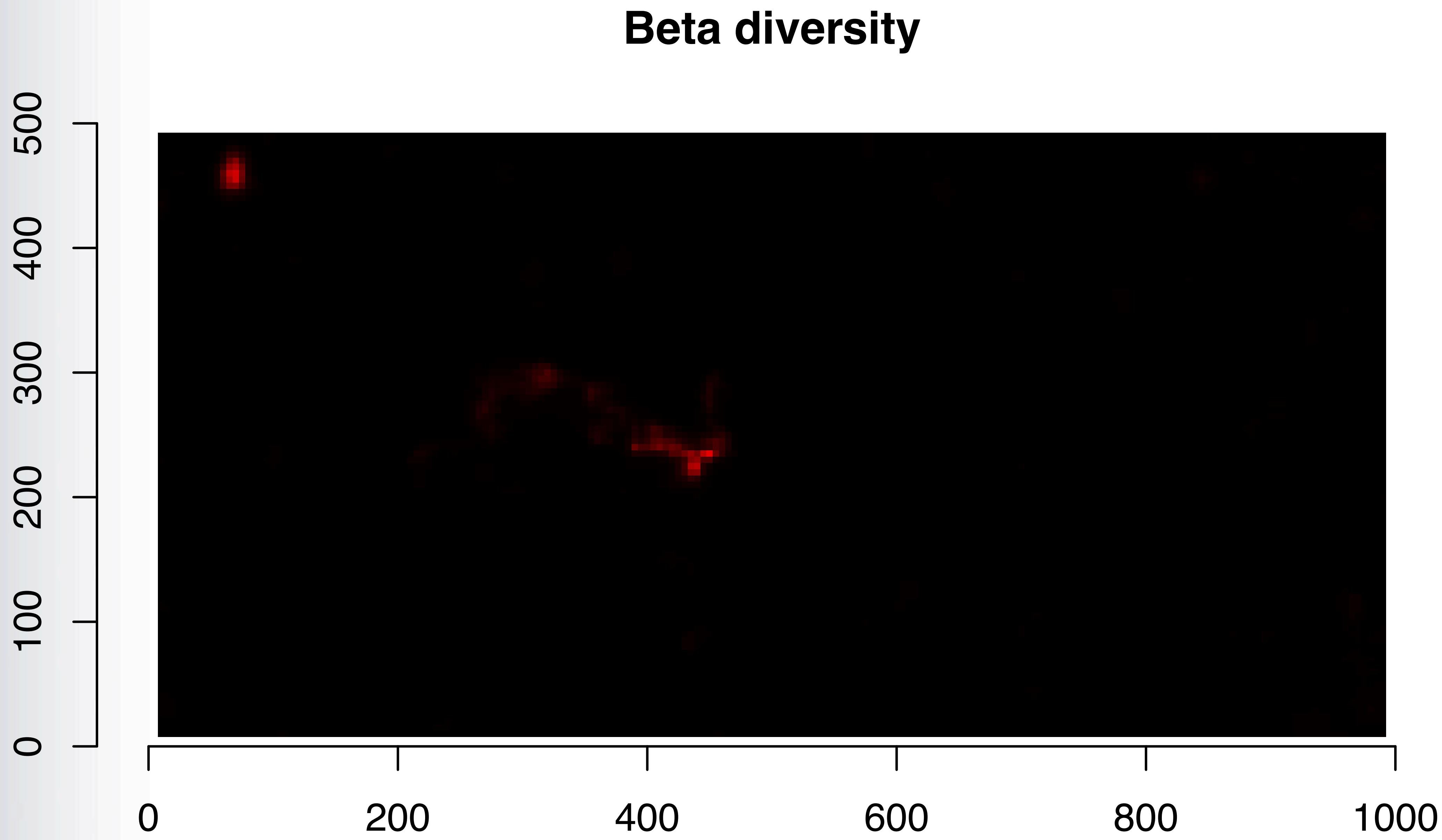
What's happening in this patch?

- The trees are filling in...

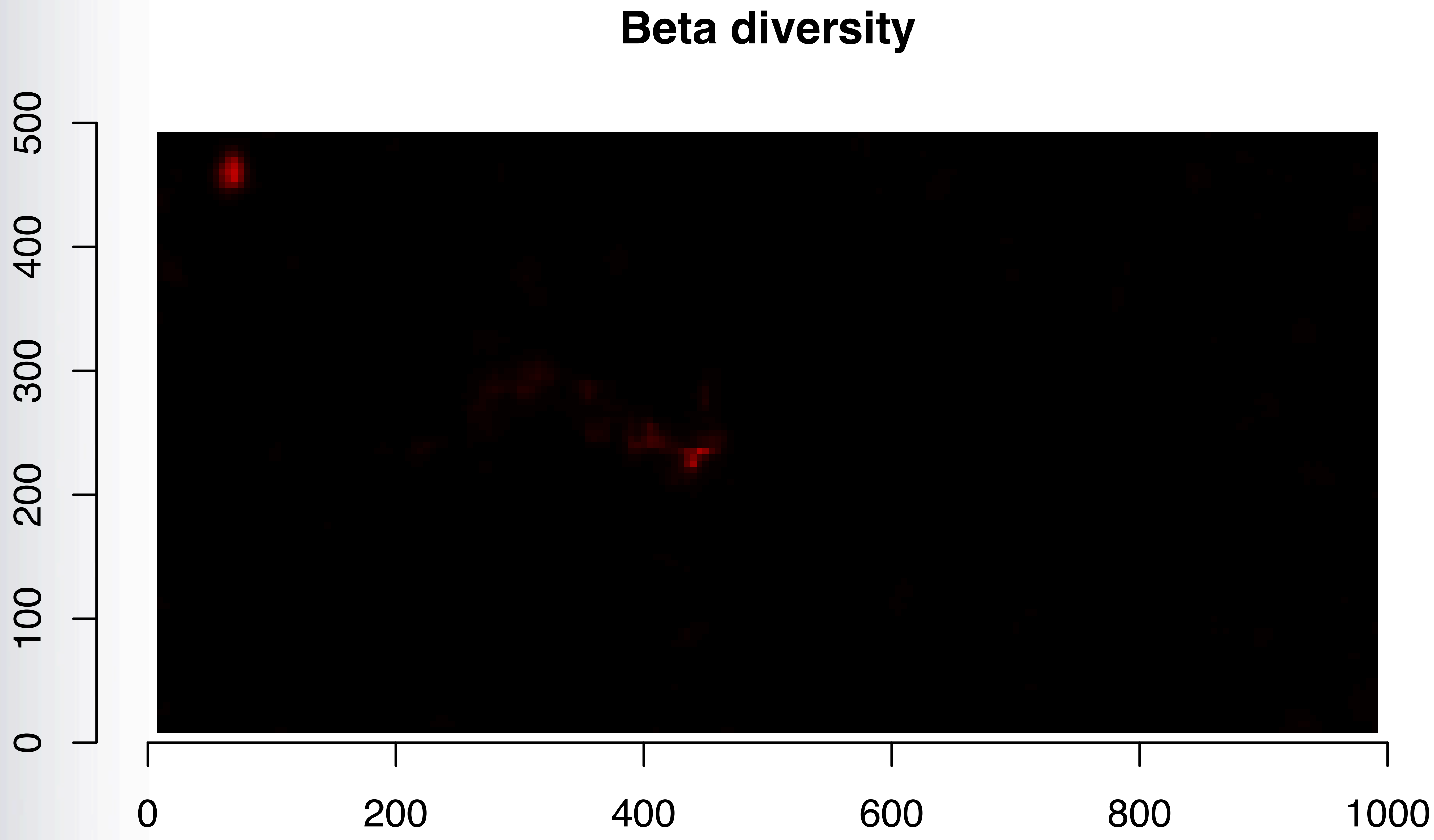
Revisiting Beta Diversity – 1981



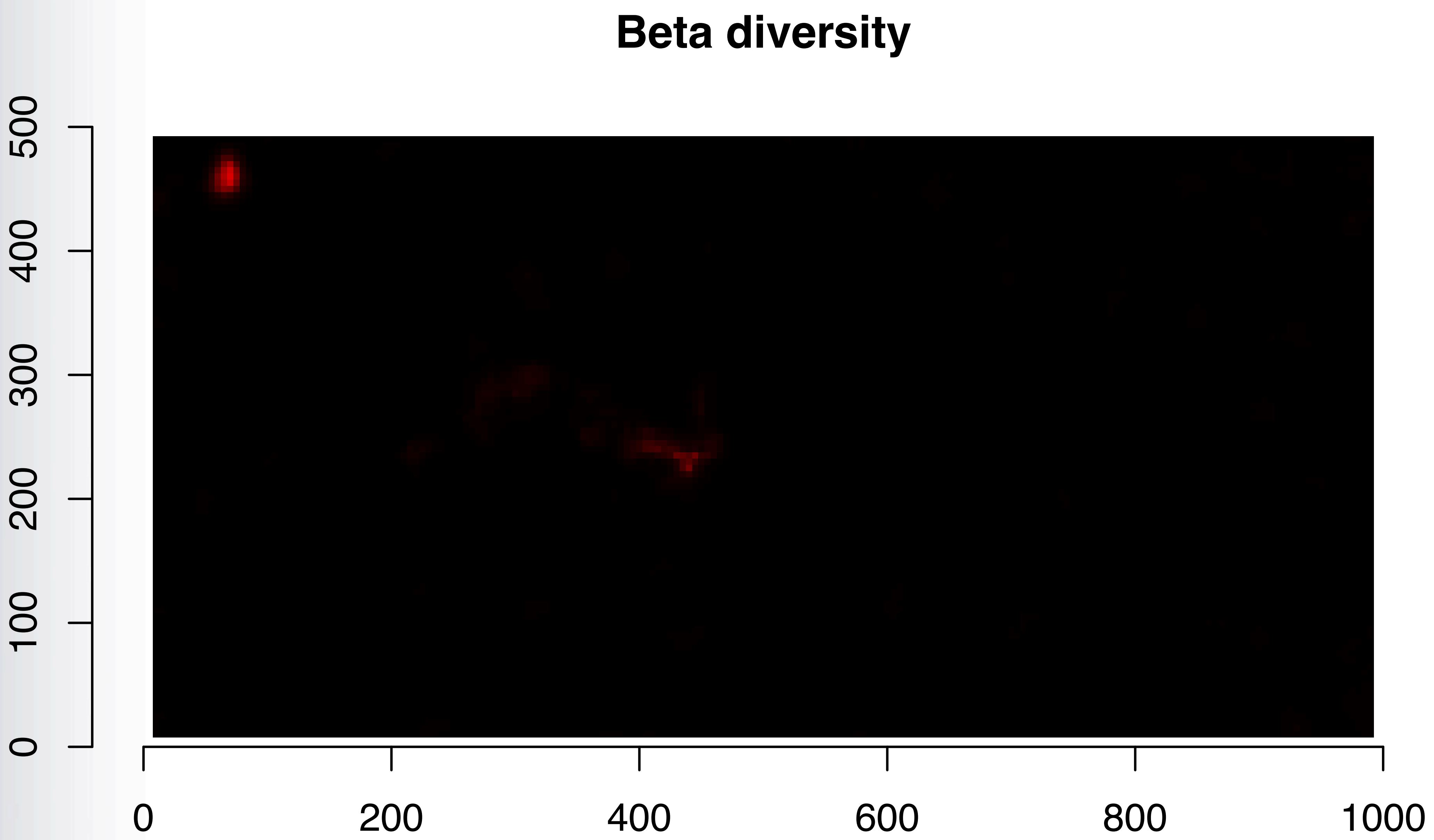
Revisiting Beta Diversity – 1985



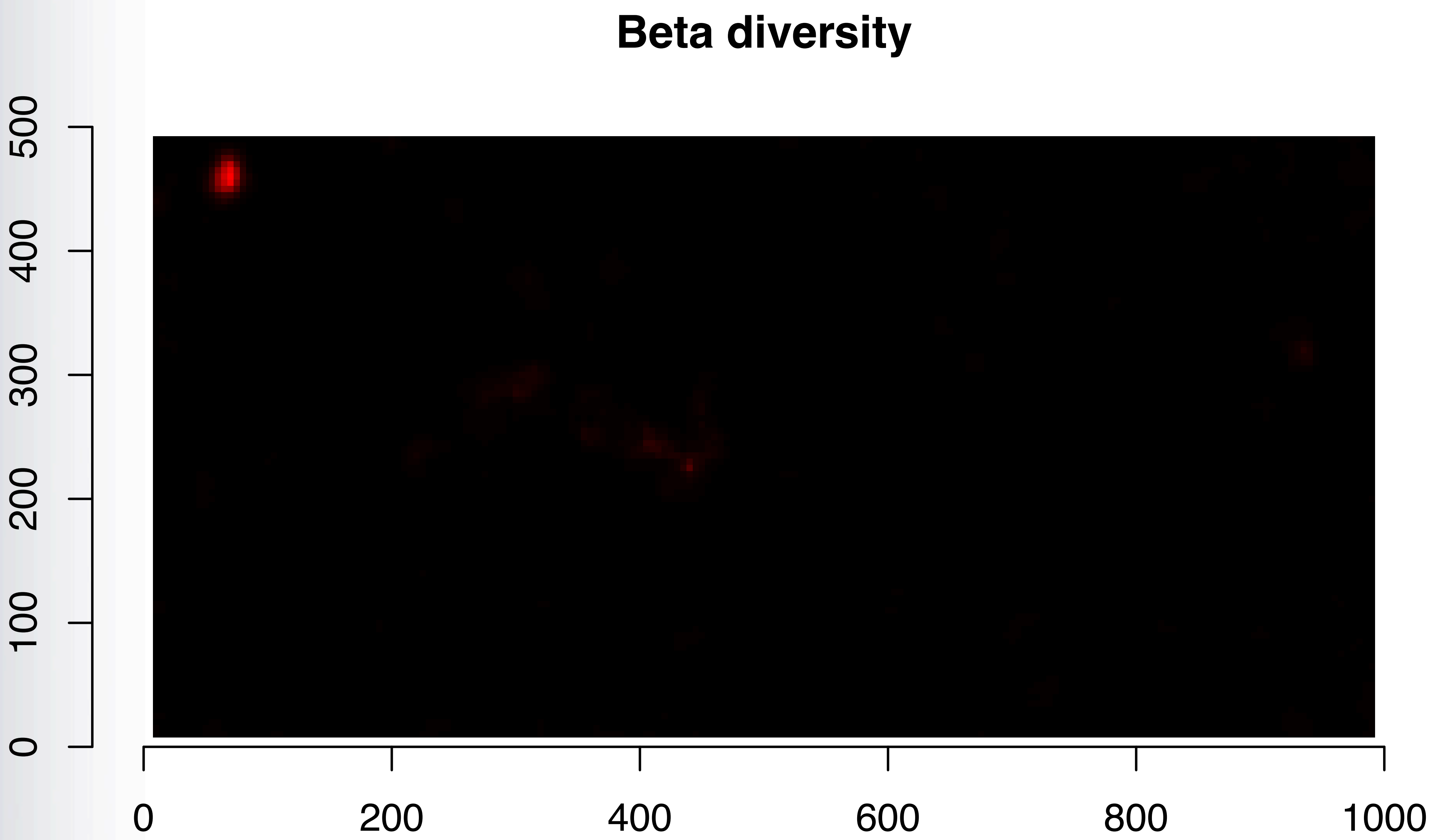
Revisiting Beta Diversity – 1990



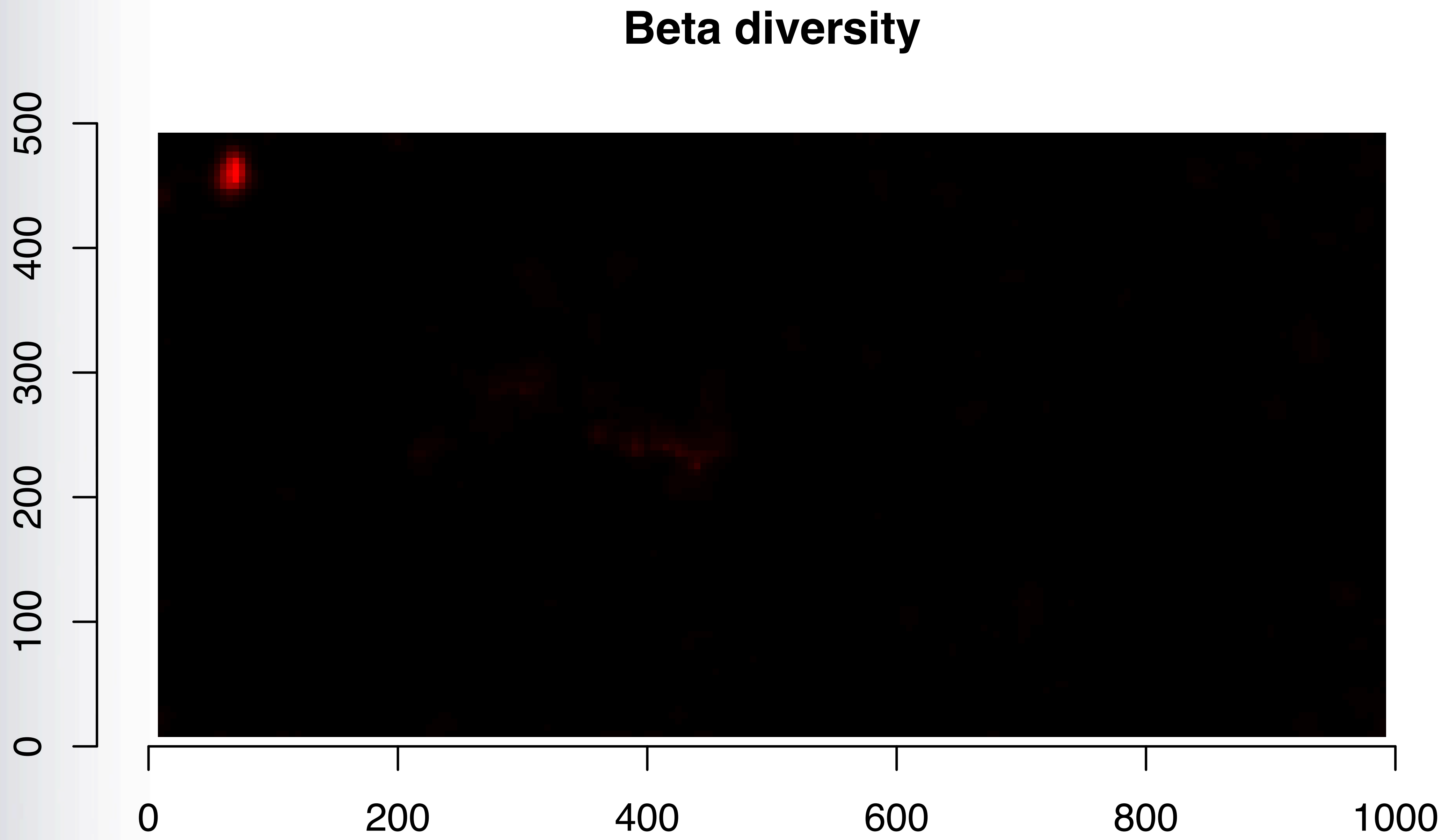
Revisiting Beta Diversity – 1995



Revisiting Beta Diversity – 2000



Revisiting Beta Diversity – 2005



Temporal beta diversity

- Correctly identifies an interesting area where there were few, but distinct, trees in the 1980s, but now the area has filled in with lots of more normal trees...

Conclusions

- We have a generalisation of existing measures of beta diversity that incorporates similarity
- We have a new concept of individual alpha, beta and gamma diversity, which tell us
  - which specific communities are most distinct
  - which contribute most to overall diversity
  - which are changing most over time
- We can use these to identify areas of interest and well as measuring overall diversity, turnover and beta diversity...

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