Vignette ecospat package

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Miscellaneous methods and utilities for spatial ecology analysis, written by current and former members and collaborators of the ecospat group of Antoine Guisan, Department of Ecology and Evolution (DEE) & Institute of Earth Surface Dynamics (IDYST), University of Lausanne, Switzerland.

ecospat offers the possibility to perform Pre-modelling Analysis, such as Spatial autocorrelation analysis, MESS (Multivariate Environmental Similarity Surfaces) analyses, Phylogenetic diversity Measures, Biotic Interactions. It also provides functions to complement biomod2 in preparing the data, calibrating and evaluating (e.g. boyce index) and projecting the models. Complementary analysis based on model predictions (e.g. co-occurrences analyses) are also provided.

In addition, the *ecospat* package includes Niche Quantification and Overlap functions that were used in Broennimann et al. 2012 and Petitpierre et al. 2012 to quantify climatic niche shifts between the native and invaded ranges of invasive species.

1 Load data

```
library(ecospat)
## Loading required package: ade4
## Warning: package 'ade4' was built under R version 4.1.3
## Loading required package: ape
## Warning: package 'ape' was built under R version 4.1.3
## Loading required package: gbm
## Loaded gbm 2.1.8
## Loading required package: sp
## Registered S3 methods overwritten by 'adehabitatMA':
    method
##
    print.SpatialPixelsDataFrame sp
    print.SpatialPixels
citation("ecospat")
## To cite package 'ecospat' in publications use:
##
##
    Olivier Broennimann, Valeria Di Cola and Antoine Guisan (2022).
    ecospat: Spatial Ecology Miscellaneous Methods. R package version
##
    http://www.unil.ch/ecospat/home/menuguid/ecospat-resources/tools.html
##
##
## A BibTeX entry for LaTeX users is
##
##
    @Manual{,
##
      title = {ecospat: Spatial Ecology Miscellaneous Methods},
       author = {Olivier Broennimann and Valeria {Di Cola} and Antoine Guisan},
##
       year = {2022},
##
       note = {R package version 3.2.2},
##
##
       url = {http://www.unil.ch/ecospat/home/menuguid/ecospat-resources/tools.html},
##
1.0.1 Test data for the ecospat library
ecospat.testData()
data(ecospat.testData)
names(ecospat.testData)
## [1] "numplots"
                                         "long"
## [3] "lat"
                                         "ddeg"
                                         "srad"
## [5] "mind"
## [7] "slp"
                                         "topo"
## [9] "Achillea_atrata"
                                         "Achillea_millefolium"
```

```
## [11] "Acinos_alpinus"
                                         "Adenostyles_glabra"
## [13] "Aposeris_foetida"
                                         "Arnica_montana"
## [15] "Aster_bellidiastrum"
                                         "Bartsia_alpina"
## [17] "Bellis_perennis"
                                         "Campanula_rotundifolia"
                                         "Cerastium_latifolium"
## [19] "Centaurea_montana"
## [21] "Cruciata_laevipes"
                                         "Doronicum_grandiflorum"
## [23] "Galium_album"
                                         "Galium_anisophyllon"
## [25] "Galium_megalospermum"
                                         "Gentiana bavarica"
## [27] "Gentiana_lutea"
                                         "Gentiana_purpurea"
## [29] "Gentiana_verna"
                                         "Globularia_cordifolia"
## [31] "Globularia_nudicaulis"
                                         "Gypsophila_repens"
## [33] "Hieracium_lactucella"
                                         "Homogyne_alpina"
## [35] "Hypochaeris_radicata"
                                         "Leontodon_autumnalis"
## [37] "Leontodon_helveticus"
                                         "Myosotis_alpestris"
                                         "Phyteuma_orbiculare"
## [39] "Myosotis_arvensis"
## [41] "Phyteuma_spicatum"
                                         "Plantago_alpina"
## [43] "Plantago_lanceolata"
                                         "Polygonum_bistorta"
                                         "Prunella_grandiflora"
## [45] "Polygonum_viviparum"
## [47] "Rhinanthus_alectorolophus"
                                         "Rumex_acetosa"
## [49] "Rumex_crispus"
                                         "Vaccinium_gaultherioides"
## [51] "Veronica_alpina"
                                         "Veronica_aphylla"
                                         "Bromus_erectus_sstr"
## [53] "Agrostis_capillaris"
## [55] "Campanula_scheuchzeri"
                                         "Carex_sempervirens"
## [57] "Cynosurus_cristatus"
                                         "Dactylis_glomerata"
## [59] "Daucus_carota"
                                         "Festuca_pratensis_sl"
## [61] "Geranium_sylvaticum"
                                         "Leontodon_hispidus_sl"
## [63] "Potentilla erecta"
                                         "Pritzelago alpina sstr"
## [65] "Prunella_vulgaris"
                                         "Ranunculus_acris_sl"
## [67] "Saxifraga_oppositifolia"
                                         "Soldanella_alpina"
## [69] "Taraxacum_officinale_aggr"
                                         "Trifolium_repens_sstr"
## [71] "Veronica_chamaedrys"
                                         "Parnassia_palustris"
## [73] "glm_Agrostis_capillaris"
                                         "glm_Leontodon_hispidus_sl"
## [75] "glm_Dactylis_glomerata"
                                         "glm_Trifolium_repens_sstr"
## [77] "glm_Geranium_sylvaticum"
                                         "glm_Ranunculus_acris_sl"
## [79] "glm_Prunella_vulgaris"
                                         "glm_Veronica_chamaedrys"
## [81] "glm_Taraxacum_officinale_aggr"
                                         "glm_Plantago_lanceolata"
## [83] "glm_Potentilla_erecta"
                                         "glm_Carex_sempervirens"
## [85] "glm_Soldanella_alpina"
                                         "glm_Cynosurus_cristatus"
## [87] "glm_Campanula_scheuchzeri"
                                         "glm_Festuca_pratensis_sl"
## [89] "glm_Bromus_erectus_sstr"
                                         "glm_Saxifraga_oppositifolia"
## [91] "glm_Daucus_carota"
                                         "glm_Pritzelago_alpina_sstr"
## [93] "gbm_Bromus_erectus_sstr"
                                         "gbm_Saxifraga_oppositifolia"
## [95] "gbm_Daucus_carota"
                                         "gbm_Pritzelago_alpina_sstr"
```

Test data for the Niche Overlap Analysis

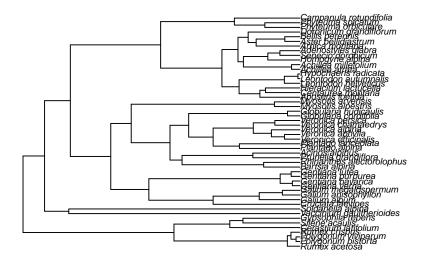
ecospat.testNiche.inv()

```
data(ecospat.testNiche.inv)
names(ecospat.testNiche.inv)
```

```
##
                        "y"
                                                                       "p"
    [1] "x"
                                        "aetpet"
                                                        "gdd"
    [6] "pet"
                        "stdp"
                                        "tmax"
                                                        "tmin"
                                                                       "tmp"
## [11] "species_occ" "predictions"
```

ecospat.testNiche.nat()

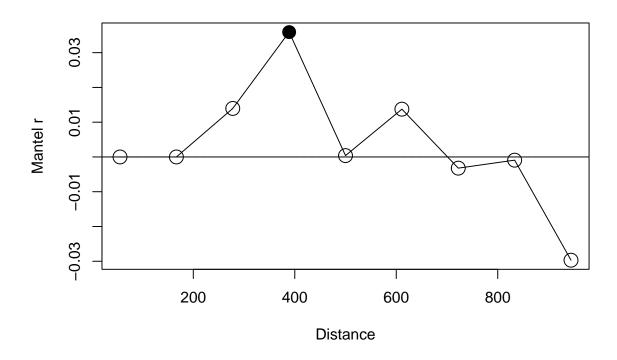
```
data(ecospat.testNiche.nat)
names(ecospat.testNiche.nat)
## [1] "x"
                       "v"
                                     "aetpet"
                                                    "gdd"
                                                                  "p"
                       "stdp"
## [6] "pet"
                                     "tmax"
                                                    "tmin"
                                                                   "tmp"
## [11] "species_occ" "predictions"
      Test tree for Phylogenetic Diversity Analysis
ecospat.testTree()
fpath <- system.file("extdata", "ecospat.testTree.tre", package="ecospat")</pre>
fpath
## [1] "C:/Users/obroenni/AppData/Local/Temp/Rtmp2dUCps/Rinst7438507de99/ecospat/extdata/ecospat.tes
tree<-read.tree(fpath)</pre>
tree$tip.label
##
    [1] "Rumex acetosa"
                                     "Polygonum_bistorta"
## [3] "Polygonum_viviparum"
                                     "Rumex_crispus"
## [5] "Cerastium_latifolium"
                                     "Silene_acaulis"
## [7] "Gypsophila_repens"
                                     "Vaccinium_gaultherioides"
## [9] "Soldanella_alpina"
                                     "Cruciata_laevipes"
## [11] "Galium_album"
                                     "Galium_anisophyllon"
## [13] "Galium_megalospermum"
                                     "Gentiana_verna"
## [15] "Gentiana_bavarica"
                                     "Gentiana_purpurea"
## [17] "Gentiana_lutea"
                                     "Bartsia_alpina"
## [19] "Rhinanthus_alectorolophus"
                                     "Prunella_grandiflora"
## [21] "Acinos_alpinus"
                                     "Plantago_alpina"
## [23] "Plantago_lanceolata"
                                     "Veronica_officinalis"
## [25] "Veronica_aphylla"
                                     "Veronica_alpina"
## [27] "Veronica_chamaedrys"
                                     "Veronica_persica"
## [29] "Globularia_cordifolia"
                                     "Globularia_nudicaulis"
## [31] "Myosotis_alpestris"
                                     "Myosotis_arvensis"
## [33] "Aposeris_foetida"
                                     "Centaurea_montana"
## [35] "Hieracium_lactucella"
                                     "Leontodon_helveticus"
## [37] "Leontodon_autumnalis"
                                     "Hypochaeris_radicata"
## [39] "Achillea atrata"
                                     "Achillea millefolium"
                                     "Senecio doronicum"
## [41] "Homogyne_alpina"
## [43] "Adenostyles_glabra"
                                     "Arnica_montana"
## [45] "Aster_bellidiastrum"
                                     "Bellis_perennis"
## [47] "Doronicum_grandiflorum"
                                     "Phyteuma_orbiculare"
## [49] "Phyteuma_spicatum"
                                     "Campanula_rotundifolia"
Plot tree
```



2 Pre-Modelling Analysis

2.1 Spatial Auto-correlation

 ${\bf 2.1.1} \quad {\bf Mantel~Correlogram~with~\it ecospat.mantel.correlogram()}$



The graph indicates that spatial autocorrelation (SA) is minimal at a distance of 180 meters. Note however that SA is not significantly different than zero for several distances (open circles).

2.2 Predictor Variable Selection

2.2.1 Number of Predictors with Pearson Correlation ecospat.npred()

```
colvar <- ecospat.testData[c(4:8)]
x <- cor(colvar, method="pearson")
ecospat.npred (x, th=0.75)</pre>
```

[1] 4

2.2.2 Number of Predictors with Spearman Correlation ecospat.npred()

```
x <- cor(colvar, method="spearman")
ecospat.npred (x, th=0.75)</pre>
```

[1] 4

2.3 Climate Analogy Tools

2.3.1 Climate Analogy with ecospat.climan()

```
x <- ecospat.testData[c(4:8)]
p<- x[1:90,] #A projection dataset.
ref<- x[91:300,] # A reference dataset</pre>
```

```
ecospat.climan(ref,p)
```

```
## [1] 0.185415746 -0.028290993 -0.032909931 -0.009237875 -0.034642032
## [6] -0.209006928 -0.084295612 -0.103622863 0.355220600 -0.136258661
## [11] -0.087182448 -0.209006928 -0.143187067 -0.124711316 -0.114844720
## [21] -0.113883908 -0.204653076 -0.001154734 -0.132217090 -0.100461894
## [26] 0.464738681 -0.416578541 -0.044457275 -0.018475751 -0.122225532
## [31] -0.137611720 -0.050808314 0.254605027 -0.062012319 0.238294633
## [41] 0.390781314 0.175132571 0.401892929 0.843703731 0.286155800
## [46] 0.321142114 0.668511130 0.252253209 0.440050672 0.177247206
## [51] 0.831525456 0.303710525 0.197182304 0.219273698 0.196637663
## [56] 0.195300816 0.142395786 0.176988160 -0.051991905 0.265163111
## [61] -0.020785219 -0.017898383 0.553965995 0.409635110 0.323633285
## [66] 0.468693064 0.124983005 -0.032909931 0.165642783 0.147046687
## [71] 0.202895471 0.341992334 0.225508458 0.133254065 0.485295264
## [76] -0.047344111 -0.012282931 0.165429659 0.134199992 0.216655251
## [81] 0.139419127 0.121254775 0.098782992 0.591393741 0.110866239
## [86] 0.146010655 0.095562156 0.093353356 0.081712342 0.160531262
```

2.3.2 Extrapolation detection, creating a MESS object with ecospat.mess()

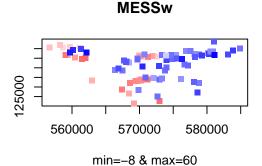
```
x <- ecospat.testData[c(2,3,4:8)]
proj<- x[1:90,] #A projection dataset.
cal<- x[91:300,] #A calibration dataset</pre>
```

```
mess.object<-ecospat.mess (proj, cal, w="default")</pre>
```

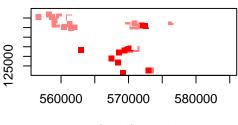
2.3.3 Plot MESS with ecospat.plot.mess()

```
ecospat.plot.mess (mess.object, cex=1, pch=15)
```

MESS 560000 570000 580000 min=-25 & max=24



#MESSneg



min=0 & max=2

In the MESS plot pixels in red indicate sites where at least one environmental predictor has values outside of the range of that predictor in the calibration dataset. In the MESSw plot, same as previous plot but with weighted by the number of predictors. Finally, the MESSneg plot shows at each site how many predictors have values outside of their calibration range.

2.4 Phylogenetic Diversity Measures

##

##

##

Γ137

[19]

[25]

38.4155607

29.0894143 89.9839758

18.9535475 34.8871800

6.5223035

```
fpath <- system.file("extdata", "ecospat.testTree.tre", package="ecospat")
tree <- read.tree(fpath)
data <- ecospat.testData[9:52]</pre>
```

2.4.1 Calculate Phylogenetic Diversity Measures ecospat.calculate.pd

```
pd<- ecospat.calculate.pd(tree, data, method = "spanning", type = "species", root = TRUE, average =
## Progress (. = 100 pixels calculated):
## ... [300]
## All 300 pixels done.
pd
           6.9782188
                       6.7981743
                                                4.9964700
                                                             4.9964700
                                                                        29.8820547
##
     [1]
                                    4.9964700
##
     [7]
          58.7451752
                       6.5223035
                                  30.6152478
                                                1.5258335
                                                            0.0000000
                                                                        44.3661803
```

78.1607950

1.5258335

38.4155607

29.0894143

1.5258335 56.7686202

39.9291325 48.5997861

27.4135569 40.2827035

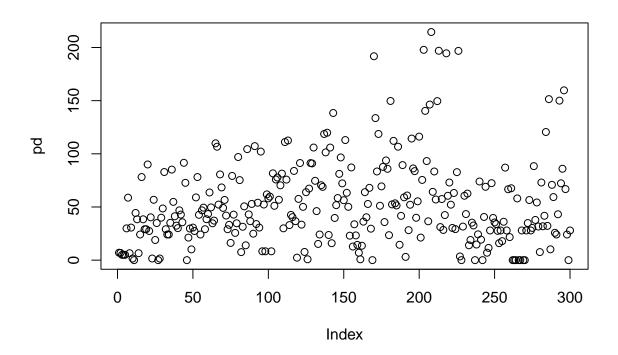
24.0929443

0.0000000

```
##
    [31]
         82.8763723 29.0894143 24.0929443 24.0929443 35.0949481 85.1406422
         54.7974724 41.2817284
                                              30.0984781 46.8247511
##
    [37]
                                 32.4100269
                                                                     42.8358475
##
    [43]
         35.6223697
                     91.5539224
                                 72.7022527
                                              0.0000000 21.1862293
                                                                     29.7320308
##
    [49]
          10.1187868
                     30.6152478 27.4135569
                                              59.0015345
                                                         78.1536692 42.6423378
    [55]
         24.0929443
                     46.8050070 49.3924266
                                              29.0894143
                                                          38.5290848 43.3611373
##
    [61]
         63.6397674
                     49.6097169
                                 34.6522309
                                              37.1871282 109.8813371 106.6971561
##
    [67]
         52.2512132
                     80.6221671
                                 68.3867818
                                             49.1362998
                                                         56.6138690
                                                                     41.9283257
##
    [73]
          29.0894143
                      33.2026673
                                 16.1897593
                                              79.1938213
                                                          42.8115427
                                                                      25.6187778
##
    [79]
         34.6805724
                     96.9902366
                                 75.2672695
                                              7.5313673
                                                          31.4078882
                                                                      50.5865673
                                                                      24.8855847
##
    [85]
         13.9570775 104.4121025
                                 43.0464918
                                              36.6693230
                                                          52.8590823
##
    [91] 107.2302322
                     33.9358604
                                 54.0048319
                                              30.6152478 102.0983385
                                                                      8.3170826
         52.3071062
                      8.3170826
                                 61.8562896
                                              58.1179346
                                                          59.7939424
    [97]
                                                                       8.3170826
## [103]
         81.6495398
                     51.1054635
                                 75.8701970
                                              77.6947419
                                                          56.7929250
                                                                     70.3693202
## [109]
                     29.9118877 111.0790432
                                             75.7518798 112.5482496
         81.3965205
                                                                      32.9763735
## [115]
         42.5644761
                     40.4507005
                                83.8955419
                                              36.6693230
                                                          2.3184739
                                                                      57.5978451
## [121]
         91.3453370
                     33.3983912
                                 50.1351419
                                              7.7084002
                                                          63.9227817
                                                                       0.7926404
## [127]
         67.2813325
                     91.2965996
                                 90.9578739 105.9024741
                                                         74.6128871
                                                                     46.1321553
         15.2479619 24.0929443 70.4802708 68.8949899 118.6657550 101.3545260
## [133]
## [139] 119.8539056
                     23.6602184 105.8968281
                                             15.9336325 138.4059855
                                                                     39.6674173
                     58.4119283 81.1388699
## [145]
         51.7391372
                                              96.6048825
                                                         72.2156025
                                                                      56.3601992
                                              23.0021994
## [151] 112.9489963
                     63.3258805
                                 50.1594468
                                                         87.1886965
                                                                      12.7714946
                                                                      13.5641350
## [157]
         33.7421666
                     23.2537702
                                 14.3226164
                                              6.9752071
                                                          0.7926404
## [163]
         36.2007616 63.9227817 40.3310946
                                              52.8264129
                                                          67.9956878
                                                                      29.5843437
## [169]
          0.0000000 191.7818606 133.6077875
                                              83.3977825 118.6711630
                                                                      51.1512871
         69.3838811 87.7066616 35.8005270
                                              93.7797077
## [175]
                                                          85.8984840
                                                                      23.4933413
## [181] 149.7094684 52.4451847 112.1873673 53.4479612 51.4341108 106.6959500
## [187]
         14.4361405
                     41.6547546 89.4018733
                                             59.1068292
                                                          3.0516670
                                                                      60.7852739
## [193]
         28.1850877
                     52.1002690 114.3651475
                                             86.2640717
                                                         83.7092232
                                                                      39.8499777
## [199]
         55.3514065 116.1795597 21.2346203 75.4593878 197.8157358 140.3806968
## [205]
         93.2192350 36.5337815 146.3370747 214.5450205
                                                        64.2439145
                                                                     83.3740177
## [211]
         57.0440643 149.5697614 196.9415036
                                              31.0984631
                                                          57.4769230
                                                                      28.4014469
## [217]
         42.3978747 194.5384819
                                 60.5204195
                                             73.0060715
                                                          52.1628582
                                                                      30.2801165
                     29.1789484
## [223]
         63.1752097
                                 82.7662787 196.8309769
                                                          3.4666557
                                                                       0.0000000
## [229]
         31.5688084
                    60.5650008 43.3334929
                                            62.5952411
                                                         13.9570775
                                                                     18.9495667
## [235]
         35.2646601
                     32.6155790
                                  0.0000000
                                             14.6693623
                                                         24.2745827
                                                                      73.9480832
## [241]
         19.2825866
                      0.0000000
                                 40.6115985
                                              68.9862341
                                                          6.9782188
                                                                     11.5030881
## [247]
         27.9105497
                     72.4020225
                                 39.6781995
                                              35.4596364
                                                          33.9160835
                                                                      27.5735165
## [253]
          15.9619740
                     27.9105497
                                 17.8628493
                                              36.0936777
                                                          87.0440848
                                                                      27.9105497
## [259]
                      21.6475811
                                  67.5969904
                                                          0.0000000
          66.6907987
                                              0.0000000
                                                                       0.0000000
## [265]
         58.0542370
                      0.0000000
                                  0.0000000
                                              27.9105497
                                                          0.0000000
                                                                       0.0000000
## [271]
         27.9105497
                      34.8887684
                                 56.5556633
                                              27.9105497
                                                                      88.4296666
                                                          30.3097595
## [277]
         37.8150727
                     54.2397810
                                 31.6243116
                                              7.5799087
                                                          73.0136833
                                                                      31.8638035
## [283]
         41.7172212 120.5228857
                                 32.2001243 151.4545228
                                                          10.1544492
                                                                      70.8133537
## [289]
         59.3255687
                     25.7211220
                                 24.1115267
                                              43.1500941 150.0299191
                                                                      72.2758570
## [295]
         85.9498096 159.7242106 66.8328159
                                              24.0929443
                                                          0.0000000
                                                                      27.9105497
```

plot(pd)

2.4.1.1 Plot the results (correlation of phylogenetic diversity with species richness)



2.5 Niche Quantification and Comparison with Ordination techniques

Loading test data for the niche dynamics analysis in the invaded range

```
inv <- ecospat.testNiche.inv</pre>
```

Loading test data for the niche dynamics analysis in the native range

nat <- ecospat.testNiche.nat</pre>

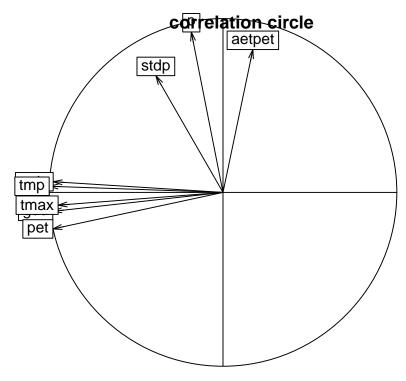
2.5.1 PCA-ENVIRONMENT

The PCA is calibrated on all the sites of the study area, including both native and invaded ranges (same as PCAenv in Broenniman et al. 2012)

```
pca.env <- dudi.pca(rbind(nat,inv)[,3:10],scannf=F,nf=2)</pre>
```

Plot Variables Contribution with ecospat.plot.contrib()

ecospat.plot.contrib(contrib=pca.env\$co, eigen=pca.env\$eig)



axis1 = 61.14 % axis2 = 25.09 %

The correlation circle indicate the contribution of original predictors to the PCA axes.

Predict the scores on the axes

```
# PCA scores for the whole study area
scores.globclim <- pca.env$li

# PCA scores for the species native distribution
scores.sp.nat <- suprow(pca.env,nat[which(nat[,11]==1),3:10])$li

# PCA scores for the species invasive distribution
scores.sp.inv <- suprow(pca.env,inv[which(inv[,11]==1),3:10])$li

# PCA scores for the whole native study area
scores.clim.nat <- suprow(pca.env,nat[,3:10])$li

# PCA scores for the whole invaded study area
scores.clim.inv <- suprow(pca.env,inv[,3:10])$li</pre>
```

2.5.2 Calculate the Occurrence Densities Grid with ecospat.grid.clim.dyn()

For a species in the native range (North America)

For a species in the invaded range (Australia)

2.5.3 Calculate Niche Overlap with ecospat.niche.overlap()

```
# Compute Schoener's D, index of niche overlap
D.overlap <- ecospat.niche.overlap (grid.clim.nat, grid.clim.inv, cor = TRUE)$D
D.overlap</pre>
```

[1] 0.224586

The niche overlap between the native and the invaded range is 22%.

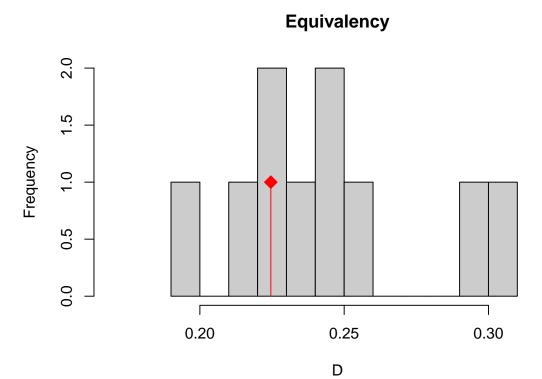
2.5.4 Perform the Niche Equivalency Test with ecospat.niche.equivalency.test() according to Warren et al. (2008)

It is recommended to use at least 1000 replications for the equivalency test. As an example we used rep = 10, to reduce the computational time.

Niche equivalency test H1: the observed overlap between the native and invaded niche is higher than if the two niches are randomized, the niche expansion of the invaded niche is lower, the niche stability is higher and the niche unfilling is lower than if the two niches are randomized.

Plot Equivalency test

```
ecospat.plot.overlap.test(eq.test, "D", "Equivalency")
```



2.5.5 Perform the Niche Similarity Test with ecospat.niche.similarity.test()

Shifts randomly on niche (here the invasive niche) in the study area It is recomended to use at least 1000 replications for the similarity test. As an example we used rep = 10, to reduce the computational time.

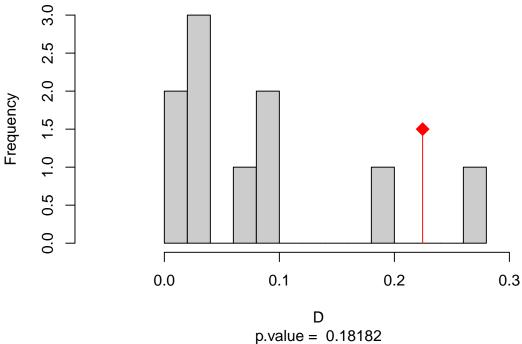
p.value = 0.63636

Niche similarity test H1: the observed overlap between the native and invaded is higher than randomly shifted invasive niches in the invaded study area, the niche expansion of the invaded niche is lower, the niche stability is higher and the niche unfilling is lower than if the two niches are randomized.

Plot Similarity test

```
ecospat.plot.overlap.test(sim.test, "D", "Similarity")
```

Similarity

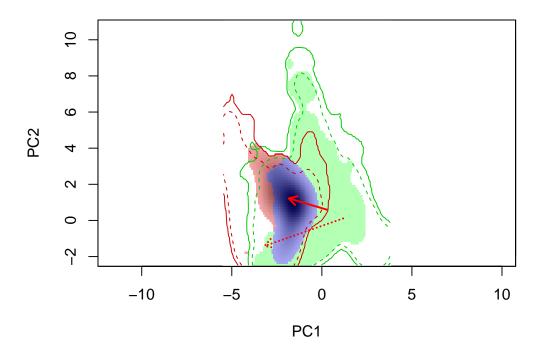


2.5.6 Delimiting niche categories and quantifying niche dynamics in analogue climates with ecospat.niche.dyn.index()

```
niche.dyn <- ecospat.niche.dyn.index (grid.clim.nat, grid.clim.inv, intersection = 0.1)</pre>
```

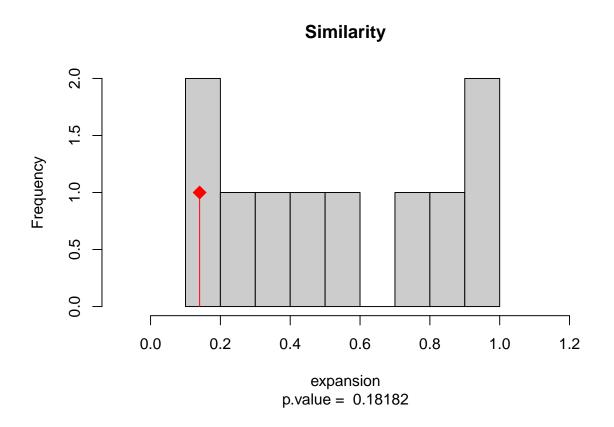
2.5.6.1 Visualizing niche categories, niche dynamics and climate analogy between ranges with ecospat.plot.niche.dyn() Plot niche overlap

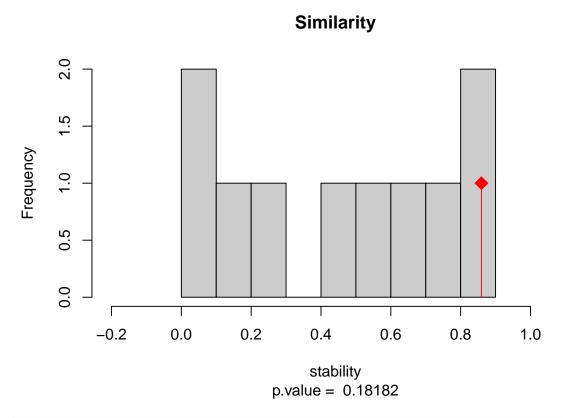
Niche Overlap



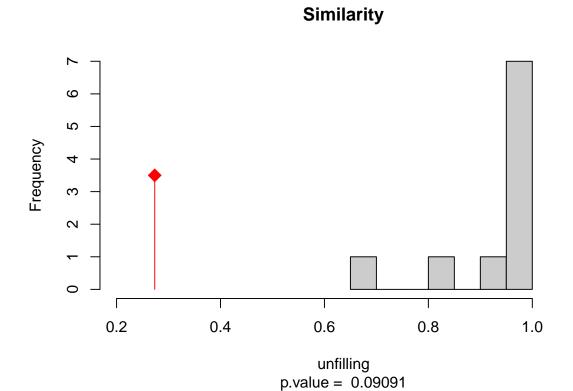
Plot Similarity test for niche expansion, stability and unfilling

ecospat.plot.overlap.test(sim.test, "expansion", "Similarity")

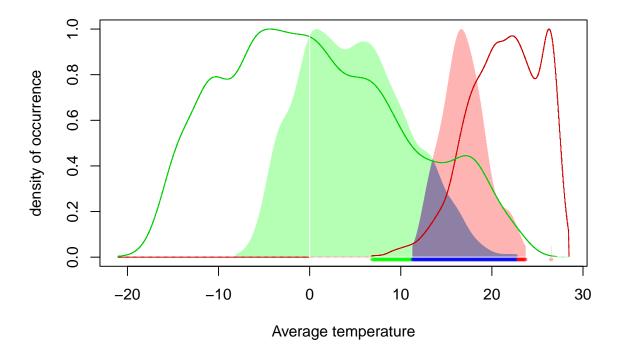




ecospat.plot.overlap.test(sim.test, "unfilling", "Similarity")



2.5.6.2 Plot the niche dynamics along one gradient (here temperature) with ecospat.plot.niche.dyn()



2.6 Biotic Interactions

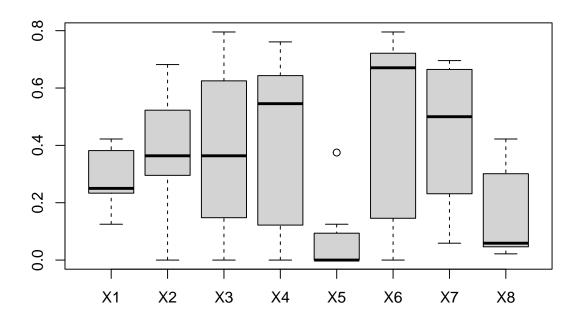
2.6.1 Species Co-occurrences Analysis with a Presence-absence matrix using the function $ecospat.co_occurrences()$

```
data <- ecospat.testData[c(9:16,54:57)]
```

For each pair of species (sp1, sp2), the number (N) of plots where both species were present is divided by the number of plots where the rarest of the two species is present. This index ranges from 0 (no co-occurrence) to 1 (always in co-occurrence) as given in eq. 1.

where N(S1 intersects S2) is the number of times species S1 and S2 co-occur, while Min(NS1, NS2) is the number of times species S1 and S2 co-occur, while is the occurrence frequency of the rarest of the two species.

ecospat.co_occurrences (data)



##		Aposeris_foetida A	Arnica_montana Aster	_bellidiastrum	
##	Aposeris_foetida	1.0000000	0.3636364	0.25000000	
##	Arnica_montana	0.3636364	1.0000000	0.36363636	
##	Aster_bellidiastrum	0.2500000	0.3636364	1.00000000	
##	Bartsia_alpina	0.222222	0.5454545	0.59090909	
##	Bromus_erectus_sstr	0.1250000	0.0000000	0.0000000	
##	Campanula_scheuchzeri	0.244444	0.6818182	0.79545455	
##	Carex_sempervirens	0.4000000	0.5000000	0.65909091	
##	Cynosurus_cristatus	0.4222222	0.2272727	0.04545455	
##		Bartsia_alpina Bro	omus_erectus_sstr Ca	mpanula_scheuchzeri	
##	Aposeris_foetida	0.2222222	0.1250	0.2444444	
##	Arnica_montana	0.54545455	0.0000	0.68181818	
	Aster_bellidiastrum	0.59090909	0.0000	0.79545455	
##	Bartsia_alpina	1.00000000	0.0000	0.76086957	
##	Bromus_erectus_sstr	0.00000000	1.0000	0.00000000	
##	Campanula_scheuchzeri	0.76086957	0.0000	1.00000000	
##	Carex_sempervirens	0.69565217	0.0625	0.67058824	
##	Cynosurus_cristatus	0.02173913	0.3750	0.04705882	
##		Carex_sempervirens	ens Cynosurus_cristatus		
##	Aposeris_foetida	0.4000000	0.4222222	22	
##	Arnica_montana	0.50000000	0.2272727	'3	
##	Aster_bellidiastrum	0.65909091	0.0454545	55	
##	Bartsia_alpina	0.69565217	7 0.0217391	.3	
##	Bromus_erectus_sstr	0.06250000	0.3750000	00	

```
## Campanula_scheuchzeri 0.67058824 0.04705882
## Carex_sempervirens 1.0000000 0.05882353
## Cynosurus_cristatus 0.05882353 1.00000000
```

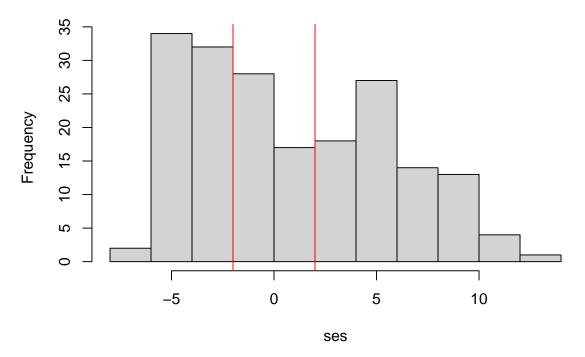
2.6.2 Pairwise co-occurrence Analysis with calculation of the C-score index using the function ecospat. Cscore()

This function allows to apply a pairwise null model analysis to a presence-absence community matrix to determine which species associations are significant across the study area. The strength of associations is quantified by the C-score index and a 'fixed-equiprobable' null model algorithm is applied.

It is recomended to use at least 10000 permutations for the test. As an example we used nperm = 100, to reduce the computational time.

```
data<- ecospat.testData[c(53,62,58,70,61,66,65,71,69,43,63,56,68,57,55,60,54,67,59,64)]
nperm <- 100
outpath <- getwd()
ecospat.Cscore(data, nperm, outpath)</pre>
```

Histogram of standardized effect size



```
## $0bsCscoreTot
## [1] 2675.468
##
## $SimCscoreTot
## [1] 2466.422
##
## $PVal.less
## [1] 1
##
## $PVal.greater
## [1] 0.00990099
```

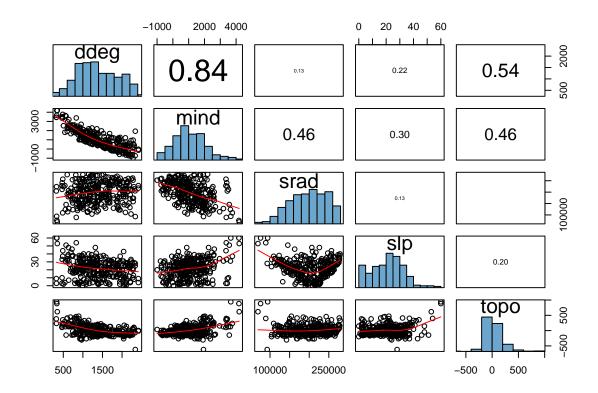
```
##
## $SES.Tot
## [1] 54.60015
```

The function returns the C-score index for the observed community (ObsCscoreTot), p.value (PValTot) and standardized effect size (SES.Tot). It saves also a table in the working directory where the same metrics are calculated for each species pair (only the table with species pairs with significant p-values is saved in this version)

2.7 Data Preparation

2.7.1 Correlation Plot of Variables with ecospat.cor.plot()

```
data <- ecospat.testData[,4:8]
ecospat.cor.plot(data)</pre>
```



A scatter plot of matrices, with bivariate scatter plots below the diagonal, histograms on the diagonal, and the Pearson correlation above the diagonal. Useful for descriptive statistics of small data sets (better with less than 10 variables).

2.7.2 Calibration And Evaluation Dataset

```
## $eval
##
     yeval yeval
## 1
       NA 102
## 2
        130
              NA
## 3
        12
              40
## 4
        240
              95
## 5
       51
              157
## 6
        15
              253
## 7
        189
              37
## 8
       11
              106
## 9
              264
        296
## 10
        79
              34
## 11
        236
              181
## 12
        225
              288
              204
## 13
        185
## 14
        133
              263
## 15
        177
              56
## 16
        75
              283
## 17
        210
              247
## 18
        100
              272
## 19
        235
              114
## 20
        84
              201
## 21
        180
              139
## 22
        116
              269
## 23
        297
              252
## 24
             94
        214
## 25
        198
              45
## 26
        71
              237
## 27
              291
        155
## 28
        292
              240
## 29
        17
              214
## 30
        113
              245
## 31
        279
              155
## 32
              189
        30
## 33
        254
              84
##
## $cal
##
     ycal ycal
## 1
       NA 138
## 2
       NA
            NA
## 3
       NA
            NA
## 4
       NA
            NA
## 5
       227
            NA
## 6
            NA
       NA
## 7
       NA
            NA
## 8
       134
            36
## 9
       154
           262
## 10 166
           228
## 11 184
            31
## 12 265
            24
## 13 266
            2
## 14
        8
           278
## 15
        3
           261
## 16
      152
            206
## 17
      186
           230
      206
## 18
            43
## 19 232
           289
## 20
       22 238
```

```
## 21 147
            171
## 22
       110
             220
## 23
       145
             223
## 24
       256
             274
## 25
        21
             275
## 26
         5
            239
## 27
       224
             268
## 28
       276
             44
## 29
       289
             193
## 30
       221
             294
## 31
        85
             241
## 32
       199
             211
## 33
       182
             222
## 34
        55
               4
## 35
       120
             140
## 36
        36
             256
             281
## 37
       249
## 38
             196
        33
## 39
        57
             156
## 40
       234
             30
## 41
       243
             212
## 42
        27
             85
## 43
       267
             270
## 44
       271
             242
## 45
       290
             188
## 46
       217
             235
## 47
        18
             168
## 48
        49
             53
## 49
       299
             15
## 50
       241
             297
             200
## 51
        14
## 52
       260
             27
## 53
       192
            293
## 54
       121
             248
## 55
       203
             295
## 56
       178
             71
## 57
       300
             300
## 58
       222
             169
## 59
       115
             251
## 60
             229
        16
## 61
       246
             255
       261
## 62
             49
## 63
        24
             244
## 64
            233
        44
## 65
        67
             123
## 66
        53
             145
## 67
       238
             180
## 68
       273
             258
## 69
        20
             23
## 70
       255
             236
## 71
       259
               3
## 72
       219
             286
## 73
       250
             178
## 74
       245
             205
## 75
       150
             152
## 76
       268
             254
## 77
       231
             210
```

We obtained an evaluation and calibration dataset with a desired ratio of disaggregation.

3 Core Niche Modelling

3.1 Model Evaluation

3.1.1 Presence-only Evaluation Indices- Boyce Index

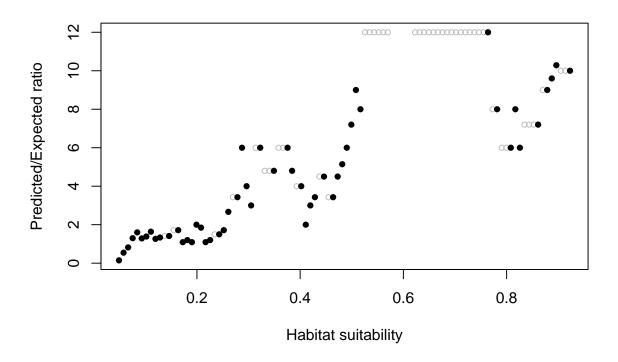
The argument fit is a vector containing the predicted suitability values

```
fit <- ecospat.testData$glm_Saxifraga_oppositifolia</pre>
```

The argument obs is a vector containing the predicted suitability values of the validation points (presence records)

```
obs<-ecospat.testData$glm_Saxifraga_oppositifolia[which(ecospat.testData$Saxifraga_oppositifolia==1)
```

Calculate and plot Boyce Index with ecospat.boyce



[1] 0.91

Here the boyce index is 0.91. If the rank of predicted expected ratio would be completely ordered along habitat suitability axis then boyce index would be 1.

3.1.2 Accuracy of Community Prediction

```
Indices of accuracy of community predictions ecospat. CommunityEval()
```

```
eval<-ecospat.testData[c(53,62,58,70,61,66,65,71,69,43,63,56,68,57,55,60,54,67,59,64)]
pred<-ecospat.testData[c(73:92)]

CommunityEval<-ecospat.CommunityEval (eval, pred, proba = TRUE, ntir=5,verbose = T)

## trial 1 on 5
## trial 2 on 5
## trial 3 on 5</pre>
```

3.2 Spatial Predictions and Projections

3.2.1 ESM Ensemble of Small Models

trial 4 on 5 ## trial 5 on 5

```
library(biomod2)
## Warning: package 'biomod2' was built under R version 4.1.3
## biomod2 3.5.1 loaded.
## Type browseVignettes(package='biomod2') to access directly biomod2 vignettes.
# species
# occurrences
xy <- inv[,1:2]</pre>
head(xy)
##
          X
## 1 142.25 -10.25
## 2 142.25 -10.75
## 3 131.25 -11.25
## 4 132.25 -11.25
## 5 142.25 -11.25
## 6 142.75 -11.25
sp_occ <- inv[11]</pre>
# env
current <- inv[3:7]</pre>
head(current)
##
        aetpet
                  gdd
                                   pet
                                            stdp
## 1 0.3180346 7965.1 1595.7 1950.320 137.8134
## 2 0.2807616 7888.9 1693.7 1991.475 156.3950
## 3 0.2638533 8165.3 1595.0 2179.968 127.0621
## 4 0.2790938 8195.6 1346.0 1919.897 114.7686
## 5 0.3030646 7858.1 1711.1 1795.255 158.3286
## 6 0.3217786 7888.5 1711.1 1788.220 151.8030
```

```
## BIOMOD
t1 <- Sys.time()
sp<-1
### Formating the data with the BIOMOD_FormatingData() function form the package biomod2
myBiomodData <- BIOMOD_FormatingData( resp.var = as.numeric(sp_occ[,sp]),</pre>
                                 expl.var = current,
                                 resp.xy = xy,
                                 resp.name = colnames(sp_occ)[sp])
##
## Response variable name was converted into species.occ
## > No pseudo absences selection !
##
       ! No data has been set aside for modeling evaluation
## ----- Done ----- Done -----
myBiomodOption <- Print_Default_ModelingOptions()</pre>
##
##
   Defaut modeling options. copy, change what you want paste it as arg to BIOMOD_ModelingOptions
##
##
## GLM = list( type = 'quadratic',
##
             interaction.level = 0,
             myFormula = NULL,
##
##
            test = 'AIC',
##
             family = binomial(link = 'logit'),
##
             mustart = 0.5,
             control = glm.control(epsilon = 1e-08, maxit = 50, trace = FALSE
##
## ) ),
##
##
## GBM = list( distribution = 'bernoulli',
##
            n.trees = 2500,
##
             interaction.depth = 7,
##
             n.minobsinnode = 5,
##
             shrinkage = 0.001,
##
             bag.fraction = 0.5,
##
             train.fraction = 1,
             cv.folds = 3,
##
##
             keep.data = FALSE,
##
             verbose = FALSE,
##
             perf.method = 'cv',
##
             n.cores = 1),
##
## GAM = list( algo = 'GAM_mgcv',
             type = 's_smoother',
##
             k = -1,
##
##
             interaction.level = 0,
```

myFormula = NULL,

##

```
##
               family = binomial(link = 'logit'),
##
               method = 'GCV.Cp',
##
               optimizer = c('outer', 'newton'),
##
               select = FALSE,
               knots = NULL,
##
               paraPen = NULL,
##
               control = list(nthreads = 1, irls.reg = 0, epsilon = 1e-07
## , maxit = 200, trace = FALSE, mgcv.tol = 1e-07, mgcv.half = 15
## , rank.tol = 1.49011611938477e-08
## , nlm = list(ndigit=7, gradtol=1e-06, stepmax=2, steptol=1e-04, iterlim=200, check.analyticals=0)
## , optim = list(factr=1e+07)
## , newton = list(conv.tol=1e-06, maxNstep=5, maxSstep=2, maxHalf=30, use.svd=0)
## , outerPIsteps = 0, idLinksBases = TRUE, scalePenalty = TRUE, efs.lspmax = 15
## , efs.tol = 0.1, keepData = FALSE, scale.est = fletcher, edge.correct = FALSE
## ) ),
##
##
## CTA = list( method = 'class',
               parms = 'default',
               cost = NULL,
##
               control = list(xval = 5, minbucket = 5, minsplit = 5, cp = 0.001
## , maxdepth = 25)),
##
##
## ANN = list( NbCV = 5,
##
               size = NULL,
##
               decay = NULL,
               rang = 0.1,
##
               maxit = 200),
##
##
## SRE = list( quant = 0.025),
## FDA = list( method = 'mars',
##
               add_args = NULL),
## MARS = list( type = 'simple',
##
                interaction.level = 0,
##
                myFormula = NULL,
                nk = NULL,
##
##
                penalty = 2
                thresh = 0.001,
##
##
                nprune = NULL,
                pmethod = 'backward'),
##
##
## RF = list( do.classif = TRUE,
              ntree = 500,
##
              mtry = 'default',
##
##
              nodesize = 5,
##
              maxnodes = NULL),
##
## MAXENT.Phillips = list( path_to_maxent.jar = 'C:/Users/obroenni/AppData/Local/Temp/Rtmp2dUCps/Rbu
##
                  memory_allocated = 512,
                  background_data_dir = 'default',
##
##
                  maximumbackground = 'default',
##
                  maximumiterations = 200,
##
                  visible = FALSE,
##
                  linear = TRUE,
##
                  quadratic = TRUE,
```

```
##
                product = TRUE,
##
                threshold = TRUE,
##
                hinge = TRUE,
##
                lq2lqptthreshold = 80,
##
                121qthreshold = 10,
##
                hingethreshold = 15,
##
                beta_threshold = -1,
##
                beta categorical = -1,
##
                beta_lqp = -1,
##
                beta_hinge = -1,
##
                betamultiplier = 1,
##
                defaultprevalence = 0.5),
##
   MAXENT.Phillips.2 =
##
##
     list(
##
       myFormula = NULL,
##
       regmult = 1,
       regfun = <function>
##
##
## )
myBiomodOption@GLM$test = 'none'
myBiomodOption@GBM$interaction.depth = 2
### Calibration of simple bivariate models
# remove insivible(capture.output)) to print output in the console
# this is just to keep the vignette short
invisible(capture.output(my.ESM <- ecospat.ESM.Modeling( data=myBiomodData,</pre>
                             models=c('GLM'),
                             models.options=myBiomodOption,
                             NbRunEval=1.
                             DataSplit=70,
                             weighting.score=c("AUC"),
                             parallel=F)
       )
### Evaluation and average of simple bivariate models to ESMs
my.ESM_EF <- ecospat.ESM.EnsembleModeling(my.ESM, weighting.score=c("SomersD"), threshold=0)
### Projection of simple bivariate models into new space
my.ESM_proj_current <- ecospat.ESM.Projection(ESM.modeling.output=my.ESM,
                                          new.env=current)
##
           ##
       ! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
##
## > Projecting ESM.BIOMOD.1_AllData_RUN2_GLM ...
## ----- Done ----- Done -----
## -----= Do Models Projections -------
##
       ! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
## > Projecting ESM.BIOMOD.2_AllData_RUN2_GLM ...
```

```
! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
 > Projecting ESM.BIOMOD.4_AllData_RUN2_GLM ...
## ----- Done ----- Done -----
##
! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
 > Projecting ESM.BIOMOD.5_AllData_RUN2_GLM ...
## ----- Done ----- Done -----
## -----=-=----- Do Models Projections -------
##
    ! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
##
  > Projecting ESM.BIOMOD.6_AllData_RUN2_GLM ...
## ----- Done ----- Done -----
##
! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
##
 > Projecting ESM.BIOMOD.7_AllData_RUN2_GLM ...
  ! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
## > Projecting ESM.BIOMOD.8_AllData_RUN2_GLM ...
## -----= Do Models Projections ------
##
##
    ! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
## > Projecting ESM.BIOMOD.9_AllData_RUN2_GLM ...
##
    ! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset
## > Projecting ESM.BIOMOD.10_AllData_RUN2_GLM ...
### Projection of calibrated ESMs into new space
my.ESM_EFproj_current <- ecospat.ESM.EnsembleProjection(ESM.prediction.output=my.ESM_proj_current,
                                ESM. EnsembleModeling.output=my.ESM EF)
```

----- Done ----- Done -----

------ Do Models Projections ------

------ Done ----- Done -----

-----= Do Models Projections ------

> Projecting ESM.BIOMOD.3_AllData_RUN2_GLM ...

##

! 'do.stack' arg is always set as TRUE for data.frame/matrix dataset

3.3 Spatial prediction of communities

Input data for the first argument (proba) as data frame of rough probabilities from SDMs for all species in columns in the considered sites in rows.

```
proba <- ecospat.testData[,73:92]</pre>
```

Input data for the second argument (sr) as data frame with richness value in the first column and sites.

```
sr <- as.data.frame(rowSums(proba))</pre>
```

3.4 SESAM framework with ecospat.SESAM.prr()

```
prr<-ecospat.SESAM.prr(proba, sr)
head(prr)[,1:4]</pre>
```

```
##
     glm_Agrostis_capillaris glm_Leontodon_hispidus_sl glm_Dactylis_glomerata
## 1
## 2
                                                          0
                             1
                                                                                   1
                                                          0
## 3
                                                                                   1
                                                          0
## 4
                             1
                                                                                   1
## 5
                             1
                                                          0
                                                                                   1
## 6
                                                                                   1
##
     glm_Trifolium_repens_sstr
## 1
## 2
                                1
## 3
                                1
## 4
## 5
                                1
## 6
```

4 Post-Modelling

4.1 Spatial Predictions of species assamblages

4.1.1 Co-occurrence analysis & Environmentally Constrained Null Models

Input data as a matrix of plots (rows) x species (columns). Input matrices should have column names (species names) and row names (sampling plots).

```
presence <-ecospat.testData[c(53,62,58,70,61,66,65,71,69,43,63,56,68,57,55,60,54,67,59,64)]
pred <-ecospat.testData[c(73:92)]
```

Define the number of permutations. It is recomended to use at least 10000 permutations for the test. As an example we used nperm = 100, to reduce the computational time.

```
nbpermut <- 100
```

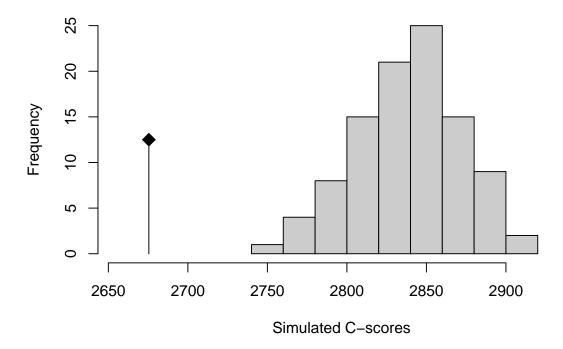
Define the outpath

outpath <- getwd()</pre>

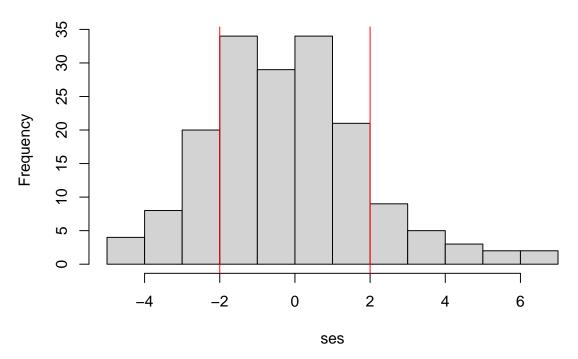
Run the function ecospat.cons_Cscore

The function tests for non-random patterns of species co-occurrence in a presence-absence matrix. It calculates the C-score index for the whole community and for each species pair. An environmental constraint is applied during the generation of the null communities.

ecospat.cons_Cscore(presence, pred, nbpermut, outpath)



Histogram of standardized effect size



```
## $0bsCscoreTot
## [1] 2675.468
##
## $SimCscoreTot
## [1] 2839.197
##
## $PVal.less
## [1] 0.00990099
##
## $PVal.greater
## [1] 1
##
## $SES.Tot
## [1] -4.854992
```

The function returns - the C-score index for the observed community (ObsCscoreTot), - the mean of C-score for the simulated communities (SimCscoreTot), - the p.values (PVal.less and PVal.greater) to evaluate the significance of the difference between the former two indices. - the standardized effect size for the whole community (SES.Tot). A SES that is greater than 2 or less than -2 is statistically significant with a tail probability of less than 0.05 (Gotelli & McCabe 2002 - Ecology). If a community is structured by competition, we would expect the C-score to be large relative to a randomly assembled community (positive SES). In this case the observed C-score is significantly lower than expected by chance, this meaning that the community is dominate by positive interactions (aggregated pattern).

A table is saved in the path specified where the same metrics are calculated for each species pair (only the table with species pairs with significant p.values is saved).