Package: spacc (via r-universe)

June 20, 2026

Title Fast Spatial Species Accumulation Curves

Version 0.8.3

Description High-performance spatial species accumulation curves using nearest-neighbor algorithms. Implements 'kNN' and 'kNCN' sampling methods with a 'C++' backend for speed. Supports Hill numbers (q=0,1,2), beta diversity partitioning (turnover/nestedness), coverage-based rarefaction and extrapolation, phylogenetic diversity (Faith's PD, mean pairwise distance, mean nearest taxon distance), functional diversity accumulation, diversity-area relationships (DAR), endemism-area curves, sampling-effort correction and fragmentation analysis, and species-area relationship (SAR) models based on extreme value theory (EVT). Multiple starting points (seeds) provide uncertainty quantification. Methods are described in 'Chao' et al. (2014) <doi:10.1890/13-0133.1>, 'Baselga' (2010) <doi:10.1111/j.1466-8238.2009.00490.x>, 'Chao' and 'Jost' (2012) <doi:10.1890/11-1952.1>, 'Faith' (1992) <doi:10.1016/0006-3207(92)91201-3>, 'Ma' (2018) <doi:10.1002/ece3.4526>, 'Borda-de-Agua' et al. (2025) <doi:10.1038/s41467-025-59239-7>, 'Hanski' et al. (2013) <doi:10.1073/pnas.1311190110>, and 'Jost' (2007) <doi:10.1890/06-1736.1>.

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Contents

`ace` *ACE Richness Estimator*

Description

Abundance-based Coverage Estimator (ACE) of total species richness (Chao & Lee 1992). Separates species into rare and abundant groups based on an abundance threshold.

Usage

```
ace(x, threshold = 10L)
```

Arguments

x	A site-by-species matrix (abundance data).
threshold	Integer. Abundance threshold separating rare from abundant species. Default 10.

Details

ACE partitions species into rare (abundance $\leq$ threshold) and abundant (abundance > threshold) groups. The estimate is:

$$S_{ACE} = S_{abund} + \frac{S_{rare}}{C_{ACE}} + \frac{f_1}{C_{ACE}}\gamma^2$$

where C_{ACE} is the sample coverage of rare species and γ^2 is the estimated coefficient of variation.

Value

An object of class `spacc_estimate`.

References

Chao, A. & Lee, S.M. (1992). Estimating the number of classes via sample coverage. Journal of the American Statistical Association, 87, 210-217.

See Also

`chao1()`, `chao2()`

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
ace(species)
```

`alphaDiversity` *Alpha Diversity (Per-Site)*

Description

Compute Hill numbers for each site individually.

Usage

```
alphaDiversity(x, q = c(0, 1, 2), coords = NULL)
```

Arguments

x	A site-by-species matrix (abundance data).
q	Numeric vector. Orders of diversity. Default c(0, 1, 2).
coords	Optional data.frame with columns x and y for spatial mapping. When provided, returns a spacc_alpha object with as_sf() and plot(type = "map") support.

Details

Alpha diversity represents local (within-site) diversity. For Hill numbers:

- q=0: Species richness
- q=1: Exponential of Shannon entropy
- q=2: Inverse Simpson concentration

Value

If coords is NULL, a data.frame with columns for each q value. If coords is provided, a spacc_alpha object.

References

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427-2439.

See Also

gammaDiversity() for regional diversity, diversityPartition() for full alpha-beta-gamma decomposition

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
alpha <- alphaDiversity(species, q = c(0, 1, 2))
head(alpha)

# Mean alpha diversity
colMeans(alpha)
```

---

analytical *Analytical Accumulation Methods*

Description

These methods compute expected species accumulation without simulation. They are faster but don't provide spatial information.

as_sf *Convert spacc_metrics to sf*

Description

Convert metrics to an sf object for spatial analysis and integration with the areaOfEffect package.

Usage

```
as_sf(x, crs = NULL)
```

Arguments

x	A spacc_metrics object.
crs	Coordinate reference system. Default NULL (no CRS). Use EPSG codes like 4326 for WGS84 or 32631 for UTM zone 31N.

Value

An sf object with POINT geometries and metric columns.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
metrics <- spaccMetrics(species, coords)
if (requireNamespace("sf", quietly = TRUE)) {
  metrics_sf <- as_sf(metrics)
}
```

autoplot.spacc *Autoplot Methods for spacc Objects*

Description

ggplot2::autoplot() methods for spacc objects. These are thin wrappers around the corresponding plot() methods, provided for ggplot2 integration.

Arguments

object	A spacc object.
...	Additional arguments passed to the corresponding plot() method.

Value

A ggplot2 object.

Examples

```
if (requireNamespace("ggplot2", quietly = TRUE)) {
  coords <- data.frame(x = runif(30), y = runif(30))
  species <- matrix(rbinom(30 * 15, 1, 0.3), nrow = 30)
  sac <- spacc(species, coords, n_seeds = 5, progress = FALSE)
  ggplot2::autoplot(sac)
}
```

---

betaDecay *Beta Distance-Decay*

Description

Compute the distance-decay of community similarity by fitting models to pairwise beta dissimilarity as a function of geographic distance.

Usage

```
betaDecay(
  x,
  coords,
  index = c("sorensen", "jaccard"),
  model = c("all", "exponential", "power", "linear"),
  distance = c("euclidean", "haversine"),
  n_bins = 50L,
  progress = TRUE
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance), or a spacc object (will use its stored coordinates).
coords	A data.frame with columns x and y, or a spacc_dist object.
index	Character. Dissimilarity index: "sorensen" (default) or "jaccard".
model	Character. Decay model to fit: "exponential", "power", "linear", or "all" (default). When "all", fits all three and selects the best by AIC.
distance	Character. Distance method: "euclidean" (default) or "haversine".
n_bins	Integer. Number of distance bins for binned means in plots. Default 50.
progress	Logical. Show progress messages? Default TRUE.

Details

Three decay models are available:

- **Exponential**: $\beta = 1 - a \cdot e^{-b \cdot d}$
- **Power**: $\beta = a \cdot d^b$
- **Linear**: $\beta = a + b \cdot d$

The half-life (exponential model) is the distance at which similarity decays to half its initial value: $d_{1/2} = \ln(2)/b$.

Value

An object of class `spacc_beta_decay` containing:

`pairs`	Data.frame with columns `distance`, `dissimilarity`, `site_i`, `site_j`
`fits`	Named list of fitted model objects
`best_model`	Name of best model by AIC
`half_life`	Distance at which similarity halves (exponential model only)
`coefficients`	Data.frame of model coefficients and AIC
`index`	Dissimilarity index used
`n_sites`	Number of sites
`n_pairs`	Number of pairwise comparisons

References

Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. Journal of Biogeography, 26, 867-878.

Morlon, H., Chuyong, G., Condit, R., et al. (2008). A general framework for the distance-decay of similarity in ecological communities. Ecology Letters, 11, 904-917.

See Also

`spaccBeta()` for spatial beta diversity accumulation, `distanceDecay()` for species similarity decay

Examples

```
coords <- data.frame(x = runif(30), y = runif(30))
species <- matrix(rbinom(30 * 20, 1, 0.3), nrow = 30)

bd <- betaDecay(species, coords)
print(bd)
plot(bd)
```

`bootstrap_richness` *Bootstrap Richness Estimator*

Description

Bootstrap estimator of total species richness (Smith & van Belle 1984). Uses species detection probabilities to estimate undetected species.

Usage

```
bootstrap_richness(x, n_boot = 200L)
```

Arguments

`x`	A site-by-species matrix (presence/absence or abundance). Automatically binarized.
`n_boot`	Integer. Number of bootstrap replicates for SE. Default 200.

Details

The bootstrap estimator is:

$$S_{boot} = S_{obs} + \sum_{i=1}^{S_{obs}} (1 - p_i)^n$$

where p_i is the proportion of sites where species i occurs.

Value

An object of class `spacc_estimate`.

References

Smith, E.P. & van Belle, G. (1984). Nonparametric estimation of species richness. Biometrics, 40, 119-129.

See Also

`jackknife()`, `chao2()`

Examples

```
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
bootstrap_richness(species, n_boot = 100)
```

c.spacc *Combine spacc Objects*

Description

Combine spacc Objects

Usage

```
## S3 method for class 'spacc'
c(...)
```

Arguments

...	Named spacc objects to combine into a grouped spacc.

Value

A grouped spacc object with per-group curves.

c.spacc_beta *Combine spacc_beta Objects*

Description

Combine multiple spacc_beta objects by stacking their curve matrices. All objects must have the same number of sites and index.

Usage

```
## S3 method for class 'spacc_beta'
c(...)
```

Arguments

...	spacc_beta objects to combine.

Value

A combined spacc_beta object with more seeds.

c.spacc_coverage *Combine spacc_coverage Objects*

Description

Combine multiple spacc_coverage objects by stacking their curve matrices. All objects must have the same number of sites.

Usage

```
## S3 method for class 'spacc_coverage'
c(...)
```

Arguments

...	spacc_coverage objects to combine.

Value

A combined spacc_coverage object with more seeds.

c.spacc_hill *Combine spacc_hill Objects*

Description

Combine multiple spacc_hill objects by stacking their curve matrices. All objects must have the same number of sites.

Usage

```
## S3 method for class 'spacc_hill'
c(...)
```

Arguments

...	spacc_hill objects to combine.

Value

A combined spacc_hill object with more seeds.

chao1 *Chao1 Richness Estimator*

Description

Estimate total species richness from abundance data using the Chao1 estimator (Chao 1984). Uses the number of singletons and doubletons to estimate undetected species.

Usage

```
chao1(x)
```

Arguments

x	A site-by-species matrix (abundance data). Columns are pooled across sites.

Details

The Chao1 estimator is:

$$S_{Chao1} = S_{obs} + \frac{f_1^2}{2f_2}$$

where f_1 is the number of singletons (species with total abundance 1) and f_2 is the number of doubletons (abundance 2).

When $f_2 = 0$, the bias-corrected form is used:

$$S_{Chao1} = S_{obs} + \frac{f_1(f_1 - 1)}{2}$$

Value

An object of class `spacc_estimate` with components:

estimator Name of the estimator (`"chao1"`)

estimate Estimated total richness

se Standard error of the estimate

lower Lower 95 percent confidence bound

upper Upper 95 percent confidence bound

S_obs Observed species richness

details List with `f1` (singletons) and `f2` (doubletons)

References

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics, 11, 265-270.

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. Biometrics, 43, 783-791.

See Also

chao2() for incidence-based estimation, ace() for abundance-based coverage estimator

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
chao1(species)
```

---

chao2 *Chao2 Richness Estimator*

Description

Estimate total species richness from incidence (presence/absence) data using the Chao2 estimator (Chao 1987).

Usage

```
chao2(x)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance). Automatically binarized.

Details

The Chao2 estimator is the incidence-based analogue of Chao1:

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

where Q_1 is the number of uniques (species found at exactly 1 site) and Q_2 is the number of duplicates (species found at exactly 2 sites).

Value

An object of class `spacc_estimate`.

References

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. Biometrics, 43, 783-791.

See Also

chao1() for abundance-based estimation

Examples

```
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
chao2(species)
```

`coleman` *Coleman Expected Accumulation*

Description

Compute the expected species accumulation curve using the Coleman method (Coleman et al. 1982). This is an analytical formula, no simulation needed.

Usage

```
coleman(x)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance).

Value

A data.frame with columns: sites, expected, sd

References

Coleman, B.D., Mares, M.A., Willig, M.R. & Hsieh, Y.H. (1982). Randomness, area, and species richness. Ecology, 63, 1121-1133.

`collector` *Collector's Curve*

Description

Compute the species accumulation curve in the order sites appear in the data (no randomization). Useful for understanding how data was collected.

Usage

```
collector(x)
```

Arguments

x	A site-by-species matrix.

Value

A data.frame with columns: sites, species

compare *Compare Two Accumulation Curves*

Description

Test whether two species accumulation curves differ significantly.

Usage

```
compare(
  x,
  y,
  method = c("permutation", "bootstrap", "auc"),
  normalize = FALSE,
  n_perm = 999L,
  ...
)
```

Arguments

x	A spacc object.
y	A spacc object.
method	Character. Comparison method: "permutation" (default), "bootstrap", or "auc" (area under curve difference).
normalize	Logical. If TRUE, each seed's curve is divided by its final value before computing AUC, so that curves are compared on a [0, 1] scale (proportion of total species). This compares the **shape** of accumulation rather than absolute species counts. Default FALSE.
n_perm	Integer. Number of permutations/bootstrap replicates. Default 999.
...	Additional arguments passed to comparison methods.

Value

An object of class spacc_comp containing:

x_name, y_name	Names of compared objects
auc_diff	Difference in area under curve
p_value	P-value from permutation test
saturation_diff	Difference in saturation points
method	Comparison method used
normalized	Whether curves were normalized before comparison

References

Colwell, R.K., Mao, C.X. & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology, 85, 2717-2727.

Gotelli, N.J. & Colwell, R.K. (2011). Estimating species richness. In: Biological Diversity: Frontiers in Measurement and Assessment, pp. 39-54. Oxford University Press.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
sp_a <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sp_b <- matrix(rbinom(50 * 30, 1, 0.5), nrow = 50)

sac_a <- spacc(sp_a, coords, n_seeds = 10)
sac_b <- spacc(sp_b, coords, n_seeds = 10)
comp <- compare(sac_a, sac_b)
print(comp)
```

`compareModels` *Compare Multiple SAR Models*

Description

Fit all (or a subset of) asymptotic species-area models and compare them using AIC, BIC, delta-AIC, and Akaike weights.

Usage

```
compareModels(
  object,
 models = c("michaelis-menten", "lomolino", "asymptotic", "weibull", "logistic", "evt"),
  ...
)
```

Arguments

`object`	A spacc object.
`models`	Character vector of models to fit. Defaults to all six: `"michaelis-menten"`, `"lomolino"`, `"asymptotic"`, `"weibull"`, `"logistic"`, `"evt"`.
`...`	Additional arguments passed to `extrapolate()`.

Value

An object of class `spacc_model_compare` containing:

`table`	Data frame with model comparison statistics
`fits`	Named list of `spacc_fit` objects
`best_model`	Name of the best model by AIC
`data`	Mean-curve data frame used for fitting
`spacc`	Original spacc object

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, coords)
cm <- compareModels(sac)
print(cm)
```

`completenessProfile` *Sample Completeness Profile*

Description

Compute the ratio of observed to estimated diversity across diversity orders, measuring how complete a sample is at each level of the Hill number spectrum.

Usage

```
completenessProfile(x, q = seq(0, 2, by = 0.2), coords = NULL)
```

Arguments

`x`	A site-by-species matrix (abundance data).
`q`	Numeric vector. Orders of diversity to evaluate. Default `seq(0, 2, by = 0.2)`.
`coords`	Optional data.frame with columns `x` and `y` for spatial mapping. When provided, enables `plot(type = "map")` and `as_sf()`.

Details

Sample completeness at order q is:

$$C_q = \frac{D_q^{obs}}{D_q^{est}}$$

where D_q^{obs} is the observed Hill number and D_q^{est} is the estimated asymptotic Hill number.

Completeness near 1 means the sample captures most of the true diversity at that order. Completeness typically increases with q because dominant species are detected early.

Asymptotic estimators used:

- q = 0: Chao1 estimator
- q = 1: Chao & Jost (2015) entropy estimator
- q = 2: Inverse Simpson estimator with bias correction
- Other q: Interpolated between adjacent integer estimates

When `coords` is provided, per-site completeness is computed by treating each site's abundance vector as an independent sample.

Value

An object of class `spacc_completeness` containing:

`completeness`	Named numeric vector of completeness ratios per q
`observed`	Named numeric vector of observed Hill numbers per q
`estimated`	Named numeric vector of estimated asymptotic Hill numbers per q
`per_site`	Matrix of per-site completeness (sites x q values), or `NULL`
`q`	Vector of diversity orders
`coords`	Coordinates if provided
`n_sites`	Number of sites
`n_species`	Number of species

References

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93, 2533-2547.

Chao, A. & Jost, L. (2015). Estimating diversity and entropy profiles via discovery rates of new species. Methods in Ecology and Evolution, 6, 873-882.

See Also

`diversityProfile()` for observed diversity profiles, `chao1()` for richness estimation

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
comp <- completenessProfile(species)
print(comp)


plot(comp)
```

dar *Diversity-Area Relationship (DAR)*

Description

Extend the classic species-area relationship (SAR) to a diversity-area relationship using Hill numbers of any order q. Instead of plotting species richness vs. sites, this plots effective diversity vs. cumulative area.

Usage

```
dar(
  x,
  coords,
  q = c(0, 1, 2),
  n_seeds = 50L,
  method = "knn",
  area_method = c("convex_hull", "voronoi", "count"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix (abundance data recommended).
coords	A data.frame with columns x and y, or a spacc_dist object.
q	Numeric vector. Diversity orders. Default c(0, 1, 2).
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method. Default "knn".
area_method	Character. How to estimate cumulative area: "voronoi" (Voronoi tessellation, requires sf), "convex_hull" (convex hull of accumulated sites, requires sf), or "count" (use site count as proxy, no dependencies). Default "convex_hull".
distance	Character. Distance method. Default "euclidean".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.

Details

The DAR (Ma, 2018) generalizes the SAR by replacing species richness (q=0) with Hill numbers of any order. This reveals how different facets of diversity scale with area:

- q=0 (richness) recovers the classic SAR
- q=1 (Shannon) shows how common species diversity scales
- q=2 (Simpson) shows how dominant species diversity scales

Value

An object of class `spacc_dar` containing:

`hill`	A `spacc_hill` object with diversity curves
`area`	Matrix of cumulative areas (n_seeds x n_sites)
`q`	Diversity orders used
`area_method`	Method used for area estimation

References

Ma, Z.S. (2018). DAR (diversity-area relationship): extending classic SAR for biodiversity and biogeography analyses. Ecology and Evolution, 8, 10023-10038.

Arrhenius, O. (1921). Species and area. Journal of Ecology, 9, 95-99.

See Also

`spaccHill()`, `extrapolate()`

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rpois(50 * 30, 2), nrow = 50)

dar <- dar(species, coords, q = c(0, 1, 2))
plot(dar)
```

`distanceDecay` *Distance-Decay Analysis*

Description

Analyze how species richness changes with distance from focal points.

Usage

```
distanceDecay(
  x,
  coords,
  n_seeds = 50L,
  breaks = NULL,
  distance = c("euclidean", "haversine"),
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix.
coords	A data.frame with x and y columns.
n_seeds	Integer. Number of focal points.
breaks	Numeric vector. Distance thresholds. Default auto-calculated.
distance	Character. Distance method.
progress	Logical. Show progress?
seed	Integer. Random seed.

Value

An object of class spacc_decay with distance-species relationships.

References

Nekola, J.C. & White, P.S. (1999). The distance decay of similarity in biogeography and ecology. Journal of Biogeography, 26, 867-878.

Soininen, J., McDonald, R. & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. Ecography, 30, 3-12.

---

distances *Compute Distance Matrix*

Description

Pre-compute pairwise distances between sites for reuse across multiple spacc() calls. Supports sf objects with accurate geodesic distances for global-scale studies.

Usage

```
distances(x, method = NULL, fun = NULL, which = NULL)
```

Arguments

x	Site locations. Can be: • A data.frame with columns x and y • An sf object with POINT geometries • An sfc_POINT object
method	Character. Distance method: • "euclidean": Euclidean distance (for projected coordinates) • "haversine": Great-circle distance (for lat/lon, fast approximation • "geodesic": Accurate ellipsoidal distance via sf/S2 (for global scale) Default is auto-detected from CRS when using sf objects.
fun	Optional custom distance function. Must take two coordinate vectors (x, y) and return a distance matrix. Overrides method.
which	For sf objects, column name containing the geometry. Default uses active geometry.

Details

For continental and global-scale studies, use sf objects with geographic CRS (e.g., EPSG:4326). The function will automatically use accurate geodesic distances via the S2 spherical geometry library.

For smaller study areas with projected coordinates (UTM, etc.), Euclidean distance is appropriate and faster.

Value

An object of class spacc_dist containing the distance matrix with coordinates stored as an attribute.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
d <- distances(coords)

# Reuse for multiple analyses
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, d)
```

`diversityPartition` *Alpha-Beta-Gamma Diversity Partitioning*

Description

Decompose regional (gamma) diversity into local (alpha) and turnover (beta) components using multiplicative partitioning of Hill numbers.

Usage

```
diversityPartition(x, q = c(0, 1, 2), weights = "equal", coords = NULL)
```

Arguments

`x`	A site-by-species matrix (abundance data).
`q`	Numeric vector. Orders of diversity. Default `c(0, 1, 2)`.
`weights`	Character or numeric. Site weights for alpha calculation: • `"equal"`: Equal weights (default) • `"proportional"`: Weights proportional to site abundance • Numeric vector of custom weights
`coords`	Optional data.frame with columns `x` and `y` for spatial mapping. When provided, enables `as_sf()` and `plot(type = "map")`.

Details

This function implements Jost (2007) multiplicative partitioning:

$$\gamma = \alpha \times \beta$$

Where:

- **Alpha**: Mean effective number of species per site
- **Beta**: Effective number of distinct communities (1 = all identical, n_sites = all completely different)
- **Gamma**: Total effective number of species in the region

Beta diversity is interpreted as the effective number of communities:

- Beta = 1: All sites have identical composition
- Beta = n_sites: Sites share no species

Value

An object of class `spacc_partition` containing:

`alpha`	Mean alpha diversity (effective number of species per site)
`beta`	Beta diversity (effective number of communities)
`gamma`	Gamma diversity (regional species pool)
`q`	Orders of diversity
`n_sites`	Number of sites
`n_species`	Total species count

References

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427-2439.

Chao, A., Chiu, C.H. & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annual Review of Ecology, Evolution, and Systematics, 45, 297-324.

See Also

`alphaDiversity()`, `gammaDiversity()`, `spaccBeta()` for spatial beta diversity accumulation

Examples

```
# Simulated community data
species <- matrix(rpois(50 * 30, 2), nrow = 50)

# Partition diversity
part <- diversityPartition(species, q = c(0, 1, 2))
print(part)

# Beta near 1 = homogeneous region
# Beta near n_sites = heterogeneous region
```

`diversityProfile` *Diversity Profile*

Description

Compute Hill numbers across a continuous range of diversity orders (q), producing a diversity profile for each site and the regional pool.

Usage

```
diversityProfile(
  x,
  q = seq(0, 3, by = 0.1),
  type = c("both", "per_site", "regional"),
  coords = NULL
)
```

Arguments

x	A site-by-species matrix (abundance data).
q	Numeric vector. Orders of diversity to evaluate. Default `seq(0, 3, by = 0.1)`.
type	Character. What to compute: `"per_site"` (per-site profiles), `"regional"` (pooled gamma), or `"both"` (default).
coords	Optional data.frame with columns `x` and `y` for spatial mapping. When provided, enables `plot(type = "map")`.

Details

A diversity profile plots effective number of species as a function of the order q. The key property is that Hill numbers are non-increasing in q: $D_q \geq D_{q'}$ for $q \leq q'$.

- q = 0: Species richness (insensitive to abundance)
- q = 1: Exponential of Shannon entropy (all species weighted equally by their proportional abundance)
- q = 2: Inverse Simpson concentration (emphasizes dominant species)
- q > 2: Increasingly dominated by common species

Value

An object of class `spacc_profile` containing:

per_site	Matrix of per-site diversity (sites x q values), or `NULL`
regional	Named numeric vector of gamma diversity per q, or `NULL`
q	Vector of diversity orders used
coords	Coordinates if provided
n_sites	Number of sites
n_species	Number of species

References

Leinster, T. & Cobbold, C.A. (2012). Measuring diversity: the importance of species similarity. Ecology, 93, 477-489.

Chao, A., Chiu, C.H. & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annual Review of Ecology, Evolution, and Systematics, 45, 297-324.

See Also

alphaDiversity() for per-site values at specific q, gammaDiversity() for regional diversity, evenness() for evenness profiles

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
prof <- diversityProfile(species)
print(prof)


plot(prof)
```

---

diversityProfileFunc *Functional Diversity Profile*

Description

Compute functional Hill numbers (Leinster & Cobbold 2012) across a continuous range of diversity orders (q), producing a functional diversity profile based on trait similarity.

Usage

```
diversityProfileFunc(
  x,
  traits,
  q = seq(0, 3, by = 0.1),
  type = c("both", "per_site", "regional"),
  dist_method = c("euclidean", "gower"),
  normalize = TRUE,
  coords = NULL
)
```

Arguments

x	A site-by-species matrix (abundance data). Column names must match row names in traits.
traits	A data.frame of species traits. Row names must match column names in x.
q	Numeric vector. Orders of diversity. Default seq(0, 3, by = 0.1).
type	Character. What to compute: "per_site", "regional", or "both" (default).
dist_method	Character. Distance method for trait matrix: "euclidean" (default) or "gower".
normalize	Logical. Normalize distances to [0, 1]? Default TRUE.
coords	Optional data.frame with x and y for spatial mapping.

Details

Functional Hill numbers (Leinster & Cobbold 2012) incorporate trait similarity via a similarity matrix Z = 1 - D. When all species are maximally dissimilar (Z = identity), this reduces to standard Hill numbers.

Value

An object of class `spacc_profile` with `$profile_type = "functional"`.

References

Leinster, T. & Cobbold, C.A. (2012). Measuring diversity: the importance of species similarity. Ecology, 93, 477-489.

See Also

`diversityProfile()` for taxonomic profiles, `diversityProfilePhylo()` for phylogenetic profiles

Examples

```
species <- matrix(rpois(20 * 10, 2), nrow = 20,
                  dimnames = list(NULL, paste0("sp", 1:10)))
traits <- data.frame(
  body_size = rnorm(10), diet = rnorm(10),
  row.names = paste0("sp", 1:10)
)
prof <- diversityProfileFunc(species, traits)
print(prof)
```

---

diversityProfilePhylo *Phylogenetic Diversity Profile*

Description

Compute phylogenetic Hill numbers (Chao et al. 2010) across a continuous range of diversity orders (q), producing a phylogenetic diversity profile.

Usage

```
diversityProfilePhylo(
  x,
  tree,
  q = seq(0, 3, by = 0.1),
  type = c("both", "per_site", "regional"),
  coords = NULL
)
```

Arguments

x	A site-by-species matrix (abundance data). Column names must match tip labels in the phylogeny.
tree	An ape::phylo object. Tips must include all species in x.
q	Numeric vector. Orders of diversity. Default seq(0, 3, by = 0.1).
type	Character. What to compute: "per_site", "regional", or "both" (default).
coords	Optional data.frame with x and y for spatial mapping.

Details

Phylogenetic Hill numbers (Chao et al. 2010) weight branches by their evolutionary distance. At q=0 this approximates normalized Faith's PD. Higher q values increasingly emphasize common lineages.

Value

An object of class spacc_profile with $profile_type = "phylogenetic".

References

Chao, A., Chiu, C.H. & Jost, L. (2010). Phylogenetic diversity measures based on Hill numbers. Philosophical Transactions of the Royal Society B, 365, 3599-3609.

See Also

diversityProfile() for taxonomic profiles, diversityProfileFunc() for functional profiles

Examples

```
if (requireNamespace("ape", quietly = TRUE)) {
  species <- matrix(rpois(20 * 10, 2), nrow = 20,
                    dimnames = list(NULL, paste0("sp", 1:10)))
  tree <- ape::rcoal(10, tip.label = paste0("sp", 1:10))
  prof <- diversityProfilePhylo(species, tree)
  print(prof)
}
```

---

evenness *Evenness Profiles*

Description

Compute species evenness across sites using Hill-based, Pielou, or Simpson evenness measures.

Usage

```
evenness(
  x,
  q = seq(0.1, 3, by = 0.1),
  type = c("hill", "pielou", "simpson"),
  coords = NULL
)
```

Arguments

x	A site-by-species matrix (abundance data).
q	Numeric vector. Orders of diversity for Hill evenness. Default `seq(0.1, 3, by = 0.1)`. Note: q = 0 is excluded by default because Hill evenness at q = 0 is trivially S/S = 1.
type	Character. Evenness type: `"hill"` (Hill evenness E_q = D_q / D_0, default), `"pielou"` (Pielou's J = log(D_1) / log(S)), or `"simpson"` (Simpson evenness = (1/D_2) / S).
coords	Optional data.frame with columns x and y for spatial mapping. When provided, enables `plot(type = "map")`.

Details

All evenness measures are bounded in $[0, 1]$:

- 0 = maximally uneven (one dominant species)
- 1 = perfectly even (all species equally abundant)

Hill evenness (Jost 2010):

$$E_q = D_q / D_0$$

This divides the effective number of species at order q by species richness.

Pielou's J (Pielou 1966):

$$J = \frac{\log(D_1)}{\log(S)} = \frac{H'}{\log(S)}$$

Simpson evenness:

$$E_{1/D} = \frac{1}{D_2 \cdot S}$$

Value

An object of class `spacc_evenness` containing:

per_site	Matrix or vector of per-site evenness values
regional	Regional (pooled) evenness
q	Orders used (for Hill type)
type	Evenness type
coords	Coordinates if provided
n_sites	Number of sites
n_species	Number of species

References

Jost, L. (2010). The relation between evenness and diversity. Diversity, 2, 207-232.

Pielou, E.C. (1966). The measurement of diversity in different types of biological collections. Journal of Theoretical Biology, 13, 131-144.

See Also

`diversityProfile()` for Hill number profiles, `alphaDiversity()` for raw diversity values

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)

# Hill evenness profile
ev <- evenness(species)
print(ev)

# Pielou's J
ev_j <- evenness(species, type = "pielou")
print(ev_j)
```

---

extrapolate *Extrapolate Total Species Richness*

Description

Fit an asymptotic model to estimate total species richness beyond the observed sampling effort.

Usage

```
extrapolate(
  object,
 model = c("michaelis-menten", "lomolino", "asymptotic", "weibull", "logistic", "evt"),
  ...
)
```

Arguments

`object`	A spacc object.
`model`	Character. Model to fit: `"michaelis-menten"` (default), `"lomolino"`, `"asymptotic"`, `"weibull"`, `"logistic"`, or `"evt"` (Extreme Value Theory, Borda-de-Agua et al. 2025).
`...`	Additional arguments passed to `stats::nls()`.

Value

An object of class `spacc_fit` containing:

`asymptote`	Estimated total species richness
`asymptote_ci`	Confidence interval for asymptote
`model`	Model name
`fit`	The nls fit object
`aic`	AIC of the model

References

Lomolino, M.V. (2000). Ecology's most general, yet protean pattern: the species-area relationship. Journal of Biogeography, 27, 17-26.

Flather, C.H. (1996). Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. Journal of Biogeography, 23, 155-168.

Borda-de-Agua, L., Whittaker, R.J., Cardoso, P., et al. (2025). Extreme value theory explains the topography and scaling of the species-area relationship. Nature Communications, 16, 5346.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, coords)
fit <- extrapolate(sac)
print(fit)
```

`extrapolateCoverage` *Extrapolate Richness Beyond Observed Coverage*

Description

Predict species richness at coverage levels beyond the empirical maximum, following the Chao et al. (2014) framework. Provides seamless interpolation and extrapolation as a function of sample coverage.

Usage

```
extrapolateCoverage(x, target_coverage = c(0.9, 0.95, 0.99), q = 0)
```

Arguments

x	A spacc_coverage object from spaccCoverage().
target_coverage	Numeric vector of target coverage levels (0 to 1). Can exceed observed coverage for extrapolation. Default c(0.90, 0.95, 0.99).
q	Numeric. Diversity order for extrapolation: 0 (richness, default), 1 (Shannon), or 2 (Simpson).

Details

For targets within observed coverage, linear interpolation is used. For targets beyond observed coverage, asymptotic estimators are applied:

- **q = 0**: Chao1 estimator: S_est = S_obs + f1^2 / (2 * f2), where f1/f2 are singleton/doubleton counts. Extrapolation via coverage deficit.
- **q = 1**: Shannon extrapolation based on the Good-Turing frequency formula.
- **q = 2**: Simpson extrapolation using the unbiased estimator.

Value

An object of class spacc_coverage_ext containing:

richness	Matrix of interpolated/extrapolated richness (n_seeds x n_targets)
target_coverage	Target coverage levels
q	Diversity order used
observed_coverage	Mean observed final coverage
observed_richness	Mean observed final richness

References

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93, 2533-2547.

Chao, A., Gotelli, N.J., Hsieh, T.C., et al. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs, 84, 45-67.

See Also

spaccCoverage(), interpolateCoverage()

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rpois(50 * 30, 2), nrow = 50)
cov <- spaccCoverage(species, coords)
ext <- extrapolateCoverage(cov, target_coverage = c(0.95, 0.99))
print(ext)
```

---

gammaDiversity *Gamma Diversity (Regional)*

Description

Compute Hill numbers for the pooled community across all sites.

Usage

```
gammaDiversity(x, q = c(0, 1, 2))
```

Arguments

x	A site-by-species matrix (abundance data).
q	Numeric vector. Orders of diversity. Default `c(0, 1, 2)`.

Details

Gamma diversity represents regional (total) diversity across all sites. It is computed by pooling abundances across all sites and calculating Hill numbers on the combined community.

Value

A named numeric vector with gamma diversity for each q.

References

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427-2439.

See Also

`alphaDiversity()` for local diversity, `diversityPartition()` for full alpha-beta-gamma decomposition

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
gammaDiversity(species, q = c(0, 1, 2))
```

`iChao1` *Improved Chao1 (iChao1) Richness Estimator*

Description

Estimate total species richness using the improved Chao1 estimator (Chiu et al. 2014). Uses singletons through quadrupletons (f1–f4) to reduce bias for small samples.

Usage

```
iChao1(x)
```

Arguments

`x`	A site-by-species matrix (abundance data). Columns are pooled across sites.

Details

The improved Chao1 estimator adds a correction term using f3 and f4:

$$S_{iChao1} = S_{Chao1} + \frac{f_3}{4f_4} \max\left(f_1 - \frac{f_2 f_3}{2f_4}, 0\right)$$

When $f_4 = 0$, the estimator collapses to Chao1.

Value

An object of class `spacc_estimate` with components:

estimator Name of the estimator (`"iChao1"`)

estimate Estimated total richness

se Standard error of the estimate

lower Lower 95 percent confidence bound

upper Upper 95 percent confidence bound

S_obs Observed species richness

details List with `f1`, `f2`, `f3`, `f4`

References

Chiu, C.H., Wang, Y.T., Walther, B.A. & Chao, A. (2014). An improved nonparametric lower bound of species richness via a modified Good-Turing frequency formula. Biometrics, 70, 671-682.

See Also

`chao1()` for the standard estimator, `iChao2()` for incidence-based version

Examples

```
species <- matrix(rpois(50 * 30, 2), nrow = 50)
iChao1(species)
```

`iChao2` *Improved Chao2 (iChao2) Richness Estimator*

Description

Estimate total species richness from incidence data using the improved Chao2 estimator (Chiu et al. 2014). Uses uniques through quadruplicates (Q1–Q4) to reduce bias for small samples.

Usage

```
iChao2(x)
```

Arguments

`x`	A site-by-species matrix (presence/absence or abundance). Automatically binarized.

Details

The improved Chao2 estimator is the incidence-based analogue of iChao1:

$$S_{iChao2} = S_{Chao2} + \frac{Q_3}{4Q_4} \max\left(Q_1 - \frac{Q_2 Q_3}{2Q_4}, 0\right)$$

When $Q_4 = 0$, the estimator collapses to Chao2.

Value

An object of class `spacc_estimate` with components:

estimator Name of the estimator (`"iChao2"`)

estimate Estimated total richness

se Standard error of the estimate

lower Lower 95 percent confidence bound

upper Upper 95 percent confidence bound

S_obs Observed species richness

details List with `Q1`, `Q2`, `Q3`, `Q4`, `n_sites`

References

Chiu, C.H., Wang, Y.T., Walther, B.A. & Chao, A. (2014). An improved nonparametric lower bound of species richness via a modified Good-Turing frequency formula. Biometrics, 70, 671-682.

See Also

chao2() for the standard estimator, iChao1() for abundance-based version

Examples

```
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
iChao2(species)
```

`interpolateCoverage` *Interpolate Richness at Target Coverage Levels*

Description

Estimate species richness at specified coverage levels by interpolation.

Usage

```
interpolateCoverage(x, target = c(0.9, 0.95, 0.99))
```

Arguments

`x`	A `spacc_coverage` object.
`target`	Numeric vector of target coverage levels (0 to 1). Default `c(0.90, 0.95, 0.99)`.

Value

A data.frame with columns for each target coverage level, showing interpolated richness for each seed.

References

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93, 2533-2547.

`jackknife` *Jackknife Richness Estimator*

Description

First- or second-order jackknife estimator of total species richness (Burnham & Overton 1978, 1979).

Usage

```
jackknife(x, order = 1L)
```

Arguments

`x`	A site-by-species matrix (presence/absence or abundance). Automatically binarized.
`order`	Integer. Jackknife order: 1 (default) or 2.

Details

First-order jackknife:

$$S_{jack1} = S_{obs} + Q_1 \frac{n-1}{n}$$

Second-order jackknife:

$$S_{jack2} = S_{obs} + \frac{Q_1(2n-3)}{n} - \frac{Q_2(n-2)^2}{n(n-1)}$$

Value

An object of class `spacc_estimate`.

References

Burnham, K.P. & Overton, W.S. (1978). Estimation of the size of a closed population when capture probabilities vary among animals. Biometrika, 65, 625-633.

Burnham, K.P. & Overton, W.S. (1979). Robust estimation of population size when capture probabilities vary among animals. Ecology, 60, 927-936.

See Also

`chao2()`, `bootstrap_richness()`

Examples

```
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
jackknife(species, order = 1)
jackknife(species, order = 2)
```

mao_tau *Exact (Mao Tau) Expected Accumulation*

Description

Compute the expected species accumulation curve using sample-based rarefaction (Mao Tau estimator). This is analytically identical to the expected curve from random permutations.

Usage

```
mao_tau(x)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance).

Value

A data.frame with columns: sites, expected, sd, lower, upper

References

Colwell, R.K., Mao, C.X. & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology, 85, 2717-2727.

plot.spacc *Plot Spatial SAC*

Description

Create a ggplot2 visualization of species accumulation curves. For grouped spacc objects, curves are overlaid with different colors.

Usage

```
## S3 method for class 'spacc'
plot(
  x,
  ci = TRUE,
  ci_level = 0.95,
  ci_alpha = 0.3,
  show_seeds = FALSE,
  saturation = FALSE,
  saturation_level = 0.9,
  facet = FALSE,
  ...
)
```

Arguments

x	A spacc or summary.spacc object.
ci	Logical. Show confidence interval ribbon? Default TRUE.
ci_level	Numeric. Confidence level for interval. Default 0.95.
ci_alpha	Numeric. Transparency of CI ribbon. Default 0.3.
show_seeds	Logical. Show individual seed curves? Default FALSE. Only available for ungrouped objects.
saturation	Logical. Mark saturation point? Default FALSE. Only available for ungrouped objects.
saturation_level	Numeric. Proportion for saturation. Default 0.9.
facet	Logical. Use faceted panels for grouped objects? Default FALSE (overlay with colors). Ignored for ungrouped objects.
...	Additional arguments (ignored).

Value

A ggplot2 object.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, coords)
plot(sac)
```

---

plot.spacc_metrics *Plot spacc_metrics*

Description

Create visualizations of per-site accumulation metrics.

Usage

```
## S3 method for class 'spacc_metrics'
plot(
  x,
  metric = NULL,
  type = c("heatmap", "points", "histogram"),
  point_size = 3,
  palette = "viridis",
  ...
)
```

Arguments

x	A spacc_metrics object from spaccMetrics().
metric	Character. Which metric to plot. Default is first metric.
type	Character. Plot type: "heatmap" Spatial heatmap colored by metric value "points" Simple point plot (same as heatmap but clearer name) "histogram" Distribution of metric values
point_size	Numeric. Size of points in heatmap. Default 3.
palette	Character. Color palette for heatmap. One of "magma" (A), "inferno" (B), "plasma" (C), "viridis" (D, default), "cividis" (E), "rocket" (F), "mako" (G), "turbo" (H). Single letters also accepted.
...	Additional arguments (unused).

Value

A ggplot2 object.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
metrics <- spaccMetrics(species, coords, metrics = c("slope_10", "auc"))
plot(metrics, metric = "slope_10", type = "heatmap")
```

---

predict.spacc *Predict from Empirical Accumulation Curve*

Description

Interpolate the mean empirical accumulation curve at arbitrary site counts using linear interpolation. Unlike the predict method for spacc_fit objects, this does not use a fitted model; it interpolates the observed curve directly.

Usage

```
## S3 method for class 'spacc'
predict(object, n = NULL, ci = TRUE, ci_level = 0.95, warn = TRUE, ...)
```

Arguments

object	A spacc object.
n	Numeric vector of site counts at which to interpolate. Defaults to 25%, 50%, and 100% of total sites.
ci	Logical. If TRUE (default), return a data frame with columns n, mean, lower, upper. If FALSE, return a named numeric vector.
ci_level	Confidence level for the interval (default 0.95).
warn	Logical. Warn when n values fall outside the observed range (default TRUE).
...	Ignored.

Value

A data frame (if ci = TRUE) or named numeric vector (if ci = FALSE). Out-of-range values return NA.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, coords, n_seeds = 10, progress = FALSE)
predict(sac, n = c(10, 25, 50))
predict(sac, n = c(10, 25), ci = FALSE)
```

---

rarefy *Individual-Based Rarefaction*

Description

Compute individual-based rarefaction curves for Hill numbers at any order q. This complements the sample-based accumulation in spacc().

Usage

```
rarefy(x, n_individuals = NULL, q = 0, n_boot = 100L)
```

Arguments

x	A site-by-species matrix with abundance data (not presence/absence).
n_individuals	Integer vector. Sample sizes to compute expected diversity for. Default NULL computes for all levels from 1 to total.
q	Numeric. Order of Hill number; any value >= 0. Default 0 (species richness). q=1 gives rarefied Shannon diversity, q=2 gives rarefied Simpson diversity. q=0, 1, and 2 use exact estimators; other orders report the Hill number of order q of the sampled composition.
n_boot	Integer. Number of bootstrap replicates for CI. Default 100.

Details

For q=0 (species richness): uses the Hurlbert (1971) formula.

For q=1 (Shannon diversity): rarefied Shannon entropy is computed and converted to effective number of species via exponentiation.

For q=2 (Simpson diversity): rarefied Simpson concentration is computed and converted to effective number of species via inversion.

Value

An object of class `spacc_rare` containing:

`n`	Sample sizes
`expected`	Expected diversity (Hill number of order q)
`sd`	Standard deviation
`lower`, `upper`	95 percent confidence bounds
`q`	Order of diversity used

References

Hurlbert, S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. Ecology, 52, 577-586.

Chao, A., Gotelli, N.J., Hsieh, T.C., et al. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs, 84, 45-67.

Examples

```
abundance_matrix <- matrix(rpois(50 * 30, 2), nrow = 50)
rare <- rarefy(abundance_matrix)
plot(rare)

# Shannon rarefaction
rare_q1 <- rarefy(abundance_matrix, q = 1)
plot(rare_q1)
```

`ses` *Standardized Effect Size (SES) via Null Models*

Description

Compute standardized effect sizes by comparing observed diversity metrics against a null distribution from randomized communities. Supports multiple null model algorithms and works with most spacc output classes.

Usage

```
ses(
  x,
  species,
  coords = NULL,
  metric = NULL,
 null_model = c("frequency", "richness", "both", "curveball", "torus", "spatial_swap"),
  n_perm = 999L,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A spacc output object. Supported classes: spacc, spacc_hill, spacc_phylo, spacc_func, spacc_beta, spacc_metrics, spacc_alpha, spacc_partition.
species	A site-by-species matrix (required). The species matrix used to produce x. Needed because spacc objects do not store the raw species matrix.
coords	Optional data.frame with columns x and y. Required if the original analysis used coordinates. If x contains stored coordinates, they will be used automatically.
metric	Character or NULL. For multi-metric objects (e.g., spacc_hill with multiple q), specify which metric to extract. If NULL, uses the first/default metric.
null_model	Character. Null model algorithm: • "frequency": Shuffle species columns independently (maintains column totals = species frequency) • "richness": Shuffle species rows independently (maintains row totals = site richness) • "both": Independent swap algorithm maintaining both row and column totals (Gotelli 2000) • "curveball": Curveball algorithm for efficient swap (Strona et al. 2014) • "torus": Toroidal shift preserving spatial autocorrelation. Shifts all coordinates by a random offset and reassigns species to shifted sites. Requires coords. • "spatial_swap": Independent swap restricted to spatially proximate site pairs. Preserves both marginals while respecting spatial structure. Requires coords.
n_perm	Integer. Number of permutations. Default 999.
parallel	Logical. Use parallel processing for the underlying analysis? Default TRUE.
n_cores	Integer. Number of cores. Default NULL (auto-detect).
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed for reproducibility.

Details

SES is computed as:

$$SES = \frac{observed - \bar{null}}{sd_{null}}$$

A two-tailed p-value is calculated as the proportion of null values at least as extreme as the observed value:

$$p = \frac{2 \cdot \min(r, n_{perm} + 1 - r)}{n_{perm} + 1}$$

where r is the rank of the observed value among null values.

Null model algorithms:

- `"frequency"`: Tests whether species composition matters given observed species frequencies
- `"richness"`: Tests whether species identity matters given observed site richness
- `"both"`: Maintains both marginal totals; tests non-random species co-occurrence patterns
- `"curveball"`: Efficient alternative to `"both"` with proven uniform sampling properties

Value

An object of class `spacc_ses` containing:

`observed`	Numeric vector of observed metric values
`null_mean`	Mean of null distribution
`null_sd`	Standard deviation of null distribution
`ses`	Standardized effect size: (observed - null_mean) / null_sd
`p_value`	Two-tailed p-value
`n_perm`	Number of permutations
`null_model`	Null model algorithm used
`metric`	Metric name
`input_class`	Class of input object

References

Gotelli, N.J. (2000). Null model analysis of species co-occurrence patterns. Ecology, 81, 2606-2621.

Strona, G., Nappo, D., Boccacci, F., Fattorini, S. & San-Miguel-Ayanz, J. (2014). A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals. Nature Communications, 5, 4114.

See Also

`spaccHill()`, `spaccBeta()`, `spaccMetrics()`

Examples

```
coords <- data.frame(x = runif(20), y = runif(20))
species <- matrix(rbinom(20 * 15, 1, 0.3), nrow = 20)

sac <- spacc(species, coords, n_seeds = 10)
result <- ses(sac, species, n_perm = 19)
print(result)
```

`sesars` *Sampling Effort Species-Area Relationship (SESARS)*

Description

Model the joint effect of sampling effort and area on species richness. Corrects for unequal survey intensity across sites, common in atlas data and citizen science datasets.

Usage

```
sesars(object, effort, model = c("power", "additive"), ...)
```

Arguments

`object`	A spacc object.
`effort`	Numeric vector. Sampling effort per site (e.g., hours, visits, trap-nights). Must have length equal to number of sites.
`model`	Character. SESARS model: • `"power"` (default): S = c * A^z * E^w (multiplicative power law) • `"additive"`: S = c + z * log(A) + w * log(E)
`...`	Additional arguments passed to `stats::nls()` or `stats::lm()`.

Details

Standard SARs assume complete sampling within each area unit. SESARS incorporates sampling effort (E) alongside area (A) to provide unbiased richness estimates across regions with unequal survey intensity.

Value

An object of class `spacc_sesars` containing:

`model`	Model type
`fit`	Fitted model object
`coef`	Model coefficients
`data`	Data frame used for fitting

References

Dennstadt, F., Horak, J. & Martin, M.D. (2019). Predictive sampling effort and species-area relationship models for estimating richness in fragmented landscapes. Diversity and Distributions, 26, 1112-1123.

See Also

`extrapolate()`, `spacc()`

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, coords)
effort <- rpois(50, 10)
ses <- sesars(sac, effort, model = "power")
print(ses)
```

---

sfar *Species-Fragmented Area Relationship (SFAR)*

Description

Separate the effects of habitat loss (area reduction) from fragmentation (splitting into patches) on species richness. Extends the classic power-law SAR with an explicit fragmentation term.

Usage

```
sfar(object, patches, model = c("power", "log"), ...)
```

Arguments

`object`	A spacc object.
`patches`	Factor or integer vector assigning each site to a habitat fragment (patch). Must have length equal to the number of sites.
`model`	Character. SFAR model: • `"power"` (default): S = c * A^z * n^(-f) • `"log"`: log(S) = log(c) + z*log(A)* - *f* log(n)
`...`	Additional arguments.

Details

The SFAR (Hanski et al. 2013) extends the power-law SAR to quantify the additional effect of habitat fragmentation on species richness. The model S = c * A^z * n^(-f) adds a penalty term for fragmentation (n = number of fragments), where f > 0 indicates that fragmentation reduces richness beyond what area loss alone would predict.

Value

An object of class `spacc_sfar` containing:

`fit`	Fitted model object
`coef`	Coefficients: c (intercept), z (area exponent), f (fragmentation exponent)
`n_patches`	Number of habitat fragments

References

Hanski, I., Zurita, G.A., Bellocq, M.I. & Rybicki, J. (2013). Species-fragmented area relationship. Proceedings of the National Academy of Sciences, 110, 12715-12720.

Rybicki, J. & Hanski, I. (2013). Species-area relationships and extinctions caused by habitat loss and fragmentation. Ecology Letters, 16, 27-38.

See Also

`extrapolate()`, `sesars()`

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
sac <- spacc(species, coords)
patches <- kmeans(coords, centers = 5)$cluster
sfar_result <- sfar(sac, patches)
print(sfar_result)
```

---

spacc *Spatial Species Accumulation Curves*

Description

Compute species accumulation curves using various spatial sampling methods with C++ backend for performance.

Usage

```
spacc(
  x,
  coords,
  n_seeds = 50L,
  method = c("knn", "kncn", "random", "radius", "gaussian", "cone", "collector"),
  distance = c("euclidean", "haversine"),
  backend = c("auto", "exact", "kdtree"),
  support = NULL,
```

```
  include_halo = TRUE,
  sigma = NULL,
  cone_width = pi/4,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  groups = NULL,
  time = NULL,
  w_space = 1,
  w_time = 1,
  seed = NULL,
  order = NULL
)
```

Arguments

x	A site-by-species matrix (rows = sites, cols = species) with presence/absence (0/1) or abundance data. Can also be a data.frame.
coords	Site coordinates. Can be: • A data.frame with columns x and y • An sf object with point geometries (CRS is preserved) • A spacc_dist object from distances()
n_seeds	Integer. Number of random starting points for uncertainty quantification. Default 50.
method	Character. Accumulation method: • "knn": k-Nearest Neighbor (always visit closest unvisited) • "kncn": k-Nearest Centroid Neighbor (visit closest to centroid) • "random": Random order (null model) • "radius": Expand by distance from seed • "gaussian": Probabilistic selection weighted by distance • "cone": Directional expansion within angular constraint • "collector": Sites in data order (no randomization, single curve)
distance	Character. Distance method: "euclidean" or "haversine".
backend	Character. Nearest-neighbor backend for knn and kncn: • "auto" (default): Uses exact (brute-force) for <=500 sites, spatial tree for >500 sites. • "exact": Always use brute-force with precomputed distance matrix. • "kdtree": Always use spatial tree. Uses k-d tree (nanoflann) for Euclidean distances and ball tree for haversine distances. Faster for large datasets, no distance matrix needed.
support	Optional. Spatial support for core/halo classification via areaOfEffect::aoe(). Can be: • "auto": Auto-detect countries and run per-country accumulation, returning a grouped spacc object with one curve per country

- Country name or ISO code: `"France"`, `"FR"`, `"FRA"`
- Vector of countries: `c("France", "Germany")`
- An `sf` polygon object
- An `aoe_result` object (pre-computed) When provided, seeds are sampled only from "core" sites (inside support), while accumulation can expand into "halo" sites (buffer zone).

`include_halo` Logical. When `support` is provided, should halo sites be included in accumulation? Default `TRUE` (ecological boundary). Set to `FALSE` for political/hard boundary.

`sigma` Numeric. Bandwidth for Gaussian method. Default auto-calculated.

`cone_width` Numeric. Half-width in radians for cone method. Default pi/4.

`parallel` Logical. Use parallel processing? Default `TRUE`.

`n_cores` Integer. Number of cores. Default `NULL` uses `detectCores() - 1`.

`progress` Logical. Show progress bar? Default `TRUE`.

`groups` Optional. A factor, character, or integer vector of length `ncol(x)` assigning each species (column) to a group. When provided, separate accumulation curves are computed for each group using the **same spatial site ordering**, and a grouped `spacc` object is returned. Useful for comparing native vs alien species, families, or any categorical split. Default `NULL` (no grouping).

`time` Optional. Numeric vector of length `nrow(x)` giving a temporal coordinate for each site. When provided, a combined spatiotemporal distance matrix is computed as `w_space * d_spatial + w_time * d_temporal` and used for accumulation. Forces exact (brute-force) backend since spatial trees cannot handle composite distances. Only supported for methods that use a distance matrix: `"knn"`, `"radius"`, `"gaussian"`.

`w_space` Numeric. Weight for spatial distance when `time` is provided. Default 1.

`w_time` Numeric. Weight for temporal distance when `time` is provided. Default 1.

`seed` Integer. Random seed for reproducibility. Default `NULL`.

`order` Optional user-defined accumulation order(s). When supplied, `method` is ignored and sites are accumulated in the given sequence(s) (no distance computation or seed sampling). Can be:

- A numeric vector of length `nrow(x)`: a single ordering (one curve).
- A list of such vectors, or a matrix with one ordering per row: each produces a curve, treated like seeds for uncertainty quantification. Each ordering must be a permutation of `seq_len(nrow(x))`. Cannot be combined with `support` or `time`. Default `NULL`.

Value

When `groups = NULL`, an object of class `spacc` containing:

`curves` Matrix of cumulative species counts (n_seeds x n_sites)

`coords` Original coordinates

`n_seeds` Number of seeds used

`method` Method used

`n_species` Total species in dataset

References

Arrhenius, O. (1921). Species and area. Journal of Ecology, 9, 95-99.

Scheiner, S.M. (2003). Six types of species-area curves. Global Ecology and Biogeography, 12, 441-447.

Chiarucci, A., Bacaro, G., Scheiner, S.M. (2011). Old and new challenges in using species diversity for assessing biodiversity. Philosophical Transactions of the Royal Society B, 366, 2426-2437.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)

# Basic usage
sac <- spacc(species, coords)
plot(sac)

# Different methods
sac_knn <- spacc(species, coords, method = "knn")
sac_rand <- spacc(species, coords, method = "random")
comp <- compare(sac_knn, sac_rand)
```

---

spaccBeta *Spatial Beta Diversity Accumulation*

Description

Analyze how beta diversity changes as sites are accumulated spatially. Partitions beta diversity into turnover (species replacement) and nestedness (species loss) components following Baselga (2010).

Usage

```
spaccBeta(
  x,
  coords,
  n_seeds = 50L,
  method = "knn",
  index = c("sorensen", "jaccard"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance).
coords	A data.frame with columns x and y, or a spacc_dist object.
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method. Default "knn".
index	Character. Dissimilarity index: "sorensen" (default) or "jaccard".
distance	Character. Distance method: "euclidean" or "haversine".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.
map	Logical. If TRUE, run accumulation from every site as seed and store per-site final beta values for spatial mapping. Enables as_sf() and plot(type = "map"). Default FALSE.

Details

At each step of spatial accumulation, beta diversity is calculated between the accumulated species pool and the newly added site. This reveals how species composition changes as you expand spatially.

Interpretation:

- High turnover: New sites contribute different species (replacement)
- High nestedness: New sites contribute subsets of existing species (loss)

The sum of turnover and nestedness equals total beta diversity.

Value

An object of class spacc_beta containing:

beta_total	Matrix of total beta diversity (n_seeds x n_sites-1)
beta_turnover	Matrix of turnover component
beta_nestedness	Matrix of nestedness component
distance	Matrix of cumulative distances
n_seeds, n_sites, method, index	Parameters used

References

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19, 134-143.

See Also

betapart::beta.pair() for pairwise beta diversity

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)

beta <- spaccBeta(species, coords, n_seeds = 30)
plot(beta)

# Compare Sorensen vs Jaccard
beta_jac <- spaccBeta(species, coords, index = "jaccard")
```

---

spaccBetaFunc *Functional Beta Diversity Accumulation*

Description

Compute spatial accumulation of functional beta diversity, partitioned into turnover and nestedness components. Measures how functional trait space composition changes as sites are accumulated spatially.

Usage

```
spaccBetaFunc(
  x,
  coords,
  traits,
  n_seeds = 50L,
  method = "knn",
  index = c("sorensen", "jaccard"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance).
coords	A data.frame with columns x and y, or a spacc_dist object.
traits	A species-by-traits matrix. Row names should match species.
n_seeds	Integer. Number of random starting points. Default 50.

`method`	Character. Accumulation method. Default `"knn"`.
`index`	Character. Dissimilarity index: `"sorensen"` (default) or `"jaccard"`.
`distance`	Character. Distance method. Default `"euclidean"`.
`parallel`	Logical. Use parallel processing? Default `TRUE`.
`n_cores`	Integer. Number of cores.
`progress`	Logical. Show progress? Default `TRUE`.
`seed`	Integer. Random seed.

Details

Functional beta diversity quantifies the turnover of functional traits across space. At each accumulation step, beta is computed based on the overlap of trait ranges (functional space) between the accumulated pool and the newly added site.

Value

An object of class `spacc_beta` with additional attribute `beta_type = "functional"`.

References

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography, 21, 1223-1232.

Cardoso, P., Rigal, F. & Carvalho, J.C. (2015). BAT – Biodiversity Assessment Tools. Methods in Ecology and Evolution, 6, 232-236.

See Also

`spaccBeta()`, `spaccBetaPhylo()`

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 20, 1, 0.3), nrow = 50)
traits <- matrix(rnorm(20 * 3), nrow = 20)
rownames(traits) <- colnames(species) <- paste0("sp", 1:20)

beta_func <- spaccBetaFunc(species, coords, traits)
plot(beta_func)
```

spaccBetaPhylo *Phylogenetic Beta Diversity Accumulation*

Description

Compute spatial accumulation of phylogenetic beta diversity, partitioned into turnover and nestedness components. Measures how evolutionary composition changes as sites are accumulated spatially.

Usage

```
spaccBetaPhylo(
  x,
  coords,
  tree,
  n_seeds = 50L,
  method = "knn",
  index = c("sorensen", "jaccard"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance).
coords	A data.frame with columns x and y, or a spacc_dist object.
tree	A phylogenetic tree of class phylo (from ape), or a pairwise phylogenetic distance matrix.
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method. Default "knn".
index	Character. Dissimilarity index: "sorensen" (default) or "jaccard".
distance	Character. Distance method. Default "euclidean".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.

Details

Phylogenetic beta diversity quantifies evolutionary turnover across space. The PhyloSor index (phylogenetic Sorensen) is used: the fraction of branch length shared between two communities relative to total branch length. Partitioned into replacement (turnover) and loss (nestedness) components.

Value

An object of class `spacc_beta` with additional attribute `beta_type = "phylogenetic"`.

References

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19, 134-143.

Chao, A., Chiu, C.H., Villeger, S., et al. (2023). Rarefaction and extrapolation with beta diversity under a framework of Hill numbers: the iNEXT.beta3D standardization. Ecological Monographs, 93, e1588.

See Also

`spaccBeta()`, `spaccBetaFunc()`

Examples

```
if (requireNamespace("ape", quietly = TRUE)) {
  tree <- ape::rtree(20)
  coords <- data.frame(x = runif(50), y = runif(50))
  species <- matrix(rbinom(50 * 20, 1, 0.3), nrow = 50)
  colnames(species) <- tree$tip.label

  beta_phylo <- spaccBetaPhylo(species, coords, tree)
  plot(beta_phylo)
}
```

---

spaccCoverage *Coverage-Based Spatial Rarefaction*

Description

Compute spatial accumulation curves with sample coverage tracking. Allows standardization by completeness (coverage) rather than sample size, following Chao & Jost (2012) or the sample-based estimator of Chiu (2023).

Usage

```
spaccCoverage(
  x,
  coords,
  n_seeds = 50L,
  method = "knn",
  distance = c("euclidean", "haversine"),
  coverage = c("chao", "chiu"),
  parallel = TRUE,
```

```
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE
)
```

Arguments

x	A site-by-species matrix with abundance data.
coords	A data.frame with columns x and y, or a spacc_dist object.
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method. Default "knn".
distance	Character. Distance method: "euclidean" or "haversine".
coverage	Character. Coverage estimator to use: "chao" (default) for the individual-based Chao & Jost (2012) estimator using singletons/doubletons, or "chiu" for the sample-based Chiu (2023) estimator using incidence frequency counts (Q1/Q2) and unique-species abundance (G1). The Chiu estimator is recommended for spatially aggregated data where sampling units are plots/sites rather than independent individuals.
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.
map	Logical. If TRUE, run accumulation from every site as seed and store per-site final coverage and richness for spatial mapping. Enables as_sf() and plot(type = "map"). Default FALSE.

Details

Sample coverage estimates the proportion of the total community abundance represented by observed species. It provides a measure of sampling completeness that is independent of sample size.

The **Chao-Jost (2012)** estimator counts singletons (f1) and doubletons (f2) in the cumulative abundance vector. It assumes individuals are sampled independently, which may not hold for plot-based spatial data.

The **Chiu (2023)** estimator uses incidence frequency counts instead: Q1 (species in exactly 1 site), Q2 (species in exactly 2 sites), and G1 (total abundance of Q1 species). It gives near-unbiased coverage estimates when organisms are spatially aggregated across sampling units.

Coverage-based rarefaction allows fair comparison of diversity across communities with different abundances by standardizing to equal completeness rather than equal sample size.

Value

An object of class spacc_coverage containing:

richness	Matrix of species richness (n_seeds x n_sites)

individuals	Matrix of individual counts
coverage	Matrix of coverage estimates
coverage_type	Coverage estimator used ("chao" or "chiu")
coords, n_seeds, n_sites, method	Parameters used

References

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93, 2533-2547.

Chiu, C.-H. (2023). A sample-based estimator for sample coverage. Ecology, 104, e4099.

See Also

iNEXT::iNEXT() for coverage-based rarefaction without spatial structure

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rpois(50 * 30, 2), nrow = 50)

cov <- spaccCoverage(species, coords)
plot(cov)

# Sample-based coverage (recommended for spatial data)
cov_chiu <- spaccCoverage(species, coords, coverage = "chiu")

# Interpolate richness at 90% and 95% coverage
interp <- interpolateCoverage(cov, target = c(0.90, 0.95))
```

---

spaccDiversity *Spatial Accumulation of a Custom Diversity Metric*

Description

Accumulate any user-supplied diversity index along a spatial ordering of sites. At each accumulation step the cumulative community is passed to fun, which returns a single number. This is the general escape hatch behind the built-in metric functions: use it for indices that spacc does not implement directly.

Usage

```
spaccDiversity(
  x,
  coords,
  fun,
  ...,
  method = c("knn", "kncn", "random", "radius", "collector"),
  incidence = FALSE,
  n_seeds = 50L,
  distance = c("euclidean", "haversine"),
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix (rows = sites, cols = species), abundance or presence/absence.
coords	A data.frame with columns x and y, or a spacc_dist object.
fun	A function applied to the cumulative community at each step. It receives a named numeric vector of length ncol(x) (cumulative summed abundances, or 0/1 incidences when incidence = TRUE) plus any arguments passed through ..., and must return a single numeric value.
...	Additional arguments passed to fun.
method	Character. Spatial ordering of sites: "knn" (default), "kncn", "random", "radius", or "collector".
incidence	Logical. If TRUE, fun receives 0/1 incidences instead of summed abundances. Default FALSE.
n_seeds	Integer. Number of random starting points / orderings. Ignored for "collector" (a single data-order curve). Default 50.
distance	Character. "euclidean" or "haversine".
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed for reproducibility.

Details

The site ordering reuses the same spatial traversals as the built-in methods (nearest-neighbour, nearest-centroid, random, distance-rank, or data order), then evaluates fun on the accumulating community. Because the index is an arbitrary R function, this trades the speed of the compiled metrics for full flexibility.

Value

An object of class spacc_diversity that inherits from spacc, so the standard summary(), plot(), as.data.frame() and predict() methods apply. curves is an n_seeds x n_sites matrix of the metric along the accumulation.

See Also

spaccHill(), spaccPhylo(), spaccFunc() for built-in metrics.

Examples

```
coords <- data.frame(x = runif(40), y = runif(40))
species <- matrix(rpois(40 * 20, 2), nrow = 40)

# Shannon entropy along the accumulation
shannon <- function(comm) {
  p <- comm[comm > 0] / sum(comm)
  -sum(p * log(p))
}
div <- spaccDiversity(species, coords, shannon, n_seeds = 20)
plot(div)
```

---

spaccEndemism *Spatial Endemism Accumulation*

Description

Compute the number of endemic species (species found only within the accumulated area) as sites are added spatially. Complements the standard SAC by tracking species unique to each spatial extent.

Usage

```
spaccEndemism(
  x,
  coords,
  n_seeds = 50L,
  method = "knn",
  distance = c("euclidean", "haversine"),
  map = FALSE,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance).
coords	A data.frame with columns x and y, or a spacc_dist object.
n_seeds	Integer. Number of random starting points. Default 50.

method	Character. Accumulation method. Default "knn".
distance	Character. Distance method: "euclidean" or "haversine".
map	Logical. If TRUE, compute per-site endemism by running accumulation from each site as seed. Stores a site_values data.frame enabling plot(type = "map") and as_sf(). Default FALSE.
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.

Details

At each accumulation step k, an endemic species is one that is present in the accumulated sites (1..k) but absent from all remaining unvisited sites (k+1..n). This tracks how many species are unique to the area sampled so far.

The endemism curve typically starts low (few endemics at small areas), increases as the region grows, and eventually equals total richness when all sites are included.

Value

An object of class spacc_endemism containing:

richness	Matrix of cumulative richness (n_seeds x n_sites)
endemism	Matrix of endemic species count (n_seeds x n_sites)
site_values	Per-site endemism data.frame (if map = TRUE)
coords, n_seeds, n_sites, method	Parameters used

References

Kier, G., Kreft, H., Lee, T.M., et al. (2009). A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences, 106, 9322-9327.

May, F., Gerstner, K., McGlinn, D.J., et al. (2018). mobsim: an R package for the simulation and measurement of biodiversity across spatial scales. Methods in Ecology and Evolution, 9, 1401-1408.

See Also

spacc(), spaccHill()

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)

end <- spaccEndemism(species, coords, n_seeds = 30)
plot(end)
```

---

spaccFunc *Spatial Functional Diversity Accumulation*

Description

Compute spatial accumulation of functional diversity metrics based on traits.

Usage

```
spaccFunc(
  x,
  coords,
  traits,
  metric = c("fdis", "fric"),
  n_seeds = 50L,
  method = "knn",
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE
)
```

Arguments

x	A site-by-species matrix (abundance data recommended).
coords	A data.frame with columns x and y, or a spacc_dist object.
traits	A species-by-traits matrix. Row names should match species (columns of x).
metric	Character vector. Metrics to compute: • "fdis": Functional Dispersion (mean distance to centroid) • "fric": Functional Richness (convex hull volume approximation) • "rao": Rao's quadratic entropy (abundance-weighted mean pairwise Euclidean trait distance)
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method. Default "knn".

distance	Character. Site distance method: "euclidean" or "haversine".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.
map	Logical. If TRUE, run accumulation from every site as seed and store per-site final values for spatial mapping. Enables as_sf() and plot(type = "map"). Default FALSE.

Details

Functional diversity metrics quantify trait space occupation:

- **FDis (Functional Dispersion)**: Abundance-weighted mean distance from the community centroid in trait space. Captures functional divergence.
- **FRic (Functional Richness)**: Volume of trait space occupied (convex hull). Requires more species than traits to compute.

Value

An object of class spacc_func containing:

curves	Named list of matrices, one per metric (n_seeds x n_sites)
metric	Metrics computed
coords, n_seeds, n_sites, method	Parameters used

References

Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91, 299-305.

See Also

FD::dbFD() for comprehensive functional diversity analysis

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rpois(50 * 20, 2), nrow = 50)

# Trait matrix (species x traits)
traits <- matrix(rnorm(20 * 3), nrow = 20)
rownames(traits) <- paste0("sp", 1:20)
colnames(species) <- rownames(traits)

func <- spaccFunc(species, coords, traits, metric = c("fdis", "fric"))
plot(func)
```

spaccHill *Spatial Accumulation with Hill Numbers*

Description

Compute spatial species accumulation curves using Hill numbers (effective number of species) instead of raw richness. Hill numbers unify diversity measures: q=0 is richness, q=1 is exponential Shannon, q=2 is inverse Simpson.

Usage

```
spaccHill(
  x,
  coords,
  q = c(0, 1, 2),
  n_seeds = 50L,
  method = "knn",
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE
)
```

Arguments

x	A site-by-species matrix (rows = sites, cols = species) with presence/absence (0/1) or abundance data.
coords	A data.frame with columns x and y containing site coordinates, or a spacc_dist object from distances().
q	Numeric vector. Orders of diversity to compute. Default c(0, 1, 2). • q = 0: Species richness • q = 1: Exponential of Shannon entropy (effective common species) • q = 2: Inverse Simpson (effective dominant species)
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method: "knn" (default).
distance	Character. Distance method: "euclidean" or "haversine".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores. Default NULL uses detectCores() - 1.
progress	Logical. Show progress bar? Default TRUE.
seed	Integer. Random seed for reproducibility.
map	Logical. If TRUE, run accumulation from every site as seed and store per-site final Hill numbers for spatial mapping. Enables as_sf() and plot(type = "map"). Default FALSE.

Details

Hill numbers (Chao et al. 2014) provide a unified framework for diversity measurement. Unlike raw richness (q=0), higher-order Hill numbers (q=1, q=2) down-weight rare species, providing different perspectives on diversity.

The spatial accumulation of Hill numbers can reveal scale-dependent diversity patterns missed by richness alone.

Value

An object of class `spacc_hill` containing:

`curves`	Named list of matrices, one per q value (n_seeds x n_sites)
`q`	Vector of q values used
`coords`	Original coordinates
`n_seeds`	Number of seeds
`n_sites`	Number of sites
`n_species`	Total species
`method`	Method used

References

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs, 84, 45-67.

See Also

`spacc()` for richness-only accumulation, `iNEXT::iNEXT()` for non-spatial Hill number rarefaction

Examples

```
# Compare diversity at different orders
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rpois(50 * 30, 2), nrow = 50)

hill <- spaccHill(species, coords, q = c(0, 1, 2))
plot(hill)

# Extract summary at final site
summary(hill)
```

`spaccHillBeta` *Spatial Hill Number Beta Diversity*

Description

Compute multisite beta diversity as gamma/alpha decomposition of Hill numbers along the spatial accumulation curve (Jost 2007 framework).

Usage

```
spaccHillBeta(
  x,
  coords,
  q = c(0, 1, 2),
  n_seeds = 50L,
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

`x`	A site-by-species matrix (rows = sites, cols = species).
`coords`	A data.frame with columns `x` and `y`, or a `spacc_dist` object.
`q`	Numeric vector. Orders of diversity. Default `c(0, 1, 2)`.
`n_seeds`	Integer. Number of random starting points. Default 50.
`distance`	Character. `"euclidean"` or `"haversine"`.
`parallel`	Logical. Use parallel processing? Default `TRUE`.
`n_cores`	Integer. Number of cores. Default `NULL`.
`progress`	Logical. Show progress? Default `TRUE`.
`seed`	Integer. Random seed.

Details

At each accumulation step k, the function computes:

- **Gamma**: Hill number of the pooled community (all k sites combined)
- **Alpha**: Generalized mean of per-site Hill numbers (Jost's power mean)
- **Beta**: gamma / alpha (effective number of distinct communities)

Beta = 1 means all sites are identical; beta = k means all sites are completely different. This provides the Hill-number analogue of the Baselga-based `spaccBeta()`.

Value

An object of class `spacc_hill_beta` containing:

`gamma`	Named list of n_seeds x n_sites matrices (one per q)
`alpha`	Named list of n_seeds x n_sites matrices (one per q)
`beta`	Named list of n_seeds x n_sites matrices (one per q)
`q`	Vector of q values
`coords`	Original coordinates
`n_seeds`, `n_sites`, `n_species`	Dimensions

References

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. Ecology, 88, 2427-2439.

See Also

`spaccBeta()` for P/A-based Baselga partitioning, `spaccHill()` for Hill accumulation without beta decomposition

Examples

```
coords <- data.frame(x = runif(40), y = runif(40))
species <- matrix(rpois(40 * 20, 2), nrow = 40)

hb <- spaccHillBeta(species, coords, n_seeds = 10, progress = FALSE)
plot(hb)
```

`spaccHillCoverage` *Spatial Hill Numbers at Standardized Coverage*

Description

Compute spatial accumulation of Hill numbers alongside sample coverage, enabling standardized comparison at equal completeness levels (iNEXT-style analysis applied spatially).

Usage

```
spaccHillCoverage(
  x,
  coords,
  q = c(0, 1, 2),
  target_coverage = NULL,
  n_seeds = 50L,
```

```
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix (rows = sites, cols = species) with abundance data.
coords	A data.frame with columns x and y containing site coordinates, or a spacc_dist object from distances().
q	Numeric vector. Orders of diversity. Default c(0, 1, 2).
target_coverage	Numeric vector. Target coverage levels for standardization. Default NULL (no standardization). Values in (0, 1).
n_seeds	Integer. Number of random starting points. Default 50.
distance	Character. Distance method: "euclidean" or "haversine".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores. Default NULL uses all minus one.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed for reproducibility.

Details

Combines spatial kNN accumulation with simultaneous Hill number and coverage computation. At each accumulation step, both the Chao-Jost sample coverage and Hill numbers for all requested orders are calculated.

When target_coverage is specified, Hill numbers are interpolated at those coverage levels using the existing interpolate_at_coverage() C++ function, enabling fair comparison between sites with different sampling completeness.

Value

An object of class spacc_hill_coverage containing:

hills	Named list of n_seeds x n_sites matrices (one per q)
coverage	n_seeds x n_sites matrix of Chao-Jost coverage
standardized	List of per-q values interpolated at target coverage, or NULL if target_coverage is NULL
q	Vector of q values
target_coverage	Target coverage levels used
coords	Original coordinates
n_seeds	Number of seeds
n_sites	Number of sites
n_species	Total species

References

Chao, A. & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology, 93, 2533-2547.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers. Ecological Monographs, 84, 45-67.

See Also

`spaccHill()` for Hill accumulation without coverage, `spaccCoverage()` for coverage accumulation without Hill numbers

Examples

```
coords <- data.frame(x = runif(40), y = runif(40))
species <- matrix(rpois(40 * 20, 2), nrow = 40)

hc <- spaccHillCoverage(species, coords, n_seeds = 10, progress = FALSE)
plot(hc)

# Standardize at 90% coverage
hc2 <- spaccHillCoverage(species, coords, target_coverage = 0.9,
                         n_seeds = 10, progress = FALSE)
summary(hc2)
```

---

spaccMetrics *Per-Site Accumulation Metrics*

Description

Compute spatial accumulation metrics for each site as a starting point. Useful for identifying sites with high or low accumulation rates, visualizing spatial patterns in diversity, and understanding edge effects.

Usage

```
spaccMetrics(
  x,
  coords,
  metrics = c("slope_10", "half_richness", "auc"),
  method = c("knn", "kncn", "random"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE
)
```

Arguments

x	A site-by-species matrix (rows = sites, cols = species).
coords	A data.frame with columns x and y containing site coordinates, or a spacc_dist object from distances().
metrics	Character vector. Metrics to compute. Options include: "slope_10" (initial slope, first 10% of sites), "slope_25" (initial slope, first 25% of sites), "half_richness" (sites to reach 50% of total species), "richness_50pct" (alias for half_richness), "richness_75pct" (sites to reach 75% of species), "richness_90pct" (sites to reach 90% of species), "auc" (area under accumulation curve), "final_richness" (total species starting from this site).
method	Character. Accumulation method: "knn", "kncn", "random". Default "knn".
distance	Character. Distance method: "euclidean" or "haversine".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores for parallel processing.
progress	Logical. Show progress bar? Default TRUE.

Details

This function runs a spatial accumulation curve starting from each site individually, then extracts summary metrics from each curve. This allows you to identify:

- Sites in species-rich areas (high initial slope)
- Core vs edge sites (fast vs slow accumulation)
- Spatial patterns in community structure

The metrics can be plotted as a heatmap using `plot(result, type = "heatmap")`, which requires the ggplot2 package. For more sophisticated spatial visualization with study area boundaries, see the areaOfEffect package.

Value

An object of class spacc_metrics containing:

metrics	Data frame with one row per site and columns for each metric
coords	Original coordinates
metric_names	Names of computed metrics
n_sites	Number of sites
n_species	Total species count

References

Soberon, J.M. & Llorente, J.B. (1993). The use of species accumulation functions for the prediction of species richness. Conservation Biology, 7, 480-488.

See Also

spacc() for standard accumulation curves

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
metrics <- spaccMetrics(species, coords,
                        metrics = c("slope_10", "auc"))
metrics$metrics$slope_10
```

`spaccPhylo` *Spatial Phylogenetic Diversity Accumulation*

Description

Compute spatial accumulation of phylogenetic diversity metrics (MPD, MNTD, PD).

Usage

```
spaccPhylo(
  x,
  coords,
  tree,
  metric = c("mpd", "mntd"),
  n_seeds = 50L,
  method = "knn",
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE
)
```

Arguments

`x`	A site-by-species matrix.
`coords`	A data.frame with columns `x` and `y`, or a `spacc_dist` object.
`tree`	A phylogenetic tree of class `phylo` (from ape package), or a pairwise phylogenetic distance matrix.
`metric`	Character vector. Metrics to compute: • `"mpd"`: Mean Pairwise Distance • `"mntd"`: Mean Nearest Taxon Distance • `"pd"`: Faith's Phylogenetic Diversity (requires tree, not distance matrix) • `"rao"`: Rao's quadratic entropy (abundance-weighted mean pairwise phylogenetic distance). Pass abundance data for weighting; with presence/absence it reduces to the equal-weight form.

n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method. Default "knn".
distance	Character. Site distance method: "euclidean" or "haversine".
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.
map	Logical. If TRUE, run accumulation from every site as seed and store per-site final values for spatial mapping. Enables as_sf() and plot(type = "map"). Default FALSE.

Details

Phylogenetic diversity metrics incorporate evolutionary relationships:

- **MPD (Mean Pairwise Distance)**: Average phylogenetic distance between all pairs of species. Sensitive to tree-wide patterns.
- **MNTD (Mean Nearest Taxon Distance)**: Average distance to closest relative. Sensitive to terminal clustering.
- **PD (Faith's Phylogenetic Diversity)**: Total branch length connecting species. Requires full tree object.

Value

An object of class spacc_phylo containing:

curves	Named list of matrices, one per metric (n_seeds x n_sites)
metric	Metrics computed
coords, n_seeds, n_sites, method	Parameters used

References

Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. Biological Conservation, 61, 1-10.

Webb, C.O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist, 156, 145-155.

See Also

picante::mpd(), picante::mntd(), picante::pd()

Examples

```
if (requireNamespace("ape", quietly = TRUE)) {
  # Create random tree
  tree <- ape::rtree(30)

  coords <- data.frame(x = runif(50), y = runif(50))
  species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
  colnames(species) <- tree$tip.label

  phylo <- spaccPhylo(species, coords, tree, metric = c("mpd", "mntd"))
  plot(phylo)
}
```

---

spatialEigenvectors *Spatial Eigenvectors (PCNM/dbMEM)*

Description

Compute spatial eigenvectors from site coordinates using Principal Coordinates of Neighbour Matrices (PCNM) or distance-based Moran's Eigenvector Maps (dbMEM).

Usage

```
spatialEigenvectors(
  coords,
  threshold = NULL,
  method = c("pcnm", "dbmem"),
  distance = c("euclidean", "haversine")
)
```

Arguments

`coords`	A data.frame with columns `x` and `y`, or a `spacc_dist` object.
`threshold`	Numeric. Distance threshold for truncation. Default `NULL` uses the largest edge in the minimum spanning tree.
`method`	Character. `"pcnm"` (default) retains all positive eigenvectors; `"dbmem"` retains only those with positive Moran's I.
`distance`	Character. `"euclidean"` (default) or `"haversine"`.

Details

PCNM (Borcard & Legendre 2002) decomposes spatial structure into orthogonal eigenvectors representing patterns at different spatial scales. Large eigenvalues correspond to broad-scale patterns (positive spatial autocorrelation), while small eigenvalues represent fine-scale patterns.

The algorithm:

1. Compute pairwise distances
2. Truncate distances beyond threshold (set to 4 * threshold)
3. Double-centre the squared truncated distance matrix
4. Extract eigenvectors with positive eigenvalues
5. For `"dbmem"`: additionally filter to Moran's I > 0

Value

An object of class `spacc_mem` containing:

`vectors`	Matrix of eigenvectors (sites x n_vectors)
`eigenvalues`	Positive eigenvalues
`moran_i`	Moran's I for each eigenvector
`threshold`	Truncation distance used
`coords`	Original coordinates
`n_sites`	Number of sites
`method`	Method used

References

Borcard, D. & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling, 153, 51-68.

Dray, S., Legendre, P. & Peres-Neto, P.R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling, 196, 483-493.

See Also

`spatialPartition()` for variance partitioning with MEMs

Examples

```
coords <- data.frame(x = runif(30), y = runif(30))
mem <- spatialEigenvectors(coords)
print(mem)
```

spatialPartition *Spatial Variance Partitioning with MEMs*

Description

Partition diversity variation into spatial and non-spatial components using forward selection of Moran's Eigenvector Maps.

Usage

```
spatialPartition(x, mem, metric = NULL, forward = TRUE, alpha = 0.05)
```

Arguments

x	A spacc result object (e.g., spacc_metrics, spacc_alpha, spacc_hill) or a numeric vector of per-site diversity values.
mem	A spacc_mem object from spatialEigenvectors().
metric	Character. Which metric to extract from x (passed to internal extraction). Default NULL uses the first available.
forward	Logical. Use forward selection? Default TRUE. If FALSE, all MEMs are included.
alpha	Numeric. Significance threshold for forward selection. Default 0.05.

Details

Forward selection of MEMs proceeds by adding the MEM that most improves the model AIC at each step, stopping when no MEM improves AIC by more than 2 units or when p > alpha.

Value

An object of class spacc_mem_partition containing:

r_squared_spatial	R-squared of the spatial model
r_squared_total	Total R-squared (same as spatial here)
selected_mems	Names of selected MEM vectors
n_selected	Number of selected MEMs
anova_table	ANOVA table from the final model
coefficients	Model coefficients

See Also

spatialEigenvectors() for computing MEMs

Examples

```
coords <- data.frame(x = runif(30), y = runif(30))
species <- matrix(rpois(30 * 15, 2), nrow = 30)

mem <- spatialEigenvectors(coords)
alpha <- alphaDiversity(species, q = 0)
part <- spatialPartition(alpha$q0, mem)
print(part)
```

---

spatialRarefaction *Spatially-Constrained Rarefaction*

Description

Compute expected species richness accounting for spatial autocorrelation (Chiarucci et al. 2009). Uses distance-weighted sampling probabilities.

Usage

```
spatialRarefaction(x, coords, n_perm = 100, bandwidth = NULL)
```

Arguments

x	A site-by-species matrix.
coords	A data.frame with x and y columns.
n_perm	Number of permutations. Default 100.
bandwidth	Distance bandwidth for spatial weighting.

Value

A data.frame with columns: sites, mean, sd, lower, upper

References

Chiarucci, A., Bacaro, G., Rocchini, D. & Fattorini, L. (2009). Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. Community Ecology, 10, 195-199.

`subsample` *Spatial Subsampling*

Description

Reduce spatial autocorrelation by subsampling sites using various methods.

Usage

```
subsample(
  coords,
  n = NULL,
  method = c("grid", "random", "thinning"),
  cell_size = NULL,
  min_dist = NULL,
  seed = NULL
)
```

Arguments

`coords`	A data.frame with columns `x` and `y` containing site coordinates.
`n`	Integer. Target number of sites to retain. If `NULL`, determined by `cell_size` or `min_dist`.
`method`	Character. Subsampling method: `"grid"` (default), `"random"`, or `"thinning"`.
`cell_size`	Numeric. Grid cell size for `method = "grid"`. One site retained per cell.
`min_dist`	Numeric. Minimum distance between retained sites for `method = "thinning"`.
`seed`	Integer. Random seed for reproducibility.

Details

Methods:

- `"grid"`: Overlay a grid and retain one random site per cell.
- `"random"`: Simple random subsample of n sites.
- `"thinning"`: Iteratively remove sites until minimum distance is achieved.

Value

Integer vector of row indices to retain.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., et al. (2015). spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38, 541-545.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2004). Contribution of rarity and commonness to patterns of species richness. Ecology Letters, 7, 81-87.

Examples

```
coords <- data.frame(x = runif(50) * 100, y = runif(50) * 100)
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)

keep <- subsample(coords, method = "grid", cell_size = 20)
sac <- spacc(species[keep, ], coords[keep, ])
```

---

wavefront *Wavefront Expansion Accumulation*

Description

Accumulate species within an expanding radius from seed points. Models invasion spread from introduction points.

Usage

```
wavefront(
  x,
  coords,
  n_seeds = 50L,
  r0 = 0,
  dr = NULL,
  n_steps = 50L,
  distance = c("euclidean", "haversine"),
  progress = TRUE,
  seed = NULL
)
```

Arguments

x	A site-by-species matrix.
coords	A data.frame with x and y columns, or a spacc_dist object.
n_seeds	Integer. Number of random starting points.
r0	Numeric. Initial radius. Default 0.
dr	Numeric. Radius increment per step. Default auto-calculated.
n_steps	Integer. Number of expansion steps. Default 50.
distance	Character. Distance method.
progress	Logical. Show progress?
seed	Integer. Random seed.

Value

An object of class `spacc_wavefront` containing:

`curves`	Matrix of species counts (n_seeds x n_steps)
`radius`	Vector of radius values
`sites_included`	Matrix of sites included at each step

References

Shigesada, N. & Kawasaki, K. (1997). Biological Invasions: Theory and Practice. Oxford University Press.

Examples

```
coords <- data.frame(x = runif(50), y = runif(50))
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
wf <- wavefront(species, coords, n_seeds = 20, n_steps = 50)
plot(wf)
```

---

zetaDiversity *Zeta Diversity*

Description

Compute zeta diversity — the mean number of species shared across k sites — for increasing orders of k. The zeta decline curve reveals community assembly processes: exponential decline suggests stochastic assembly, while power-law decline indicates niche-based assembly.

Usage

```
zetaDiversity(
  x,
  coords,
  orders = 1:10,
  n_samples = 100L,
  method = c("knn", "random"),
  distance = c("euclidean", "haversine"),
  seed = NULL,
  progress = TRUE
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance). Automatically binarized.
coords	A data.frame with columns x and y, or a spacc_dist object.
orders	Integer vector. Orders of zeta diversity to compute (number of sites in each combination). Default 1:10.
n_samples	Integer. Number of random combinations to sample per order. Default 100.
method	Character. Method for selecting k-site combinations: "knn" (spatially nearest sites) or "random" (random combinations). Default "knn".
distance	Character. Distance method: "euclidean" or "haversine".
seed	Integer. Random seed for reproducibility. Default NULL.
progress	Logical. Show progress? Default TRUE.

Details

Zeta diversity of order k (ζ_k) is the mean number of species shared across k sites. Key properties:

- ζ_1 = mean species richness per site
- ζ_2 = mean number of species shared by any two sites
- ζ_k decreases monotonically with k

The zeta decline ratio (ζ_k / ζ_{k-1}) is diagnostic:

- Constant ratio: exponential decline (stochastic assembly)
- Increasing ratio: power-law decline (deterministic/niche-based assembly)

The knn method selects spatially nearest k sites from each focal site, which is ecologically meaningful for testing spatial turnover. The random method samples random k-site combinations, providing a null expectation.

Value

An object of class spacc_zeta containing:

zeta	Mean zeta values per order
zeta_sd	Standard deviations per order
orders	The k values
n_samples	Number of samples per order
ratio	Zeta ratio: zeta_k / zeta_(k-1)
decline	Data.frame with exponential and power-law fit statistics
method	Method used
n_sites	Number of sites
n_species	Total species count

References

Hui, C. & McGeoch, M.A. (2014). Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. The American Naturalist, 184, 684-694.

Latombe, G., McGeoch, M.A., Nipperess, D.A. & Hui, C. (2018). zetadiv: an R package for computing compositional change across multiple sites, assemblages or cases. bioRxiv, 324897.

See Also

`spaccBeta()` for pairwise beta diversity, `distanceDecay()` for distance-decay relationships

Examples

```
coords <- data.frame(x = runif(30), y = runif(30))
species <- matrix(rbinom(30 * 20, 1, 0.3), nrow = 30)
zeta <- zetaDiversity(species, coords, orders = 1:5, n_samples = 50)
plot(zeta)
```

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