

Package ‘space’

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Title Fast Spatial Species Accumulation Curves

Version 0.11.0

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Description High-performance spatial species accumulation curves using fixed-focus spatially constrained rarefaction, nearest-centroid expansion, and nearest-neighbor walks with a C++ backend for speed. Supports Hill numbers ($q=0,1,2$), beta diversity partitioning (turnover/nestedness) at site and pooled resolution, coverage-based rarefaction and extrapolation of alpha and beta diversity, phylogenetic diversity (PD; Faith's PD, EvoHeritage, mean pairwise distance, mean nearest taxon distance), functional diversity accumulation including aggregated functional diversity and intraspecific trait variation, phylogenetic and functional redundancy, interaction network accumulation, diversity-area relationships (DAR), endemism-area curves, sampling-effort correction and fragmentation analysis, species-area relationship (SAR) models based on extreme value theory (EVT), and area-based richness extrapolation via the total-species curve. Total richness is also estimated from frequency counts, including the accumulation rate curve estimator and an estimator for sites sampled without replacement, and shift-and-rotate null models test the position of a sampling design. 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/ece3.4425>, Borda-de-Agua et al. (2025) <doi:10.1038/s41467-025-59239-7>, Hanski et al. (2013) <doi:10.1073/pnas.1311190110>, Jost (2007) <doi:10.1890/06-1736.1>, Ugland et al. (2003) <doi:10.1046/j.1365-2656.2003.00748.x>, Chao et al. (2023) <doi:10.1002/ecm.1588>, Chiu (2023) <doi:10.1111/2041-210X.14146>, Chiu et al. (2023) <doi:10.1098/rstb.2022.0183>, Rosindell et al. (2024) <doi:10.1093/sysbio/syad072>.

Wojcik et al. (2024) <[doi:10.1111/2041-210X.14470](https://doi.org/10.1111/2041-210X.14470)>,
Ridder et al. (2024) <[doi:10.1111/2041-210X.14443](https://doi.org/10.1111/2041-210X.14443)>,
Jones et al. (2025) <[doi:10.1111/ddi.70080](https://doi.org/10.1111/ddi.70080)>,
and Shestopaloff (2025) <[doi:10.1007/s10651-025-00644-y](https://doi.org/10.1007/s10651-025-00644-y)>.

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ace	<i>ACE Richness Estimator</i>
-----	-------------------------------

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	<i>Alpha Diversity (Per-Site)</i>
----------------	-----------------------------------

Description

Compute Hill numbers for each site individually.

Usage

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

Arguments

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

Description

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

arc	<i>Accumulation Rate Curve (ARC) Richness Estimator</i>
-----	---

Description

Estimate total species richness from the rate at which new species appear along a random reordering of the observations (Shestopaloff 2025). The rate curve is extrapolated with three decay curves whose tails give the number of species not yet seen, combined with bounded weights.

Usage

```
arc(
  x,
  data = c("abundance", "incidence"),
  K = 20L,
  adjust = FALSE,
  n_boot = 2000L,
  parallel = TRUE,
  n_cores = NULL
)
```

Arguments

x	A site-by-species matrix. For data = "abundance" the columns are pooled into species abundances; for data = "incidence" the matrix is binarized and each species counts the sites it occupies.
data	Character. "abundance" (default) treats every individual as one observation; "incidence" treats every species-site occurrence as one.
K	Integer. Species seen more than K times are left out of the rate curve. Default 20.
adjust	Logical. Apply the smoothing adjustment of Eq. 11 with a log-linear fit to the frequency counts? Default FALSE. See Details.
n_boot	Integer. Parametric bootstrap draws for the interval. Default 2000. 0 returns the point estimate only.
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.

Details

Let y_k be the number of species observed k times and N the number of observations of the species with $k \leq K$. Drawing the observations in random order, the expected number of these species seen after n draws is

$$S(n) = \sum_{k=1}^K y_k [1 - (1 - n/N)^k],$$

and the accumulation rate is $s_n = S(n) - S(n-1)$, evaluated at up to 1000 points. Three curves are fitted to the tail of s_n by least squares with weights proportional to the squared point index: the log-normal $1 - \Phi((\log n - \mu)/\sigma)$, the log-logistic $1/(1 + \alpha n^\gamma)$ and the Weibull $\exp(-\lambda n^\gamma)$, the last on the log scale. Each curve's integral from N to infinity is its number of undetected species; the log-logistic integral is finite only for $\gamma > 1$.

The estimate combines the three with weights fitted by the squared misfit to s_n plus a penalty on the product of the log-logistic and Weibull weights (Eq. 8), each bounded by caps built from the three estimates and the observed richness (Eq. 7). The undetected species are averaged over fits to the last 100, 95, ..., 70 percent of the curve.

The penalty is there to make the fit prefer either the log-logistic or the Weibull, and gives the loss one local minimum for each. The weights are the end point of the projected gradient flow of the loss started at zero weights, which `arc()` solves in closed form face by face of the box of admissible weights. This is the minimum the author's reference code reaches (L-BFGS within an augmented Lagrangian, started at zero). In Poisson-Gamma samples of intermediate sparsity it is the log-logistic one, with median bias between -1 and +4 percent; the global minimum of the loss is the Weibull one there, with median bias between -9 and -17 percent (`vignette("richness-estimation")`).

With `adjust = TRUE` the counts $y_1, \dots, y_{k_1}$ (the first run of positive counts) are mixed half and half with a log-linear fit $\log y_k = b_0 + b_1 k$, and fully replaced by it; the adjusted estimate is $2S_{0.5} - S_1$. The adjustment assumes the ratios $(k+1)y_{k+1}/y_k$ are linear in k .

The interval comes from a parametric bootstrap of the counts. Their covariance is that of a mixture of 30 Poisson distributions whose weights are fitted to $(y_1, \dots, y_K, y_{K+})$ by penalised least squares (Eq. 12-15). The penalty is chosen by resampling species: 1500 resamples are ordered

by their distance to the left-out species and split into deciles, and the first decile whose out-of-sample error is smallest at a non-zero penalty sets it. `n_boot` count vectors are drawn from a normal distribution with that covariance, rounded to non-negative integers and re-estimated; the interval is their 2.5 and 97.5 percent quantiles and the standard error their standard deviation. In Poisson-Gamma simulations the 95 percent interval covered the truth in 93 to 96 percent of samples for sparse data and about 89 percent for dense data, where the point estimate is biased upwards (`vignette("richness-estimation")`).

With `data = "incidence"` the observations are species-site occurrences and y_k becomes Q_k , the number of species found at k sites, the substitution that turns Chao1 into Chao2.

Value

An object of class `spacc_estimate` with `estimator = "ARC"`. Its details hold undetected (undetected species from each curve) and weights (their weights), both averaged over the curve portions, `K`, `data`, `penalty` (the selected Poisson-mixture penalty) and `boot` (the bootstrap estimates).

References

Shestopaloff, K. (2025). An accumulation rate curve estimator for total species. *Environmental and Ecological Statistics*, 32, 311-345. doi:10.1007/s1065102500644y

See Also

`chao1()`, `chao2()`, `ace()`

Examples

```
set.seed(1)
species <- matrix(rpois(40 * 300, rgamma(300, 0.4, 2)), nrow = 40, byrow = TRUE)
arc(species, n_boot = 0)

arc(species, n_boot = 200)
```

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)
}
```

as_spacc	<i>Convert an Accumulation Curve from Another Package to a spacc Object</i>
----------	---

Description

Bring an existing species accumulation curve into the spacc object system so it can be summarised, plotted, extrapolated and compared with [compare\(\)](#) alongside spatial curves.

Usage

```
as_spacc(x, ...)
```

Default S3 method:

```
as_spacc(x, ...)
```

S3 method for class 'specaccum'

```
as_spacc(x, ...)
```

S3 method for class 'numeric'

```
as_spacc(x, ...)
```

S3 method for class 'data.frame'

```
as_spacc(x, column = NULL, ...)
```

Arguments

<code>x</code>	An object to convert: a <code>specaccum</code> object from <code>vegan::specaccum()</code> , a numeric vector holding one accumulation curve, or a data frame with such a curve in one column (for example the output of <code>Rarefy::directionalSAC()</code> or <code>Rarefy::rare_alpha()</code>).
<code>...</code>	Ignored, for method extensibility.
<code>column</code>	For a data frame, the name of the column holding the curve. <code>NULL</code> (default) uses <code>N_SCR</code> (the spatially constrained curve of <code>Rarefy::directionalSAC()</code>) or <code>Rarefaction</code> (<code>Rarefy::rare_alpha()</code>), whichever is present.

Details

A `specaccum` object built with `method = "random"` stores one richness curve per permutation in its `perm` matrix. Those curves become the rows of the returned curves matrix and behave exactly like `spacc` seeds, so the across-curve confidence band and the `compare()` permutation, bootstrap, and AUC tests carry over unchanged. A `specaccum` object without a permutation matrix (for example `method = "exact"` or `"collector"`), a numeric vector and a data frame column each contribute a single mean curve, entry `k` being the value after `k` sites.

`Rarefy::directionalSAC(community, gradient)` with a site distance matrix as `gradient` orders the sites by distance from each plot in turn and averages the collector curves; this is `spacc(x, coords, method = "knn", focal_points = coords)`, so the two curves agree up to the order of sites at tied distances.

Coordinates cannot be recovered from these objects, so the result carries no `coords`: it is a curve container for plotting and comparison, not a re-runnable spatial object.

Value

An object of class `spacc` with `print()`, `summary()`, `plot()`, `as.data.frame()`, and `compare()` support.

References

Thouverai, E., Pavoine, S., Tordoni, E., Chiarucci, A., Ricotta, C., Rocchini, D. & Bacaro, G. (2026). Rarefy: an R package for the calculation of taxonomic, functional and phylogenetic sample-based spatially explicit rarefaction curves. *Ecological Informatics*, 103803. doi:10.1016/j.ecoinf.2026.103803

See Also

`compare()` to test a converted curve against a spatial one.

Examples

```
if (requireNamespace("vegan", quietly = TRUE)) {
  data(BCI, package = "vegan")
  classic <- vegan::specaccum(BCI, method = "random")
  sp <- as_spacc(classic)
  summary(sp)
  plot(sp)
```

```

}

as_spacc(c(5, 8, 10, 11, 12))

```

autoplot.spacc	<i>Autoplot Methods for spacc Objects</i>
----------------	---

Description

`ggplot2::autoplot()` methods for `spacc` objects. Each one calls the corresponding `plot()` method, which already returns a `ggplot2` object.

Usage

```

## S3 method for class 'spacc'
autoplot(object, ...)

```

Arguments

<code>object</code>	A <code>spacc</code> object.
<code>...</code>	Additional arguments passed to the corresponding <code>plot()</code> 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:

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

<code>bootstrap_richness</code>	<i>Bootstrap Richness Estimator</i>
---------------------------------	-------------------------------------

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	<i>Combine spacc_beta Objects</i>
--------------	-----------------------------------

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	<i>Combine spacc_coverage Objects</i>
------------------	---------------------------------------

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	<i>Combine spacc_hill Objects</i>
--------------	-----------------------------------

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	<i>Chao1 Richness Estimator</i>
-------	---------------------------------

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	<i>Chao2 Richness Estimator</i>
-------	---------------------------------

Description

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

Usage

```
chao2(x, n_units = NULL)
```

Arguments

- x** A site-by-species matrix (presence/absence or abundance). Automatically binarized.
- n_units** Total number of sampling units in the study region, when the rows of `x` are a sample drawn without replacement from a finite set of units (atlas cells, a plot network). `NULL` (default) or `Inf` assumes sampling with replacement and gives Chao2; a finite value gives the MoRE estimator of Chiu (2023).

Details

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

$$S_{Chao2} = S_{obs} + \frac{t-1}{t} \frac{Q_1^2}{2Q_2}$$

where t is the number of sites, 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).

Chao2 assumes the sites are drawn with replacement, or from an effectively infinite set of units. When they are a large fraction $w = t/T$ of a finite set of T units it overestimates richness and does not reach the true richness as $w \rightarrow 1$. With `n_units = T`, `chao2()` returns the moment-based estimator for sampling without replacement (MoRE, Chiu 2023, Eq. 5):

$$S_{MoRE} = S_{obs} + \frac{t-1}{t} \frac{(1-w)Q_1^2}{Q_2 + w(Q_1 - Q_2)^+}$$

where $(A)^+$ is A for $A > 0$ and 1 otherwise; for $Q_2 = 0$ the undetected term is $\frac{t-1}{t} \frac{1-w}{w} (Q_1 - 1)$. MoRE equals the observed richness at $w = 1$. Its standard error is the delta-method variance of Chiu (2023) and the interval is the log-normal one used for Chao2.

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.
- Chiu, C.-H. (2023). A species richness estimator for sample-based incidence data sampled without replacement. *Methods in Ecology and Evolution*, 14, 2482-2493. doi:10.1111/2041210X.14146

See Also

[chao1\(\)](#) for abundance-based estimation

Examples

```
species <- matrix(rbinom(50 * 30, 1, 0.3), nrow = 50)
chao2(species)
# the 50 sites are 80% of a 62-cell grid
chao2(species, n_units = 62)
```

coleman	<i>Coleman Expected Accumulation</i>
---------	--------------------------------------

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	<i>Collector's Curve</i>
-----------	--------------------------

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:

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

<code>completenessProfile</code>	<i>Sample Completeness Profile</i>
----------------------------------	------------------------------------

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

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

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:

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

<code>confint.spacc_fit</code>	<i>Confidence interval for an extrapolated asymptote</i>
--------------------------------	--

Description

Returns the calibrated bootstrap interval stored on the fit by default. With `method = "profile"` the (over-confident) nls profile interval is computed instead. The interval is for the asymptote *parameter*; see the bias caveat in [extrapolate\(\)](#).

Usage

```
## S3 method for class 'spacc_fit'
confint(object, parm, level = 0.95, method = c("stored", "profile"), ...)
```

Arguments

<code>object</code>	A <code>spacc_fit</code> object.
<code>parm</code>	Ignored; the asymptote (" <i>a</i> ") is always returned.
<code>level</code>	Confidence level. Recomputed from stored bootstrap draws.
<code>method</code>	"stored" (default) or "profile".
<code>...</code>	Passed to stats::confint() when <code>method = "profile"</code> .

Value

A 1-row matrix with the lower and upper bound for *a*.

<code>dar</code>	<i>Diversity-Area Relationship (DAR)</i>
------------------	--

Description

Diversity against cumulative area along a spatial accumulation, for Hill numbers (Ma 2018) or for any curve `spacc` computes: species richness, phylogenetic and functional metrics, redundancy.

Usage

```
dar(x, ...)

## Default S3 method:
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,
    focal_points = NULL,
    focal_domain = NULL,
    ...
)

## S3 method for class 'spacc'
dar(x, area_method = c("convex_hull", "voronoi", "count"), ...)

## S3 method for class 'spacc_hill'
dar(x, area_method = c("convex_hull", "voronoi", "count"), ...)

## S3 method for class 'spacc_phylo'
dar(x, area_method = c("convex_hull", "voronoi", "count"), ...)

## S3 method for class 'spacc_func'
dar(x, area_method = c("convex_hull", "voronoi", "count"), ...)

## S3 method for class 'spacc_redundancy'
dar(x, area_method = c("convex_hull", "voronoi", "count"), ...)

```

Arguments

<code>x</code>	A site-by-species matrix (abundance data recommended), or a curve object: <code>spacc</code> , <code>spacc_hill</code> , <code>spacc_phylo</code> , <code>spacc_func</code> or <code>spacc_redundancy</code> . A matrix is first passed to <code>spaccHill()</code> with <code>q</code> .
<code>...</code>	Arguments passed to methods.
<code>coords</code>	A <code>data.frame</code> with columns <code>x</code> and <code>y</code> , or a <code>spacc_dist</code> object (matrix input only).
<code>q</code>	Numeric vector. Diversity orders (matrix input only). Default <code>c(0, 1, 2)</code> .
<code>n_seeds</code>	Integer. Number of random starting points. Default 50.
<code>method</code>	Character. Accumulation method: <code>"knn"</code> or <code>"nn_walk"</code> .
<code>area_method</code>	Character. How to measure the area covered by the first <code>k</code> sites of an order: <code>"convex_hull"</code> (area of their convex hull, 0 until three sites span a polygon), <code>"voronoi"</code> (summed area of their Voronoi cells within the bounding box of all sites) or <code>"count"</code> (number of sites). Areas are in squared coordinate units. Default <code>"convex_hull"</code> .
<code>distance</code>	Character. Distance method. Default <code>"euclidean"</code> .
<code>parallel</code>	Logical. Use parallel processing? Default <code>TRUE</code> .
<code>n_cores</code>	Integer. Number of cores.
<code>progress</code>	Logical. Show progress? Default <code>TRUE</code> .

seed	Integer. Random seed.
focal_points	Optional focal points for method = "knn". See spacc() .
focal_domain	Optional polygonal focal domain. See spacc() .

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

The area is accumulated along the same site orders as the diversity curve, so any curve object gives its own diversity-area relationship: functional richness, dispersion and other facets can scale with area differently from richness (Dias et al. 2025). The power-law exponent z is the slope of log mean diversity against log mean area over the steps where both are positive.

Value

An object of class `spacc_dar` containing:

curves	Named list of diversity curves ($n\_seeds \times n\_sites$), one per metric or order
metric	Names of the curves
area	Matrix of cumulative areas ($n\_seeds \times n\_sites$)
power_law	Data frame with the power-law fit $D = cA^z$ of each mean curve (metric, c, z)
q	Diversity orders for Hill-number input, else NULL
area_method	Method used for area estimation
source	Class of the curve object the DAR was built from
object	That curve object

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.
- Dias, R.A., Bastazini, V.A.G., Gianuca, A.T. & Matthews, T.J. (2025). The spatial scaling of multiple dimensions of functional diversity in habitat islands. *Functional Ecology*. doi:10.1111/1365-2435.70158

See Also

[spaccHill\(\)](#), [spaccFunc\(\)](#), [spaccPhylo\(\)](#), [extrapolate\(\)](#)

Examples

```

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

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

traits <- matrix(rnorm(30 * 2), nrow = 30)
func <- spaccFunc(species, coords, traits, metric = c("fdis", "fric"))
dar(func)

```

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	<i>Compute Distance Matrix</i>
-----------	--------------------------------

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 <code>data.frame</code> with columns <code>x</code> and <code>y</code> • An <code>sf</code> object with <code>POINT</code> geometries • An <code>sfc_POINT</code> 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 <code>sf/S2</code> (for global scale) Default is auto-detected from CRS when using <code>sf</code> objects.
fun	Optional custom distance function. Must take two coordinate vectors (<code>x</code> , <code>y</code>) and return a distance matrix. Overrides <code>method</code> .
which	For <code>sf</code> 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

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

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:

<code>alpha</code>	Mean alpha diversity (effective number of species per site)
<code>beta</code>	Beta diversity (effective number of communities)
<code>gamma</code>	Gamma diversity (regional species pool)
<code>q</code>	Orders of diversity
<code>n_sites</code>	Number of sites
<code>n_species</code>	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"),
  traits = NULL,
  tree = NULL,
  dist_method = c("euclidean", "gower"),
  normalize = TRUE,
  coords = NULL
)
```

Arguments

<code>x</code>	A site-by-species matrix (abundance data). Column names must match trait row names / tree tip labels when <code>traits</code> / <code>tree</code> is supplied.
<code>q</code>	Numeric vector. Orders of diversity to evaluate. Default <code>seq(0, 3, by = 0.1)</code> .
<code>type</code>	Character. What to compute: "per_site" (per-site profiles), "regional" (pooled gamma), or "both" (default).
<code>traits</code>	Optional species-by-traits data.frame (row names matching species). When supplied, functional Hill numbers (Leinster & Cobbold 2012) are computed.
<code>tree</code>	Optional <code>ape::phylo</code> object. When supplied, phylogenetic Hill numbers (Chao et al. 2010) are computed. Supply at most one of <code>traits</code> or <code>tree</code> .
<code>dist_method</code>	Character. Trait distance for the functional profile: "euclidean" (default) or "gower". Ignored unless <code>traits</code> is supplied.
<code>normalize</code>	Logical. Normalize trait distances to [0, 1]? Default TRUE. Ignored unless <code>traits</code> is supplied.
<code>coords</code>	Optional data.frame with columns <code>x</code> and <code>y</code> for spatial mapping. When provided, enables <code>plot(type = "map")</code> .

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

Supplying `traits` computes functional Hill numbers via a trait-similarity matrix (Leinster & Cobbold 2012); supplying `tree` computes phylogenetic Hill numbers weighted by branch length (Chao et al. 2010). Both return a `spacc_profile` whose `profile_type` records which was computed.

Value

An object of class `spacc_profile` containing:

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

# Functional profile (pass a species-by-traits data.frame)
colnames(species) <- paste0("sp", 1:30)
traits <- data.frame(size = rnorm(30), row.names = paste0("sp", 1:30))
fp <- diversityProfile(species, traits = traits)
```

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:

<code>per_site</code>	Matrix or vector of per-site evenness values
<code>regional</code>	Regional (pooled) evenness
<code>q</code>	Orders used (for Hill type)
<code>type</code>	Evenness type
<code>coords</code>	Coordinates if provided
<code>n_sites</code>	Number of sites
<code>n_species</code>	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 the spatial accumulation curve and estimate total species richness beyond the observed sampling effort.

Usage

```

extrapolate(
  object,
  model = c("michaelis-menten", "lomolino", "asymptotic", "weibull", "logistic", "evt"),
  interval = c("bootstrap", "profile", "none"),
  R = 200L,
  level = 0.95,
  compare = TRUE,
  n_units = NULL,
  warn_ratio = 2,
  ...
)

```

Arguments

<code>object</code>	A spacc object.
<code>model</code>	Character. Model to fit: "michaelis-menten" (default), "lomolino", "asymptotic", "weibull", "logistic", or "evt" (Extreme Value Theory, Borda-de-Agua et al. 2025).
<code>interval</code>	Character. How to build the asymptote confidence interval: "bootstrap" (default) refits the model across resampled seed curves and takes percentile bounds; "profile" uses the (over-confident) nls profile interval on the mean-curve fit; "none" skips it.
<code>R</code>	Integer. Number of bootstrap refits when <code>interval = "bootstrap"</code> . Default 200.
<code>level</code>	Numeric. Confidence level for the interval. Default 0.95.
<code>compare</code>	Logical. If TRUE (default) and the object carries incidence frequencies, compare the asymptote to the nonparametric <code>chao2()</code> / <code>iChao2()</code> estimates and flag large disagreement.
<code>n_units</code>	Total number of sampling units in the region when the sites are drawn without replacement from a finite set. With <code>compare = TRUE</code> the asymptote is then also compared with the MoRE estimator (<code>chao2(x, n_units =)</code> , Chiu 2023), which is the reference for the disagreement warning. Default NULL (sampling with replacement).
<code>warn_ratio</code>	Numeric. Warn when the fitted asymptote exceeds the observed richness by more than this factor. Default 2. Set to Inf to silence.
<code>...</code>	Additional arguments passed to <code>stats::nls()</code> .

Value

An object of class `spacc_fit` containing:

<code>asymptote</code>	Estimated total species richness (asymptote of the model)
<code>asymptote_ci</code>	Confidence interval for the asymptote
<code>model</code>	Model name

interval	Interval method used
fit	The nls fit object
aic	AIC of the model
gof	List with residual rmse and relative rmse_rel over the observed range
compare	Nonparametric chao2 / iChao2 estimates, and MoRE when n_units is given, if available
boot	Bootstrap coefficient draws, if interval = "bootstrap"

Bias caveat

The asymptote is a *parametric extrapolation* of the accumulation curve. On clustered or strongly under-sampled presence-absence data it tends to overestimate true richness, sometimes substantially, because the curve is far from saturation. The bootstrap interval quantifies the uncertainty of the fitted asymptote (curve-fit and across-seed variability) and is much wider than the nls profile interval, but it is *not* a calibrated interval for true total richness: it is centred on a possibly biased point estimate. For calibrated total-richness estimates prefer the nonparametric estimators [chao2\(\)](#) / [iChao2\(\)](#), which are unbiased on the same data. The printout shows their values alongside the asymptote for comparison.

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.

See Also

[extrapolateArea\(\)](#) for area-based extrapolation to a region larger than the one sampled; [chao2\(\)](#), [iChao2\(\)](#) for nonparametric richness.

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)
```

extrapolateArea	<i>Extrapolate Richness to a Larger Area (Ugland T-S Curve)</i>
-----------------	---

Description

Estimate species richness for a spatial extent larger than the one sampled, using the total-species (T-S) curve of Ugland, Gray & Ellingsen (2003). Sites are partitioned into spatial subareas; the T-S curve is the expected total richness of random combinations of subareas plotted against their (convex-hull) area; an asymptotic model is fitted to that curve and extrapolated to a target area, with a site-bootstrap confidence interval.

Usage

```
extrapolateArea(
  x,
  coords,
  target_area = NULL,
  n_subareas = 10L,
  model = c("michaelis-menten", "asymptotic", "weibull", "lomolino", "logistic"),
  n_combos = 30L,
  R = 200L,
  level = 0.95,
  seed = NULL,
  progress = TRUE
)
```

Arguments

x	A site-by-species matrix (presence/absence or abundance; binarized).
coords	A two-column matrix or data frame of site coordinates (x, y).
target_area	Numeric. Area to extrapolate to, in the squared units of coords. Defaults to twice the observed (convex-hull) area.
n_subareas	Integer. Number of spatial subareas to partition sites into (k-means on coordinates). Default 10; must be between 4 and the number of sites.
model	Character. Area model to fit: "michaelis-menten" (default), "asymptotic", "weibull", "lomolino", or "logistic".
n_combos	Integer. Number of random subarea combinations averaged per T-S point (all combinations are used when there are fewer). Default 30.
R	Integer. Number of site-bootstrap replicates for the confidence interval. Default 200.
level	Numeric. Confidence level. Default 0.95.
seed	Optional integer for reproducibility.
progress	Logical. Show a progress message. Default TRUE.

Details

Unlike `extrapolate()`, which extends the curve in *sample count*, this answers "how many species in a region of a given *area*", including areas beyond the sampled extent.

Value

An object of class `spacc_area` with components:

<code>ts_curve</code>	Data frame of the T-S curve (<code>n_sub</code> , <code>area</code> , <code>richness</code> , <code>richness_sd</code>)
<code>fit</code>	The fitted nls area model
<code>observed_area</code> , <code>observed_richness</code>	Convex-hull area and richness of the full sample
<code>target_area</code>	Area extrapolated to
<code>predicted_richness</code> , <code>predicted_ci</code>	Extrapolated richness and its bootstrap interval
<code>asymptote</code> , <code>asymptote_ci</code>	Model asymptote and its bootstrap interval

References

Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003). The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, 72, 888-897. doi:[10.1046/j.13652656.2003.00748.x](https://doi.org/10.1046/j.13652656.2003.00748.x)

See Also

`extrapolate()` for sample-count extrapolation; `chao2()` for nonparametric richness.

Examples

```
coords <- data.frame(x = runif(150), y = runif(150))
species <- matrix(rbinom(150 * 60, 1, 0.15), nrow = 150)
area_fit <- extrapolateArea(species, coords, n_subareas = 8, progress = FALSE)
print(area_fit)
```

extrapolateCoverage *Extrapolate Diversity Beyond Observed Coverage*

Description

Hill numbers at target sample coverages along a coverage-tracking accumulation, interpolated within the observed coverage and extrapolated beyond it (Chao et al. 2014).

Usage

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

Arguments

x	A spacc_coverage object from spaccCoverage() (richness, q = 0 only) or a spacc_hill_coverage object from spaccHillCoverage() (any of its orders).
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: 0 (richness, default), or for a spacc_hill_coverage object one of its orders.

Details

A target at or below a seed's final coverage is read off that seed's spatial accumulation curve by linear interpolation in coverage. Above it, every seed has accumulated the same pooled sample, so the value is the coverage-based extrapolation of the pooled abundances (Chao et al. 2014): the sample size reaching the target coverage is found from the Chao-Jost coverage deficit, and the Hill number at that size approaches the Chao1 (q = 0), Chao et al. (2013) Shannon (q = 1) or unbiased Simpson (q = 2) asymptote; target_coverage = 1 gives the asymptote itself. Extrapolation is defined for integer q and for the individual-based coverage (coverage = "chao").

Value

An object of class spacc_coverage_ext containing:

richness	Matrix of interpolated/extrapolated Hill numbers of order q (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 Hill number of order q

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	<i>Gamma Diversity (Regional)</i>
----------------	-----------------------------------

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:

$$S_{iChao2} = S_{Chao2} + \frac{Q_3}{4Q_4} \max\left(Q_1 - \frac{Q_2Q_3}{2Q_4}, 0\right)$$

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	<i>Interpolate Richness at Target Coverage Levels</i>
---------------------	---

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	<i>Exact (Mao Tau) Expected Accumulation</i>
---------	--

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	<i>Plot Spatial SAC</i>
------------	-------------------------

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

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

<code>plot.spacc_metrics</code>	<i>Plot spacc_metrics</i>
---------------------------------	---------------------------

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 <code>spaccMetrics()</code> .
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)
```

predict.spacc_area	<i>Predict richness at a given area</i>
--------------------	---

Description

Predict richness at a given area

Usage

```
## S3 method for class 'spacc_area'
predict(
  object,
  area = NULL,
  interval = c("none", "bootstrap"),
  level = NULL,
  ...
)
```

Arguments

object	A spacc_area object.
area	Numeric vector of areas. Defaults to the observed T-S areas.
interval	"none" (default) or "bootstrap" for percentile bounds.
level	Confidence level. Defaults to the fit's level.
...	Unused.

Value

A numeric vector (point) or a data frame with area, fit, lower, upper.

predict.spacc_fit	<i>Predict richness at a given sampling effort</i>
-------------------	--

Description

Predict richness at a given sampling effort

Usage

```
## S3 method for class 'spacc_fit'
predict(object, n = NULL, interval = c("none", "bootstrap"), level = NULL, ...)
```

Arguments

object	A spacc_fit object.
n	Integer vector of site counts. Defaults to the observed range.
interval	"none" (default) returns point predictions; "bootstrap" returns a data frame with percentile bounds from the stored bootstrap draws.
level	Confidence level for the interval. Defaults to the fit's level.
...	Unused.

Value

A numeric vector (point) or a data frame with n, fit, lower, upper (interval).

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

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

Details

The expected Hill number of a random subsample of n individuals drawn without replacement from the pooled sample (Chao et al. 2014). Each species' subsample count is hypergeometric, and

$${}^qD(n) = \left(\sum_i E[(Y_i/n)^q] \right)^{1/(1-q)},$$

with the exponential of the expected Shannon entropy at $q = 1$. At $q = 0$ this is the Hurlbert (1971) formula. Sizes above the sample size are extrapolated towards the asymptotic estimators (Chao et al. 2014; integer q only).

Value

An object of class `spacc_rare` containing:

<code>n</code>	Sample sizes
<code>expected</code>	Expected diversity (Hill number of order q)
<code>sd</code>	Standard deviation
<code>lower, upper</code>	95 percent confidence bounds
<code>q</code>	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",
    "shift_rotate"),
  n_perm = 999L,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL
)
```

Arguments

<code>x</code>	A spacc output object. Supported classes: <code>spacc</code> , <code>spacc_hill</code> , <code>spacc_phylo</code> , <code>spacc_func</code> , <code>spacc_beta</code> , <code>spacc_metrics</code> , <code>spacc_alpha</code> , <code>spacc_partition</code> .
<code>species</code>	A site-by-species matrix (required). The species matrix used to produce <code>x</code> . Needed because <code>spacc</code> objects do not store the raw species matrix.
<code>coords</code>	Optional data.frame with columns <code>x</code> and <code>y</code> . Required if the original analysis used coordinates. If <code>x</code> contains stored coordinates, they will be used automatically.
<code>metric</code>	Character or NULL. For multi-metric objects (e.g., <code>spacc_hill</code> with multiple <code>q</code>), specify which metric to extract. If NULL, uses the first/default metric.
<code>null_model</code>	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 <code>coords</code>. • "spatial_swap": Independent swap restricted to spatially proximate site pairs. Preserves both marginals while respecting spatial structure. Requires <code>coords</code>. • "shift_rotate": Keeps the community and moves the sampling design: the user-supplied focal points of a method = "knn" analysis are rotated by a random angle and shifted by a random offset (Ridder et al. 2024). Requires <code>coords</code>.
<code>n_perm</code>	Integer. Number of permutations. Default 999.
<code>parallel</code>	Logical. Use parallel processing for the underlying analysis? Default TRUE.
<code>n_cores</code>	Integer. Number of cores. Default NULL (auto-detect).
<code>progress</code>	Logical. Show progress? Default TRUE.
<code>seed</code>	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
- "shift_rotate": The permutation nulls destroy the spatial structure of the community, so a spatially structured curve differs from almost any of them. The shift-and-rotate null keeps that structure intact and asks instead whether the curve depends on where the fixed design sits within it: each replicate moves the focal points by a rigid motion (rotation about their centroid, shift within the extent of the sites), drops those that leave the convex hull of the sites, and recomputes the curve. It is defined only for a fixed design; randomly drawn focal points are already a sample over all positions.

For method = "knn" analyses the permutation nulls reuse the observed focal points, so observed and null curves share one design.

Value

An object of class `spacc_ses` containing:

<code>observed</code>	Numeric vector of observed metric values
<code>null_mean</code>	Mean of null distribution
<code>null_sd</code>	Standard deviation of null distribution
<code>ses</code>	Standardized effect size: $(\text{observed} - \text{null\_mean}) / \text{null\_sd}$
<code>p_value</code>	Two-tailed p-value
<code>n_perm</code>	Number of permutations
<code>null_model</code>	Null model algorithm used
<code>metric</code>	Metric name
<code>input_class</code>	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.
- Ridder, G., Hardy, O.J. & Ovaskainen, O. (2024). Generating spatially realistic environmental null models with the shift-&-rotate approach helps evaluate false positives in species distribution modelling. *Methods in Ecology and Evolution*, 15, 2331-2342. doi:[10.1111/2041210X.14443](https://doi.org/10.1111/2041210X.14443)

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	<i>Sampling Effort Species-Area Relationship (SESARS)</i>
--------	---

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 <code>stats::nls()</code> or <code>stats::lm()</code> .

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

<code>object</code>	A <code>spacc</code> object.
<code>patches</code>	Factor or integer vector assigning each site to a habitat fragment (patch). Must have length equal to the number of sites.
<code>model</code>	Character. SFAR model: "power" (default): $S = c * A^z * n^{-f}$ "log": $\log(S) = \log(c) + z\log(A) - f\log(n)$
<code>...</code>	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:

<code>fit</code>	Fitted model object
<code>coef</code>	Coefficients: <code>c</code> (intercept), <code>z</code> (area exponent), <code>f</code> (fragmentation exponent)
<code>n_patches</code>	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", "nn_walk", "random", "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,
focal_points = NULL,
focal_domain = 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 focal points or starting sites for uncertainty quantification. Default 50.
method	Character. Accumulation method: • "knn": fixed-focus spatially constrained rarefaction • "kncn": k-Nearest Centroid Neighbor (visit closest to centroid) • "nn_walk": nearest-neighbour walk (move from the current site to the closest unvisited site) • "random": Random order (null model) • "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 nn_walk 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. A supplied distance matrix (spacc_dist coordinates or the spatiotemporal composite built from time) is always used as given, so those inputs take the exact backend.

support	Optional. Spatial support for core/halo classification via <code>areaOfEffect::aoe()</code> . 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: <code>c("France", "Germany")</code> • 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 <code>detectCores()</code> - 1.
progress	Logical. Show progress bar? Default TRUE.
groups	Optional. A factor, character, or integer vector of length <code>ncol(x)</code> 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 <code>nrow(x)</code> giving a temporal coordinate for each site. When provided, a combined spatiotemporal distance matrix is computed as <code>w_space * d_spatial + w_time * d_temporal</code> 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: "nn_walk", "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.
focal_points	Optional data frame or sf point object with x and y coordinates. For method = "knn", each row is a fixed focal point and sites are accumulated by increasing distance from it. When supplied, <code>n_seeds</code> is set to the number of focal points. Default NULL samples continuous focal points uniformly from the spatial domain.
focal_domain	Optional sf or sfc polygon defining the domain from which continuous knn focal points are sampled. When omitted, the convex hull of the eligible site coordinates is used. For haversine distances, hull sampling uses a local equal-area projection. Supplying the study polygon preserves concavities, holes, and disconnected components in irregular sampling domains. Its coordinates must use the same coordinate reference system as <code>coords</code> .

- 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`.

Details

The canonical knn method follows Chiarucci et al. (2009): each curve uses one fixed focal point and accumulates sites by increasing distance from that point. The `nn_walk` method is a greedy traversal whose reference point moves to the most recently selected site. The two methods represent different spatial sampling models.

Every method is a rule for ordering the sites; the species data are then accumulated along those orders. The `orders` element of the result lets the same traversals be reused, for example through the `order` argument.

Value

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

<code>curves</code>	Matrix of cumulative species counts (<code>n_seeds</code> x <code>n_sites</code>)
<code>orders</code>	Matrix of 1-based site indices (<code>n_seeds</code> x <code>n_sites</code>): the order in which each curve visited the sites
<code>coords</code>	Original coordinates
<code>n_seeds</code>	Number of seeds used
<code>method</code>	Method used
<code>n_species</code>	Total species in dataset
<code>focal_points</code>	Continuous focal points used by <code>method = "knn"</code>

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., Rocchini, D., Ricotta, C., Palmer, M.W. & Scheiner, S.M. (2009). Spatially constrained rarefaction: incorporating the autocorrelated structure of biological communities into sample-based rarefaction. *Community Ecology*, 10, 209-214.

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,
  traits = NULL,
  tree = NULL,
  n_seeds = 50L,
  method = c("knn", "nn_walk"),
  index = c("sorensen", "jaccard"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE,
  focal_points = NULL,
  focal_domain = NULL,
  pool = 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	Optional species-by-traits matrix or data.frame (row names matching species). When supplied, functional beta diversity is computed.
tree	Optional phylogenetic tree of class phylo, or a pairwise phylogenetic distance matrix. When supplied, phylogenetic beta diversity is computed. Supply at most one of traits or tree.

n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method: "knn" or "nn_walk".
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 <code>as_sf()</code> and <code>plot(type = "map")</code> . Default FALSE.
focal_points	Optional focal points for method = "knn". See <code>spacc()</code> .
focal_domain	Optional polygonal focal domain. See <code>spacc()</code> .
pool	Optional vector with one value per site (habitat, degradation level, region) grouping sites into pools. The partition is then also computed between pooled assemblages along the same orders.

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.

Supplying `traits` computes functional beta diversity, weighting the partition by the trait distinctiveness of the species exchanged between the accumulated pool and each new site. Supplying `tree` computes phylogenetic beta diversity (PhyloSor), weighting by shared branch length. The taxonomic, functional, and phylogenetic variants all return a `spacc_beta` object whose `beta_type` field records which was computed. `map = TRUE` is supported for the taxonomic variant only.

With `pool`, sites are aggregated into pooled assemblages (a species is present in a pool if it occurs in any of its sites) and the partition is repeated between pools: each site order becomes the order in which its pools are first reached, and the distance between two pools is the mean distance between their sites. Partitions at the two resolutions can disagree, for example when degraded habitats are homogenised at the pool level while individual sites still differ (Jones et al. 2025). `summary(x, resolution = "pooled")` and `plot(x, resolution = "pooled")` or "both" show the pooled partition.

Value

An object of class `spacc_beta` containing:

<code>beta_total</code>	Matrix of total beta diversity (<code>n_seeds</code> x <code>n_sites</code> -1)
<code>beta_turnover</code>	Matrix of turnover component
<code>beta_nestedness</code>	Matrix of nestedness component
<code>distance</code>	Matrix of cumulative distances
<code>pooled</code>	With <code>pool</code> : the same four matrices for the pooled assemblages (<code>n_seeds</code> x <code>n_pools</code> -1), plus <code>pool</code> and <code>n_pools</code> ; else <code>NULL</code>
<code>n_seeds</code> , <code>n_sites</code> , <code>method</code> , <code>index</code>	Parameters used

References

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

Jones, F.A.M., Hardenbol, A.A., Hekkala, A.-M., et al. (2025). Partitioning beta diversity at two spatial resolutions reveals biotic homogenisation with habitat degradation. *Diversity and Distributions*, 31, e70080. doi:[10.1111/ddi.70080](https://doi.org/10.1111/ddi.70080)

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")

# Functional beta diversity (pass a species-by-traits matrix)
traits <- matrix(rnorm(30 * 3), nrow = 30)
rownames(traits) <- colnames(species) <- paste0("sp", 1:30)
beta_func <- spaccBeta(species, coords, traits = traits)
```

spaccCoverage	<i>Coverage-Based Spatial Rarefaction</i>
---------------	---

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 = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  coverage = c("chao", "chiu"),
  n_units = NULL,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE,
  focal_points = NULL,
  focal_domain = NULL
)
```

Arguments

<code>x</code>	A site-by-species matrix with abundance data.
<code>coords</code>	A data.frame with columns <code>x</code> and <code>y</code> , or a <code>spacc_dist</code> object.
<code>n_seeds</code>	Integer. Number of random starting points. Default 50.
<code>method</code>	Character. Accumulation method: canonical fixed-focus "knn" or "nn_walk". Default "knn".
<code>distance</code>	Character. Distance method: "euclidean" or "haversine".
<code>coverage</code>	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.
<code>n_units</code>	Total number of sampling units in the study region, when the sites are drawn without replacement from a finite set of units (atlas cells, a plot network). Requires <code>coverage = "chiu"</code> . NULL (default) or Inf assumes sampling with replacement. See Details.

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 <code>as_sf()</code> and <code>plot(type = "map")</code> . Default FALSE.
focal_points	Optional focal points for method = "knn". See <code>spacc()</code> .
focal_domain	Optional polygonal focal domain. See <code>spacc()</code> .

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 (f_1) and doubletons (f_2) 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: Q_1 (species in exactly 1 site), Q_2 (species in exactly 2 sites), and G_1 (total abundance of Q_1 species). It gives near-unbiased coverage estimates when organisms are spatially aggregated across sampling units. It writes the abundance of undetected species as the Chao2 estimate of their number, $\frac{t-1}{t} \frac{Q_1^2}{2Q_2}$ after t sites, times the mean abundance of a unique species, G_1/Q_1 .

With $n\_units = T$, the t sites are a fraction $w = t/T$ of a finite set of units drawn without replacement, and the number of undetected species is the MoRE term of `chao2(x, n_units = )` (Chiu 2023, Methods in Ecology and Evolution, Eq. 5),

$$\frac{t-1}{t} \frac{(1-w)Q_1^2}{Q_2 + w(Q_1 - Q_2)^+},$$

so richness and coverage of the same sample rest on one estimate of the undetected species. It vanishes at $w = 1$: the coverage reaches 1 once the accumulation has visited every unit. On simulated grids its error is lower than that of the with-replacement form from $w = 0.5$ on, and several-fold lower near a census; it is about equal at $w = 0.3$ and larger at $w = 0.1$ on a sparse grid (`vignette("extrapolation")`).

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 ($n\_seeds \times n\_sites$)
individuals	Matrix of individual counts
coverage	Matrix of coverage estimates
pooled	Species abundances pooled over all sites

coverage_type Coverage estimator used ("chao" or "chiu")
 n_units Number of units in the finite population, or NULL
 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 species richness estimator for sample-based incidence data sampled without replacement. *Methods in Ecology and Evolution*, 14, 2482-2493. doi:10.1111/2041210X.14146
- 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")

# The 50 sites are 80% of a 62-cell grid
cov_grid <- spaccCoverage(species, coords, coverage = "chiu", n_units = 62)

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

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", "nn_walk", "random", "collector"),
  incidence = FALSE,
  n_seeds = 50L,
  distance = c("euclidean", "haversine"),
  progress = TRUE,
  seed = NULL,
  focal_points = NULL,
  focal_domain = NULL
)

```

Arguments

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

Details

The site ordering reuses the same spatial traversals as the built-in methods (fixed-focus, nearest-neighbour walk, nearest-centroid, random, 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 = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  map = FALSE,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  focal_points = NULL,
  focal_domain = NULL
)
```

Arguments

<code>x</code>	A site-by-species matrix (presence/absence or abundance).
<code>coords</code>	A data.frame with columns <code>x</code> and <code>y</code> , or a <code>spacc_dist</code> object.
<code>n_seeds</code>	Integer. Number of random starting points. Default 50.
<code>method</code>	Character. Accumulation method. Default "knn".
<code>distance</code>	Character. Distance method: "euclidean" or "haversine".
<code>map</code>	Logical. If TRUE, compute per-site endemism by running accumulation from each site as seed. Stores a <code>site_values</code> data.frame enabling <code>plot(type = "map")</code> and <code>as_sf()</code> . Default FALSE.
<code>parallel</code>	Logical. Use parallel processing? Default TRUE.
<code>n_cores</code>	Integer. Number of cores.
<code>progress</code>	Logical. Show progress? Default TRUE.
<code>seed</code>	Integer. Random seed.
<code>focal_points</code>	Optional focal points for <code>method = "knn"</code> . See <code>spacc()</code> .
<code>focal_domain</code>	Optional polygonal focal domain. See <code>spacc()</code> .

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:

<code>richness</code>	Matrix of cumulative richness ($n\_seeds \times n\_sites$)
<code>endemism</code>	Matrix of endemic species count ($n\_seeds \times n\_sites$)
<code>site_values</code>	Per-site endemism data.frame (if <code>map = TRUE</code>)
<code>coords, n_seeds, n_sites, method</code>	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 = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE,
  focal_points = NULL,
  focal_domain = NULL,
  axis_length_k = NULL,
  itv = 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) • "K": aggregated functional diversity (Wojcik et al. 2024), reported with its four facets as k_richness, k_biomass_evenness, k_trait_evenness, k_dispersion and K
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method: "knn" or "nn_walk".
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 <code>plot(type = "map")</code> . Default FALSE.
focal_points	Optional focal points for method = "knn". See spacc() .
focal_domain	Optional polygonal focal domain. See spacc() .
axis_length_k	Numeric vector, one value per trait. Length of each trait axis for the richness facet of "K". Default NULL uses the range of each trait over all species in traits.
itv	Logical. Use intraspecific trait variability: traits is then a long data frame with one row per individual or population, a species column, an optional site column (matched like the sites of spaccNetwork()) and numeric trait columns. 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.
- **K (aggregated functional diversity)**: the geometric mean of four facets between 0 and 1, each equal to 1 when species are spread uniformly along the trait axis with equal abundances (Wojcik et al. 2024). Per trait, with the n present species sorted by trait value and relative abundances b_i : functional richness is the trait range over the axis length; biomass evenness compares the b_i with $1/n$; trait evenness compares the gaps between neighbouring trait values with an even spacing; dispersion is the abundance-weighted trait variance over that of a uniform distribution on the same range, capped at 1. Several traits combine as the geometric mean over traits, and each reported facet is its geometric mean over traits. Trait evenness needs three species: with two, K is the cube root of the other three facets and k_trait_evenness is NA. With fewer than two species K is 0. With presence/absence data biomass evenness is 1.

Intraspecific trait variability (`itv = TRUE`; Palacio et al. 2025). Each trait row is a unit of the community in place of a species: at each step the metrics are evaluated on the rows describing the accumulated sites, each weighted by its species' abundance at its site, shared equally among the rows describing that species there. Rows without a site (no `site` column, or NA) stand for the species at every site where it has no site-specific rows, so one row per species reproduces the species-mean curves. A widespread species whose traits change along a gradient then adds trait range as the accumulation reaches new parts of the gradient, which its mean trait value hides.

Value

An object of class `spacc_func` containing:

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

References

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

Palacio, F.X., Ottaviani, G., Mammola, S., Graco-Roza, C., de Bello, F. & Carmona, C.P. (2025). Integrating intraspecific trait variability in functional diversity: an overview of methods and a guide for ecologists. *Ecological Monographs*, 95, e70024. doi:10.1002/ecm.70024

Wojcik, L.A., Gaedke, U., van Velzen, E. & Klauschies, T. (2024). Measuring overall functional diversity by aggregating its multiple facets: functional richness, biomass evenness, trait evenness and dispersion. *Methods in Ecology and Evolution*, 16, 215-227. doi:10.1111/2041210X.14470

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 = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  map = FALSE,
  focal_points = NULL,
  focal_domain = NULL
)
```

Arguments

<code>x</code>	A site-by-species matrix (rows = sites, cols = species) with presence/absence (0/1) or abundance data.
<code>coords</code>	A data.frame with columns <code>x</code> and <code>y</code> containing site coordinates, or a <code>spacc_dist</code> object from distances() .
<code>q</code>	Numeric vector. Orders of diversity to compute. Default <code>c(0, 1, 2)</code> . • $q = 0$: Species richness • $q = 1$: Exponential of Shannon entropy (effective common species) • $q = 2$: Inverse Simpson (effective dominant species)
<code>n_seeds</code>	Integer. Number of random starting points. Default 50.
<code>method</code>	Character. Accumulation method: "knn" or "nn_walk".
<code>distance</code>	Character. Distance method: "euclidean" or "haversine".
<code>parallel</code>	Logical. Use parallel processing? Default TRUE.
<code>n_cores</code>	Integer. Number of cores. Default NULL uses <code>detectCores()</code> - 1.
<code>progress</code>	Logical. Show progress bar? Default TRUE.
<code>seed</code>	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 <code>as_sf()</code> and <code>plot(type = "map")</code> . Default FALSE.
focal_points	Optional focal points for method = "knn". See <code>spacc()</code> .
focal_domain	Optional polygonal focal domain. See <code>spacc()</code> .

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 ($n_{\text{seeds}} \times n_{\text{sites}}$)
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,
  method = c("knn", "nn_walk"),
  focal_points = NULL,
  focal_domain = NULL,
  standardize = c("none", "coverage"),
  coverage = 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.
method	Character. Accumulation method: "knn" or "nn_walk".
focal_points	Optional focal points for method = "knn". See spacc() .
focal_domain	Optional polygonal focal domain. See spacc() .
standardize	Character. "none" (default) decomposes the observed samples; "coverage" standardises gamma and alpha to a common sample coverage at every step (iN-EXT.beta3D, Chao et al. 2023). Needs integer abundances.

coverage Numeric in (0, 1]. Fixed coverage for `standardize = "coverage"`, the same at every step. NULL (default) uses, at each step, the lower of the observed coverages of the pooled and joint samples.

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:** $\text{gamma} / \text{alpha}$ (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:

<code>gamma</code>	Named list of $n\_seeds \times n\_sites$ matrices (one per q)
<code>alpha</code>	Named list of $n\_seeds \times n\_sites$ matrices (one per q)
<code>beta</code>	Named list of $n\_seeds \times n\_sites$ matrices (one per q)
<code>dissimilarity</code>	With <code>standardize = "coverage"</code> : list of the four dissimilarities 1-CqN, 1-UqN, 1-VqN, 1-SqN, each a named list of $n\_seeds \times n\_sites$ matrices (one per q); NULL otherwise
<code>coverage</code>	With <code>standardize = "coverage"</code> : $n\_seeds \times n\_sites$ matrix of the coverage used at each step
<code>q</code>	Vector of q values
<code>coords</code>	Original coordinates
<code>n_seeds, n_sites, n_species</code>	Dimensions

Coverage standardisation

Observed beta depends on sampling completeness: gamma and alpha approach their asymptotes at different rates, so the ratio moves along the curve even where composition does not change. With `standardize = "coverage"`, gamma is the Hill number of the pooled sample and alpha the Hill number of the joint sample (every species-by-site cell treated as a unit) divided by k (Chiu et al. 2014), both rarefied or extrapolated to the same sample coverage C with the estimators of Chao et al. (2014); beta is their ratio (Chao et al. 2023). By default C is, at each step, the lower of the two observed coverages, so both values come from the observed samples or their rarefaction. A fixed coverage makes the curve comparable across steps and datasets, at the cost of extrapolation where a step's sample is less complete; for $q = 0$, Chao et al. (2023) advise against extrapolating beyond the coverage of twice the sample size.

The standardised beta is transformed to four dissimilarities between 0 and 1 (Chao et al. 2023): 1-CqN (Sorensen-type, the classic Sorensen index at $q = 0$), 1-UqN (Jaccard-type), 1-VqN and 1-SqN. They are NA at the first step, where there is one site.

References

- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427-2439.
- Chiu, C.-H., Jost, L. & Chao, A. (2014). Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. *Ecological Monographs*, 84, 21-44.
- 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.
- Chao, A., Thorn, S., Chiu, C.-H., et al. (2023). Rarefaction and extrapolation with beta diversity under a framework of Hill numbers: the iNEXT.beta3D standardization. *Ecological Monographs*, 93, e1588. [doi:10.1002/ecm.1588](https://doi.org/10.1002/ecm.1588)

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,
method = c("knn", "nn_walk"),
focal_points = NULL,
focal_domain = NULL
)

```

Arguments

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

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:

<code>hills</code>	Named list of <code>n_seeds</code> x <code>n_sites</code> matrices (one per <code>q</code>)
<code>coverage</code>	<code>n_seeds</code> x <code>n_sites</code> matrix of Chao-Jost coverage
<code>pooled</code>	Species abundances pooled over all sites
<code>standardized</code>	List of per- <code>q</code> values interpolated at target coverage, or <code>NULL</code> if <code>target_coverage</code> is <code>NULL</code>

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

Arguments

<code>x</code>	A site-by-species matrix (rows = sites, cols = species).
<code>coords</code>	A data.frame with columns <code>x</code> and <code>y</code> containing site coordinates, or a <code>spacc_dist</code> object from <code>distances()</code> .
<code>metrics</code>	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).
<code>method</code>	Character. Accumulation method: "knn", "kncn", "nn_walk", or "random". Default "knn".
<code>distance</code>	Character. Distance method: "euclidean" or "haversine".
<code>parallel</code>	Logical. Use parallel processing? Default TRUE.
<code>n_cores</code>	Integer. Number of cores for parallel processing.
<code>progress</code>	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:

<code>metrics</code>	Data frame with one row per site and columns for each metric
<code>coords</code>	Original coordinates
<code>metric_names</code>	Names of computed metrics
<code>n_sites</code>	Number of sites
<code>n_species</code>	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
```

spaccNetwork

Spatial Accumulation of Interaction Diversity

Description

Accumulate an interaction network over space: interaction richness and interaction Hill numbers, sample coverage, the richness of the two interacting levels (for example plants and pollinators) and connectance, all along the same site orders.

Usage

```
spaccNetwork(
  interactions,
  coords,
  q = c(0, 1, 2),
  n_seeds = 50L,
  method = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
```

```

    n_cores = NULL,
    progress = TRUE,
    seed = NULL,
    focal_points = NULL,
    focal_domain = NULL
  )

```

Arguments

interactions	A data frame of observed interactions with columns site, lower, upper and optionally count (interaction frequency, default 1 per row). lower and upper name the species of the two levels; an interaction is a lower-upper pair.
coords	A data frame with columns x and y, one row per site. Sites in interactions are matched to coords\$site if present, otherwise to the row names of coords, otherwise taken as row numbers.
q	Numeric vector. Orders of diversity. Default <code>c(0, 1, 2)</code> .
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method: "knn" or "nn_walk".
distance	Character. "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.
focal_points	Optional focal points for method = "knn". See spacc() .
focal_domain	Optional polygonal focal domain. See spacc() .

Details

Each unique lower-upper pair is a unit of diversity and its frequency its abundance, so the interaction Hill number of order q is the ordinary Hill number of the interaction frequencies of the accumulated sites, the effective number of equally frequent interactions, and the sample coverage is the Chao & Jost (2012) coverage of those frequencies (Chiu et al. 2023). The species curves of the two levels use each species' summed interaction frequency. Connectance is the realised share of the possible interactions between the species detected so far.

Value

An object of class `spacc_network` containing:

interaction, lower, upper	Named lists (one per q) of $n\_seeds \times n\_sites$ matrices: Hill numbers of the interaction frequencies and of the summed frequencies of each level's species
coverage	List with the $n\_seeds \times n\_sites$ sample coverage matrices of interaction, lower and upper
connectance	$n\_seeds \times n\_sites$ matrix of interaction richness divided by the product of the two species richnesses

q, coords, n_seeds, n_sites, n_interactions, n_lower, n_upper, method,
orders

Parameters, dimensions and site orders

References

Chiu, C.-H., Chao, A., Vogel, S., Kriegel, P. & Thorn, S. (2023). Quantifying and estimating ecological network diversity based on incomplete sampling data. *Philosophical Transactions of the Royal Society B*, 378, 20220183. doi:10.1098/rstb.2022.0183

See Also

[spaccHillCoverage\(\)](#) for the same quantities on species

Examples

```
set.seed(1)
coords <- data.frame(x = runif(30), y = runif(30))
interactions <- data.frame(
  site = sample(30, 400, replace = TRUE),
  lower = paste0("plant", sample(12, 400, replace = TRUE)),
  upper = paste0("bee", sample(20, 400, replace = TRUE))
)
net <- spaccNetwork(interactions, coords, n_seeds = 10)
net
plot(net)
```

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"),
  rho = 0,
  n_seeds = 50L,
  method = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  parallel = TRUE,
  n_cores = NULL,
```

```

    progress = TRUE,
    seed = NULL,
    map = FALSE,
    focal_points = NULL,
    focal_domain = NULL
  )

```

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) • "evoheritage": EvoHeritage (Rosindell et al. 2024), PD with attrition of evolutionary heritage at rate rho (requires tree) • "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.
rho	Non-negative numeric vector. Attrition rate(s) for "evoheritage", per unit of branch length. rho = 0 gives Faith's PD. Several values give one curve each, named evoheritage_rho<value>.
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method: "knn" or "nn_walk".
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 <code>as_sf()</code> and <code>plot(type = "map")</code> . Default FALSE.
focal_points	Optional focal points for method = "knn". See <code>spacc()</code> .
focal_domain	Optional polygonal focal domain. See <code>spacc()</code> .

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 to the root. Requires full tree object.
- **EvoHeritage:** Features accumulate along each branch and are lost at rate ρ , so a branch of length L passes on a fraction $\exp(-\rho * L)$ of what entered it. A feature counts once if it survives to at least one present species. The value is in standardised units (the heritage at the end of a single branch of unit length), so $\rho = 0$ gives PD and large ρ tends to species richness. Scanning ρ places a community between its richness and PD curves.

Tree-based metrics match the columns of `x` to `tree$tip.label` by name; the tree may contain species absent from `x`.

Value

An object of class `spacc_phylo` containing:

<code>curves</code>	Named list of matrices, one per metric (<code>n_seeds</code> x <code>n_sites</code>)
<code>metric</code>	Metrics computed
<code>tree</code>	The tree or distance matrix used
<code>coords, n_seeds, n_sites, method</code>	Parameters used

References

- Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1-10.
- Rosindell, J., Manson, K., Gumbs, R., Pearse, W.D. & Steel, M. (2024). Phylogenetic biodiversity metrics should account for both accumulation and attrition of evolutionary heritage. *Systematic Biology*, 73, 158-182. [doi:10.1093/sysbio/syad072](https://doi.org/10.1093/sysbio/syad072)
- 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)
```

```
}
```

spaccRedundancy

Spatial Phylogenetic or Functional Redundancy Accumulation

Description

Track how much of the taxonomic diversity added along the spatial accumulation is new phylogenetic or functional diversity, as the ratio of the taxonomic Hill number to the phylogenetic or functional Hill number of the accumulated community.

Usage

```
spaccRedundancy(
  x,
  coords,
  tree = NULL,
  traits = NULL,
  q = c(0, 1, 2),
  n_seeds = 50L,
  method = c("knn", "nn_walk"),
  distance = c("euclidean", "haversine"),
  dist_method = c("euclidean", "gower"),
  normalize = TRUE,
  parallel = TRUE,
  n_cores = NULL,
  progress = TRUE,
  seed = NULL,
  focal_points = NULL,
  focal_domain = NULL
)
```

Arguments

x	A site-by-species matrix (abundance or presence/absence).
coords	A data.frame with columns x and y, or a spacc_dist object.
tree	A phylogenetic tree of class phylo with branch lengths. Supply either tree or traits.
traits	A species-by-traits matrix or data.frame, row names matching the columns of x.
q	Numeric vector. Orders of diversity. Default c(0, 1, 2).
n_seeds	Integer. Number of random starting points. Default 50.
method	Character. Accumulation method: "knn" or "nn_walk".
distance	Character. Site distance method: "euclidean" or "haversine".

dist_method	Character. Trait distance for traits: "euclidean" on standardised traits (default) or "gower".
normalize	Logical. Rescale trait distances to a maximum of 1. Default TRUE.
parallel	Logical. Use parallel processing? Default TRUE.
n_cores	Integer. Number of cores.
progress	Logical. Show progress? Default TRUE.
seed	Integer. Random seed.
focal_points	Optional focal points for method = "knn". See spacc() .
focal_domain	Optional polygonal focal domain. See spacc() .

Details

At each accumulation step the function computes, for every order q , the taxonomic Hill number ${}^qD$ of the accumulated community and either its phylogenetic Hill number ${}^qD(T)$ (Chao et al. 2010; effective number of equally abundant, equally distinct lineages, with T the abundance-weighted mean root-to-tip depth) or its similarity-sensitive functional Hill number ${}^qD^Z$ (Leinster & Cobbold 2012; with $Z = 1 - d$ from trait distances). The ratio

$$R_q = {}^qD / {}^qD(T) \quad \text{or} \quad {}^qD / {}^qD^Z$$

is at least 1, equal to 1 when species are maximally distinct (a star tree, or every pair of species at the maximal trait distance), and grows as the species added are close relatives or functionally similar to those already present. A ratio rising along the curve says the area is adding species faster than lineages or trait combinations.

Value

An object of class `spacc_redundancy` containing:

curves	Named list (one per q) of $n\_seeds \times n\_sites$ matrices of the ratio taxonomic / phylogenetic or functional Hill number
taxonomic	The taxonomic Hill numbers, same layout
dimension	The phylogenetic or functional Hill numbers, same layout
type	"phylogenetic" or "functional"
q, coords, n_seeds, n_sites, n_species, method, orders	Parameters and the site orders used

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.
- Leinster, T. & Cobbold, C.A. (2012). Measuring diversity: the importance of species similarity. *Ecology*, 93, 477-489.
- Alberdi, A. & Gilbert, M.T.P. (2019). A guide to the application of Hill numbers to DNA-based diversity analyses. *Molecular Ecology Resources*, 19, 804-817. doi:10.1111/17550998.13014

See Also

[spaccHill\(\)](#), [spaccPhylo\(\)](#), [spaccFunc\(\)](#), [diversityProfile\(\)](#)

Examples

```
if (requireNamespace("ape", quietly = TRUE)) {
  tree <- ape::rcoal(25)
  coords <- data.frame(x = runif(40), y = runif(40))
  species <- matrix(rpois(40 * 25, 1), nrow = 40,
                    dimnames = list(NULL, tree$tip.label))
  red <- spaccRedundancy(species, coords, tree = tree, n_seeds = 10)
  plot(red)
}
```

spaccWavefront

Wavefront Expansion Accumulation

Description

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

Usage

```
spaccWavefront(
  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 <- spaccWavefront(species, coords, n_seeds = 20, n_steps = 50)
plot(wf)
```

spatialEigenvectors	<i>Spatial Eigenvectors (PCNM/dbMEM)</i>
---------------------	--

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	<i>Spatial Variance Partitioning with MEMs</i>
------------------	--

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	<i>Spatially-Constrained Rarefaction</i>
--------------------	--

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

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

```

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

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

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:

<code>zeta</code>	Mean zeta values per order
<code>zeta_sd</code>	Standard deviations per order
<code>orders</code>	The k values
<code>n_samples</code>	Number of samples per order
<code>ratio</code>	Zeta ratio: $\text{zeta}_k / \text{zeta}_{(k-1)}$
<code>decline</code>	Data.frame with exponential and power-law fit statistics
<code>method</code>	Method used
<code>n_sites</code>	Number of sites
<code>n_species</code>	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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