Appendix S4. Methods to calculate the Spatial Individual Specialization Indices

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1 Introduction

As explained in Appendix S3, the Spatial Individual Specialization Index (*SpatIS*) and the Spatial Individual Complementary Specialization Index (*SpatICS*) measure the overlap between individual's space use and the space use of the whole (rest of the) population. Since there are several ways of quantifying use of space and the overlap in the use of space, here we describe the different methods that can be used to calculate *SpatIS* and *SpatICS*.

The two indices are based on the assessment of the overlap between the individual's and the (rest of the) population's space use, which is operationalized in R through the function `adehabitatHR::kerneloverlap` (Calenge, 2006). A general definition of *SpatIS* and *SpatICS* are

$$SpatIS_{i,pop} = 1 - OverlapIndex_{i,pop}$$
$$SpatICS_{i,rest} = 1 - OverlapIndex_{i,rest}$$

where $OverlapIndex_{i,pop}$ is a measure of overlap between the space use of the individual i and the whole population (*pop*), and $OverlapIndex_{i,rest}$ is a measure of overlap between the space use of the individual i and the rest of the population (*rest*, all individuals polled but the individual i). We defined the default method to assess the overlap in space use the `VI` index from the `kerneloverlap` function, that calculates the intersection between the volumes of the individual and the population utilization distributions (UDs). However, since other methods to assess overlap in space use are available in the `kerneloverlap` function, here we present all of them and how *SpatIS* and *SpatICS* are defined for each one.

2 Methods to assess *SpatIS* and *SpatICS*

There are five methods available to calculate *SpatIS* and *SpatICS*. Here we define each of them for the calculation of *SpatIS*. The definition of the same indices for *SpatICS* is similar, with the difference that the calculations made over the whole population (subscript *pop*) are replaced by the rest of population, i.e., all individuals of the population but the one being analyzed (subscript *rest*). All the following definitions are direct adaptations from the indices described in Fieberg and Kochanny (2005), with the modification that one of the individuals for which the overlap is calculated is represented by the whole (rest of the) population. Please refer to Fieberg and Kochanny (2005) for further details and for an in-depth discussion on the potential and limitations of each index.

2.1) Index HR: overlap of home ranges between the individuals and the population

The calculation of the overlap in space use through the `HR` index ignores the UDs and considers only polygons that represent the home range (or, in this context, the areas of use - those used most intensely by the individuals and the population). It measures the proportion of the whole population's area of use which overlaps with the area of use of each individual. As our assessment of space use is based on the UD, this method can be represented by the overlap between kernel density estimation areas of different levels. The *SpatIS* index for `HR` is defined as:

$$SpatIS(HR)_{i,pop} = 1 - HR_{i,pop}$$
$$= 1 - \frac{A_{i,pop}}{A_{pop}}$$

where $A_{i,pop}$ is the area of intersection between the area of use (or x% KDE, for a given x between 0 and 100, defined by the user) of the individual i and the area of use of the whole population, and A_{pop} is the area of use of the whole population.

SpatIS(HR) is 0 when the individual area of use overlaps completely the population's area of use, and increase towards 1 as the the individual i uses a smaller part of the population's area of use. $SpatICS(HR)_{i,rest}$ is defined accordingly by replacing `pop` by the assessment of the area of use of the rest of the population (`rest`), excluding individual i.

2.2) Index PHR: probability of finding an animal in the population home range

The index `PHR` assesses the volume of the UD of the animal i that is inside the home range (or area of use) of the whole population, i.e., the probability of finding animal i within the population's area of use. According to that, the SpatIS is defined as:

$$SpatIS(PHR)_{i,pop} = 1 - PHR_{i,pop}$$
$$= 1 - \iint_{A_{pop}} UD_i(x,y) \, dx \, dy$$

where UD_i is the estimated UD for the animal i and A_{pop} is the area of use of the whole population.

SpatIS(PHR) is 0 when the whole UD of the individual i is within A_{pop} and increases towards 1 as the the individual i uses a smaller part of the population's area of use. $SpatICS(PHR)_{i,rest}$ is defined accordingly by replacing `pop` by the assessment of the area of use of the rest of the population (`rest`), excluding individual i.

2.3) Index VI: volume intersection between individual and population UDs

The index `VI` assesses the intersection between the volume of the individual UD and the population UD and is the default method for calculating *SpatIS* and *SpatICS*. As presented in the main text of the Kerches-Rogeri et al., the SpatIS is defined as:

$$SpatIS(VI)_{i,pop} = 1 - VI_{i,pop}$$
$$= 1 - \iint_{-\infty}^{\infty} min[UD_i(x,y), UD_{pop}(x,y)] \, dx \, dy$$

where UD_i is the estimated UD for the animal i, UD_{pop} is the estimated UD for the whole population, and the `min` function computes the minimum value between the two probability density functions.

SpatIS(VI) is 0 when the UD of the individual i and the whole population coincide, and increases towards 1 as the the volume shared by the UDs decrease. $SpatICS(VI)_{i,rest}$ is defined accordingly by replacing `pop` by the assessment of the area of use of the rest of the population (`rest`), excluding individual i.

2.4) Index BA: Bhattacharyya's affinity

The `BA` index was originally defined as a statistical measure of affinity between two populations. Here, it represents the affinity between the individual's and the population's use of space. `BA` is based on the product of the individual and the population UDs, under the assumption that they use the space independently. For *SpatIS* this condition does not hold since individual i is also part of the population. Therefore, we advise users not to use *SpatIS(BA)* but only *SpatICS(BA)*, for which this assumption may be accomplished. The *SpatICS* for `BA` is defined as:

$$SpatICS(BA)_{i,rest} = 1 - BA_{i,rest}$$

$$= 1 - \iint_{-\infty}^{\infty} \sqrt{UD_i(x,y)}\sqrt{UD_{rest}(x,y)}\,dx\,dy$$

where UD_i is the estimated UD for the animal i and UD_{rest} is the estimated UD for the rest of the population, excluding the individual i.

SpatICS(BA) is 0 when the UD of the individual i and the rest of population coincide, and 1 when the individual i uses areas completely different from the rest of the population.

2.5) Index UDOI: UD overlap index

The `UDOI` index was created based on Hurlbert's (1978) $E/E_{uniform}$ index, which measures the niche overlap between populations. For pairs of individuals, it measures the amount of overlap relative to two individuals using the same space uniformly. As `BA`, `UDOI` is defined based on the product of the UDs and also assumes that both UDs are independent. Because of that, we recoment the use of *SpatICS* (but not *SpatIS*) for this index, defined as below:

$$SpatICS(UDOI)_{i,rest} = 1 - UDOI_{i,rest}$$

$$= 1 - A_{i,rest} \iint_{-\infty}^{\infty} UD_i(x,y) \times UD_{rest}(x,y)\,dx\,dy$$

where UD_i is the estimated UD for the animal i, UD_{rest} is the estimated UD for the rest of the population, excluding the individual i, and $A_{i,rest}$ is the overlap area between the individual i's and the rest of the population's areas of use. Here, the areas of use can be defined as the x% KDE area, for a given x defined by the user.

SpatICS(UDOI) is 0 when there is complete overlap between the UDs and 1 when there is no overlap. However, differently from the other indices, *SpatICS(UDOI)* may also assume negative values, when the UD of the individual i and the rest of the population are nonuniformly distributed and have a high degree of overlap. Positive *SpatICS(UDOI)* values indicate there is less overlap relative to what it would be expected under a uniform space use, and negative *SpatICS(UDOI)* values indicate there is higher overlap than expected under uniform space use.

2.6) Index HD: the Hellinger's distance

The index `HD`, also present as an option at the function `adehabitatHR::kerneloverlap`, is not consider here as a valid method to assess the overlap between individual and population space use because its definition may be writen as a linear function of the `BA` index. Since $HD = 2 \times (1 - BA)$, this means that $HD = 2 \times SpatICS(BA)$, so it would be redundant to define SpatICS for this spatial overlap measure.

3 Computing *SpatIS* and *SpatICS* through practical examples

3.1) Simulated specialist individuals from Appendix S3

Here we used the data on the 5 individuals (e.g. bats) simulated in Appendix S3 to test the difference between the methods to calculate *SpatIS* and *SpatICS*. Look at the Appendix S3 for more information on the context of these simulated individuals' movement.

```
# Loading from the local environment, after downloading and unpacking
# Path to code folder in your computer
# setwd("/home/leecb/Github/SpatIS/code/")
source("spatis_source_code_v1_0.R")
```

```
## Warning: package 'adehabitatHR' was built under R version 3.6.2
```

```
# read data
dat <- readRDS("inputdata_appS3.RDS")
```

3.1.1) *SpatIS(HR)*

Below we calculate *SpatIS* and *SpatICS* for the HR index, considering the area of use as the 95% KDE.

```
# Calculate SpatIS for a given method and index
# here we create an auxiliary function to calculate and print the SpatIS and
# SpatICS values for each method
spat.vals <- function(x, method, index = c("spatis", "spatics"), ...) {
  res <- SpatIS(x, individuals.col = "ID", population.ID = NULL,
                index = index, method = method, ...)
  return(res[3:6])
}

(spatis.hr <- spat.vals(dat, "HR", percent = 95))
```

```
## $SpatIS.individual
##          1          2          3          4          5
## 0.01492537 0.00000000 0.00000000 0.00000000 0.00000000
##
## $SpatIS.population
## [1] 0.002985075
##
## $SpatICS.individual
##          1          2          3          4          5
## 0.5820896 0.5820896 0.6301370 0.7464789 0.5833333
##
## $SpatICS.population
## [1] 0.6248257
```

It is possible to notice that, for the 95% KDE, *SpatIS(HR)* is very low or zero for most individuals, since for most of them the individual 95% KDE overlaps completely with the population 95% KDE (see the figure in section 4 of the Appendix S3). This is a consequence of using HR, that does not consider the UD but only the polygon encompassing the KDE. Reducing the KDE level for only the core areas (50% KDE, through the argument `percent` of the function `spat.vals`created here, which is used by the `kernelUD` and `kerneloverlap` functions), for instance, would reduce the overlap, increasing the measure of *SpatIS*, as shown below. However, this index should be interpreted carefully as a measure of individual specialization in the use of space.

```
(spatis.hr50 <- spat.vals(dat, "HR", percent = 50))
```

```
## $SpatIS.individual
##      1      2      3      4      5
## 0.1875 0.4500 0.6500 0.2500 0.0000
##
## $SpatIS.population
## [1] 0.3075
##
## $SpatICS.individual
##      1      2      3      4      5
## 0.9375 0.9375 0.8000 1.0000 0.8125
##
## $SpatICS.population
## [1] 0.8975
```

On the other hand, *SpatICS(HR)* is not so affected by the choice of the KDE threshold: this index can show individual specialization in relation to rest of the population even for the 95% KDE HR measure, as shown above.

3.1.2) *SpatIS(PHR)*

Below we calculate *SpatIS* and *SpatICS* for the `PHR` index, considering the population area of use as the 95% KDE. In this case, it is already possible to identify the individual specialization though SpatIS, given that the overlap is calculated through the individual UD instead of the individual area of use.

```
(spatis.phr <- spat.vals(dat, "PHR", percent = 95))
```

```
## $SpatIS.individual
##         1         2         3         4         5
## 0.6441998 0.6434557 0.7355954 0.6665676 0.8272283
##
## $SpatIS.population
## [1] 0.7034093
##
## $SpatICS.individual
##         1         2         3         4         5
## 0.7564015 0.7564015 0.7612023 0.8806711 0.7851968
##
## $SpatICS.population
## [1] 0.7879746
```

3.1.3) *SpatIS(VI)*

The values of *SpatIS* and *SpatICS* for the `VI` index were already presented in Appendix S3 and are reproduced here only to easy the comparison between methods.

```
(spatis.vi <- spat.vals(dat, "VI"))
```

```
## $SpatIS.individual
##         1         2         3         4         5
## 0.6661083 0.6567337 0.7330505 0.6594467 0.7847597
##
## $SpatIS.population
## [1] 0.7000198
##
## $SpatICS.individual
##         1         2         3         4         5
## 0.8141360 0.8141360 0.8117282 0.9064550 0.8040123
##
## $SpatICS.population
## [1] 0.8300935
```

3.1.4) *SpatICS(BA)* and *SpatICS(UDOI)*

Below we calculate *SpatICS* for the `BA` index and for the `UDOI` index. The 95% KDE is used for the latter. It is possible to notice that *SpatICS(UDOI)* present higher values than all the other methods for this example.

```
# BA index
(spatis.ba <- spat.vals(dat, "BA", index = "SpatICS"))
```

```
## $SpatIS.individual
## NULL
```

```
## 
## $SpatIS.population
## NULL
## 
## $SpatICS.individual
##         1         2         3         4         5
## 0.6799514 0.6799514 0.6901478 0.7886191 0.6732872
## 
## $SpatICS.population
## [1] 0.7023914
```

```r
# UDOI index
(spatis.udoi <- spat.vals(dat, "UDOI", index = "SpatICS", percent = 95))
```

```
## $SpatIS.individual
## NULL
## 
## $SpatIS.population
## NULL
## 
## $SpatICS.individual
##         1         2         3         4         5
## 0.9256324 0.9256324 0.9288778 0.9786022 0.9285924
## 
## $SpatICS.population
## [1] 0.9374674
```

3.1.5) Comparison between the *SpatIS* methods

Below we calculate the correlation between *SpatIS* and *SpatICS* individual values among the different methods to compute the overlap in space use. For *SpatIS*, the correlation is positive between the `PHR` and `VI` indices, but not for the `HR`, since the individual *SpatIS* is null for most individuals for this index.

```r
# Package ggcorrplot to compute correlation between
# individual SpatIS and SpatICS indices
library(ggcorrplot)
```

```
## Warning: package 'ggcorrplot' was built under R version 3.6.3
```

```
## Loading required package: ggplot2
```

```r
# Computing correlations between SpatIS
cormat <- cor(cbind(spatis.hr$SpatIS.individual,
                    spatis.phr$SpatIS.individual,
                    spatis.vi$SpatIS.individual))
rownames(cormat) <- colnames(cormat) <- c("HR", "PHR", "VI")
ggcorrplot(cormat, hc.order = FALSE, type = "lower",
    outline.col = "white", lab = TRUE, legend.title = "Pearson's r")
```
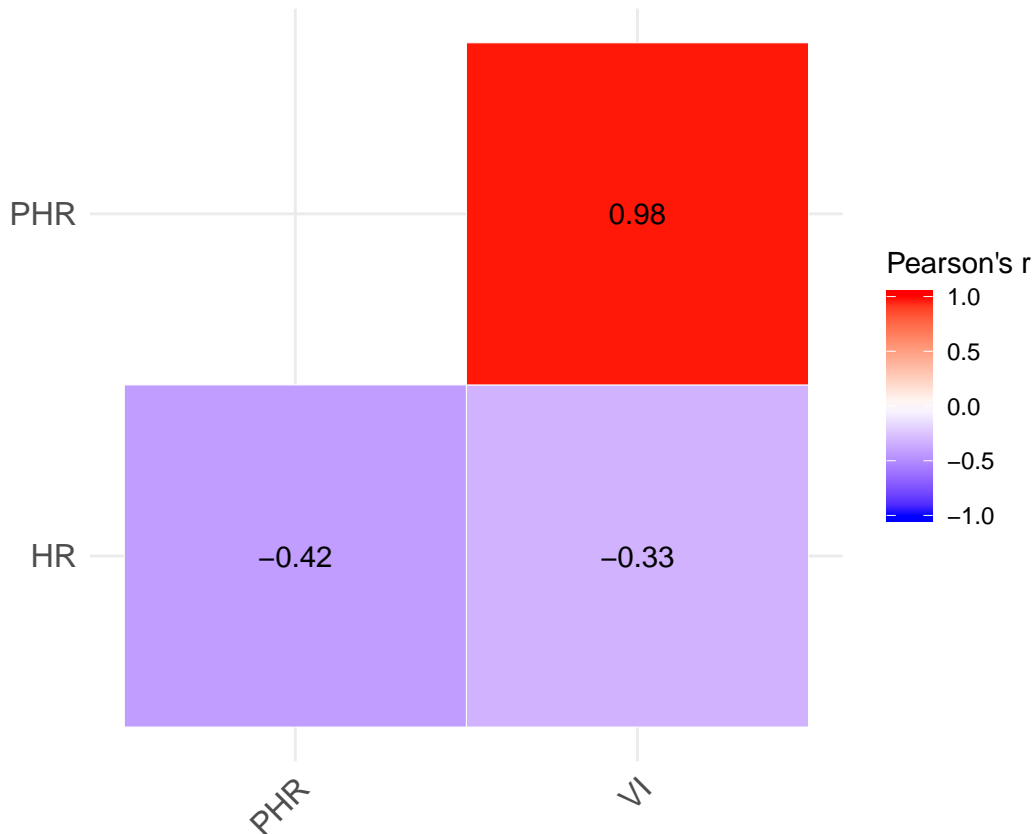
When one looks into *SpatICS*, however, we can see that all methods to assess individual complementary specialization are highly correlated.

```
# Computing correlations between SpatICS
cormat <- cor(cbind(spatis.hr$SpatICS.individual,
                    spatis.phr$SpatICS.individual,
                    spatis.vi$SpatICS.individual,
                    spatis.ba$SpatICS.individual,
                    spatis.udoi$SpatICS.individual))
rownames(cormat) <- colnames(cormat) <- c("HR", "PHR", "VI", "BA", "UDOI")
ggcorrplot(cormat, hc.order = FALSE, type = "lower",
    outline.col = "white", lab = TRUE)
```
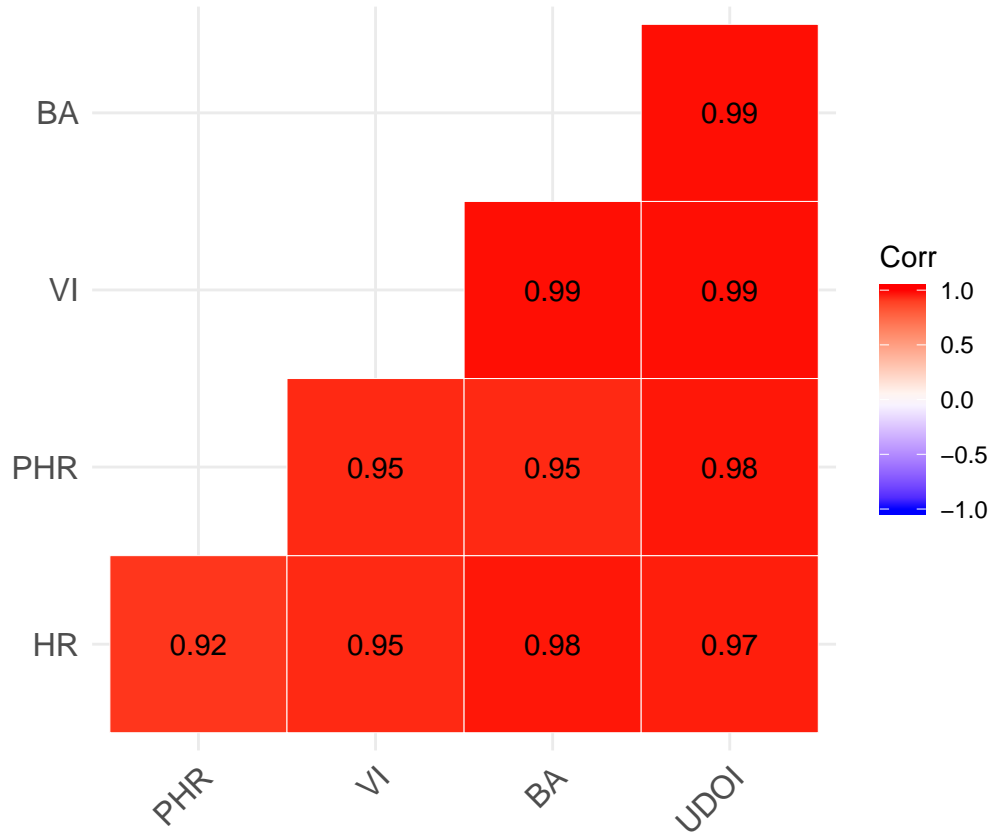
3.2) Bat tracking data from Kerches-Rogeri et al. main text

Here we calculate *SpatIS* and *SpatICS* for the ten bat individuals radio-tracked from the main text of Kerches-Rogeri et al., using the five calculation methods presented above. The absolute values of the two indices for each method vary greatly: population level *SpatIS* varies from 0.18 for `PHR` to 0.69 for `VI`, while population *SpatICS* varies from 0.20 for `PHR` to 0.75 for `VI`, and is even negative for the `UDOI` method (-0.40). This is shown below.

```
# read data
spdados <- readRDS("bat_spdados2.RDS")

# methods and indexes to be calculated
# spatis is not calculated for BA and UDOI
methods <- c("HR", "PHR", "VI", "BA", "UDOI")
index <- list(c("spatis", "spatics"), c("spatis", "spatics"), c("spatis", "spatics"),
              "spatics", "spatics")

# calculate SpatIS and SpatICS with all 5 methods
out <- mapply(SpatIS, method = methods, index = index,
              MoreArgs = list(data = spdados, individuals.col = "ID",
                              percent = 99, grid = 200, extent = 1.5))

# Population SpatIS
out[4,]

## $HR
## [1] 0.5670036
```

```
##
## $PHR
## [1] 0.1865459
##
## $VI
## [1] 0.6964447
##
## $BA
## NULL
##
## $UDOI
## NULL
```

```
# Population SpatICS
out[6,]
```
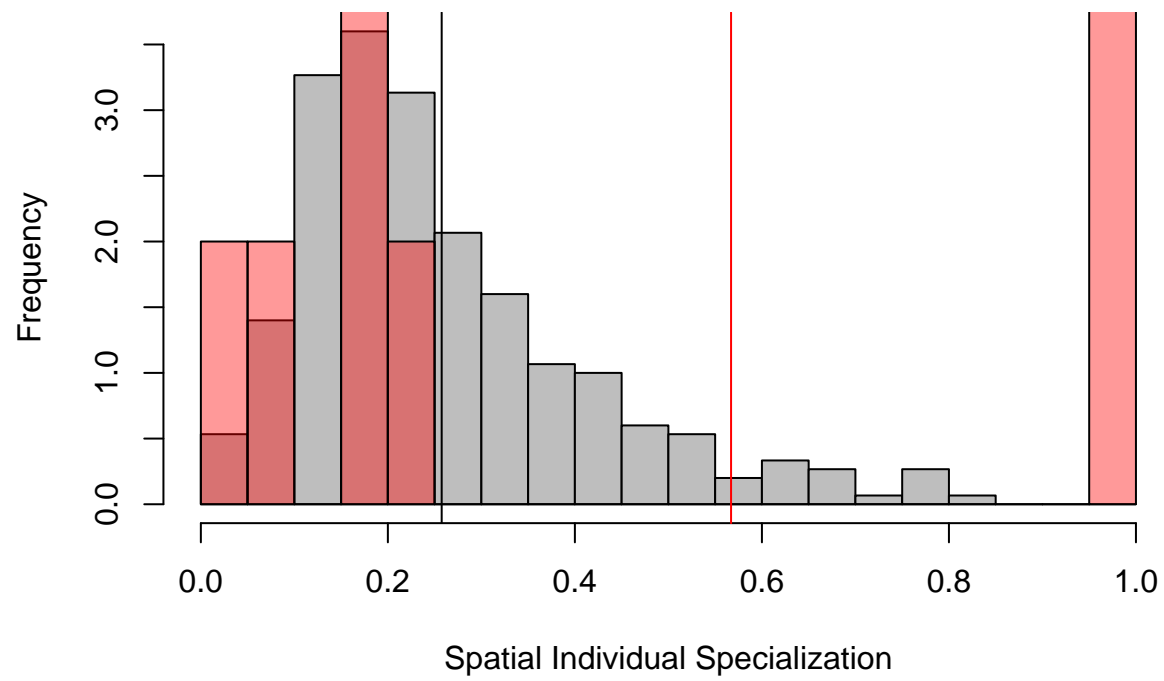
```
## $HR
## [1] 0.6220276
##
## $PHR
## [1] 0.2067028
##
## $VI
## [1] 0.7569617
##
## $BA
## [1] 0.5464079
##
## $UDOI
## [1] -0.4111708
```
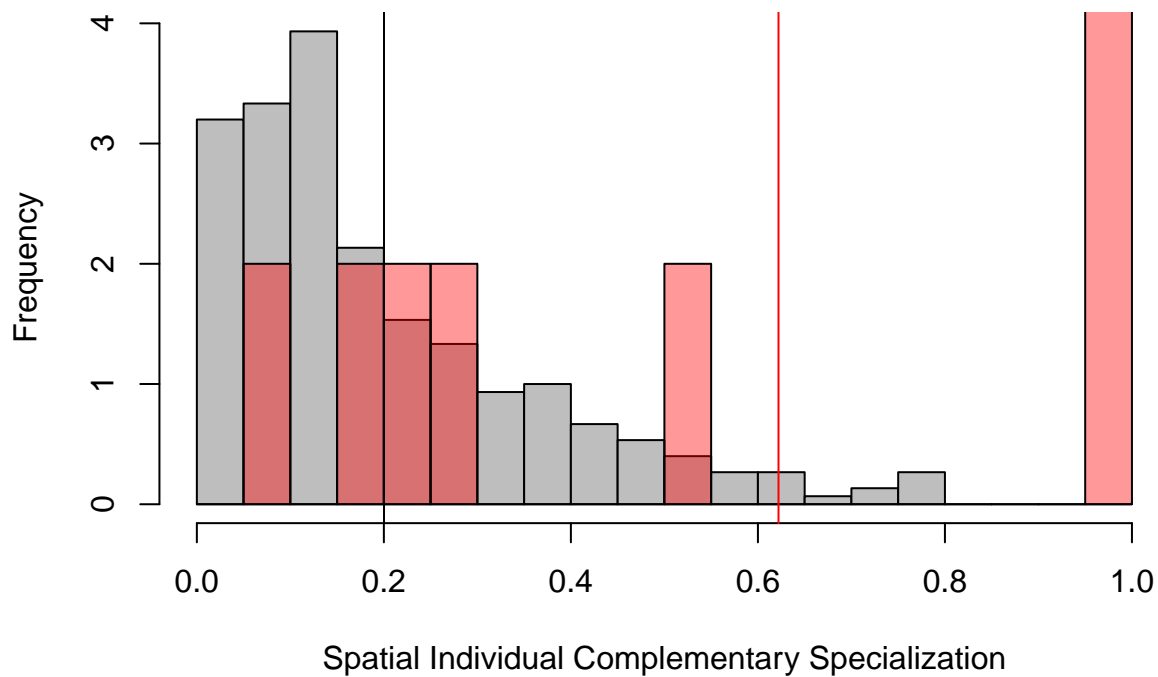
Despite differing in absolute values, the *SpatIS* and *SpatICS* indices are both higher for the observed population compared to a population where the locations were randomized to remove any spatial preference pattern. This indicates that all *SpatIS* methods are coherent and that the *Sturnira lilium* bats of this population indeed present individual specialization in their use of space.

Below we plot, for each *SpatIS* method, a histogram of the real observed individual *SpatIS* and *SpatICS* values in red, and the values of the histograms after 30 randomizations of the locations in grey. The respective mean of the observed and randomized index values are show by the vertical lines. As in the main text, the locations corresponding to the roost are not randomized and are kept the same for each individual. Besides, for each index we show the result of the *t-test* to compare the observed and randomized *SpatIS* and *SpatICS* individual values.

```
# recalculate SpatIS and have the output as a list
out.list <- mapply(SpatIS, method = methods, index = index,
               MoreArgs = list(data = spdados, individuals.col = "ID",
                               percent = 99, grid = 200, extent = 1.5),
               SIMPLIFY = F)
```

```
# For HR
randomized.HR <- try(SpatIS.randomize(out.list$HR, not.randomize.col = "nest",
                               not.randomize.val = 1, iterations = 30))
```

Spatial Individual Specialization

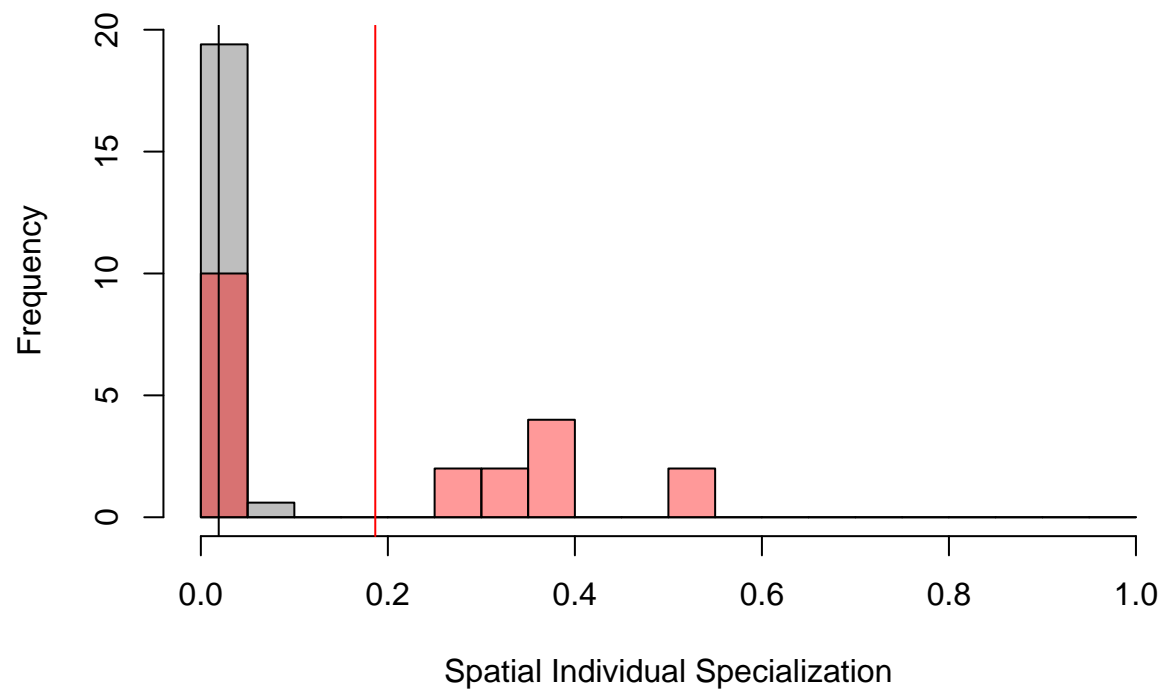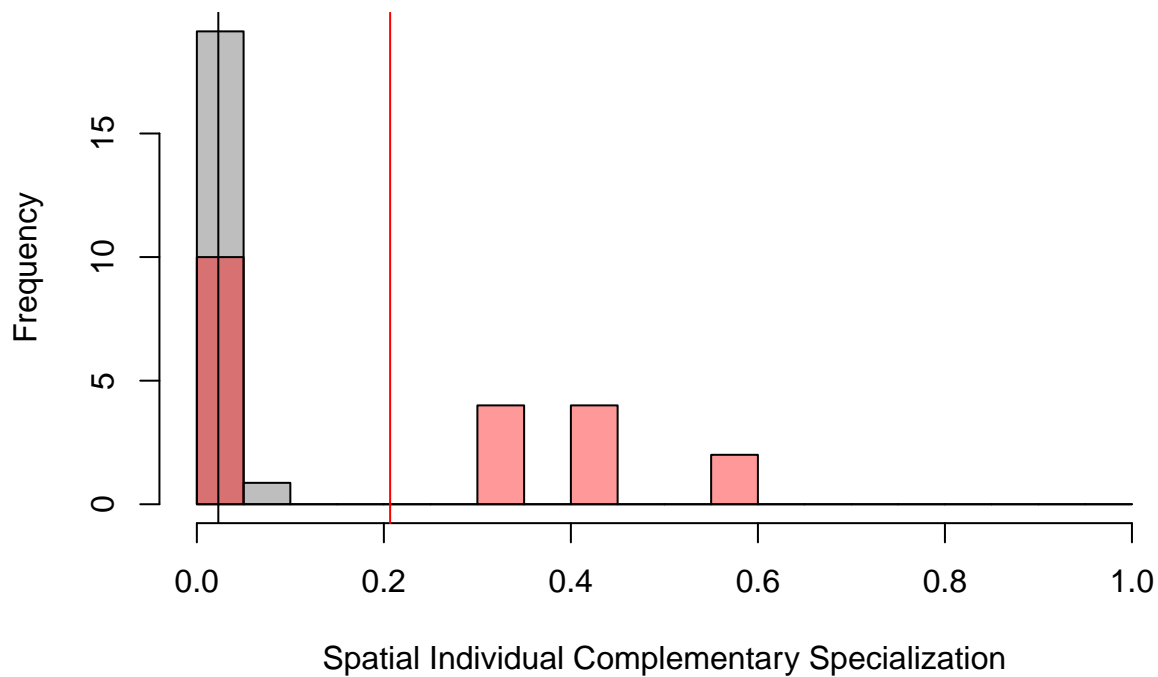Spatial Individual Complementary Specialization

```
# HR, significance for SpatIS
#randomized.HR[[1]]$SpatIS.significance
# HR, significance for SpatICS
randomized.HR[[2]]$SpatICS.significance
```

```
##
##  Welch Two Sample t-test
##
## data:  observed.C and expected.polled.C
## t = 3.3036, df = 9.1083, p-value = 0.004514
## alternative hypothesis: true difference in means is greater than 0
## 5 percent confidence interval:
##  0.6571167        Inf
## sample estimates:
## mean of x mean of y
## 0.6220276 0.1992070
```

```
# For PHR
randomized.PHR <- try(SpatIS.randomize(out.list$PHR, not.randomize.col = "nest",
                              not.randomize.val = 1, iterations = 30))
```

```
# PHR, significance for SpatIS
randomized.PHR[[1]]$SpatIS.significance
```

```
##
##  Welch Two Sample t-test
##
## data:  observed and expected.polled
## t = 2.5748, df = 9.0017, p-value = 0.01497
## alternative hypothesis: true difference in means is greater than 0
## 5 percent confidence interval:
##  0.2866949      Inf
## sample estimates:
##  mean of x  mean of y
## 0.18654593 0.01907743
```

```
# PHR, significance for SpatICS
randomized.PHR[[2]]$SpatICS.significance
```

```
##
##  Welch Two Sample t-test
##
## data:  observed.C and expected.polled.C
## t = 2.582, df = 9.0019, p-value = 0.0148
## alternative hypothesis: true difference in means is greater than 0
## 5 percent confidence interval:
##  0.3142888      Inf
## sample estimates:
```
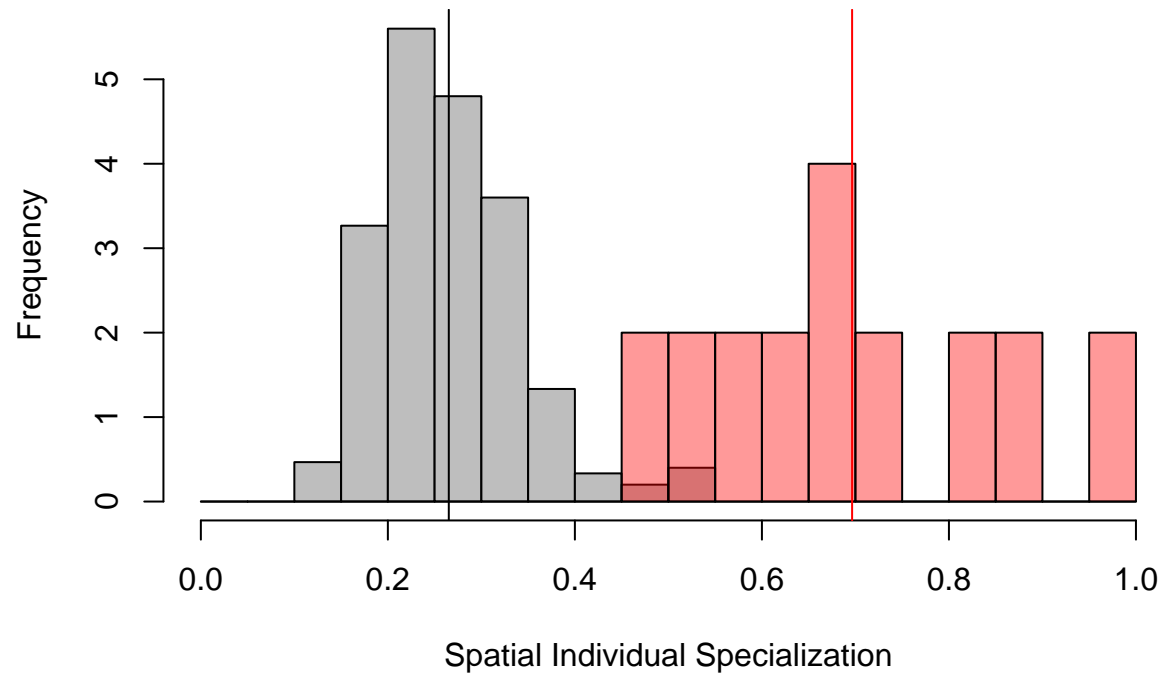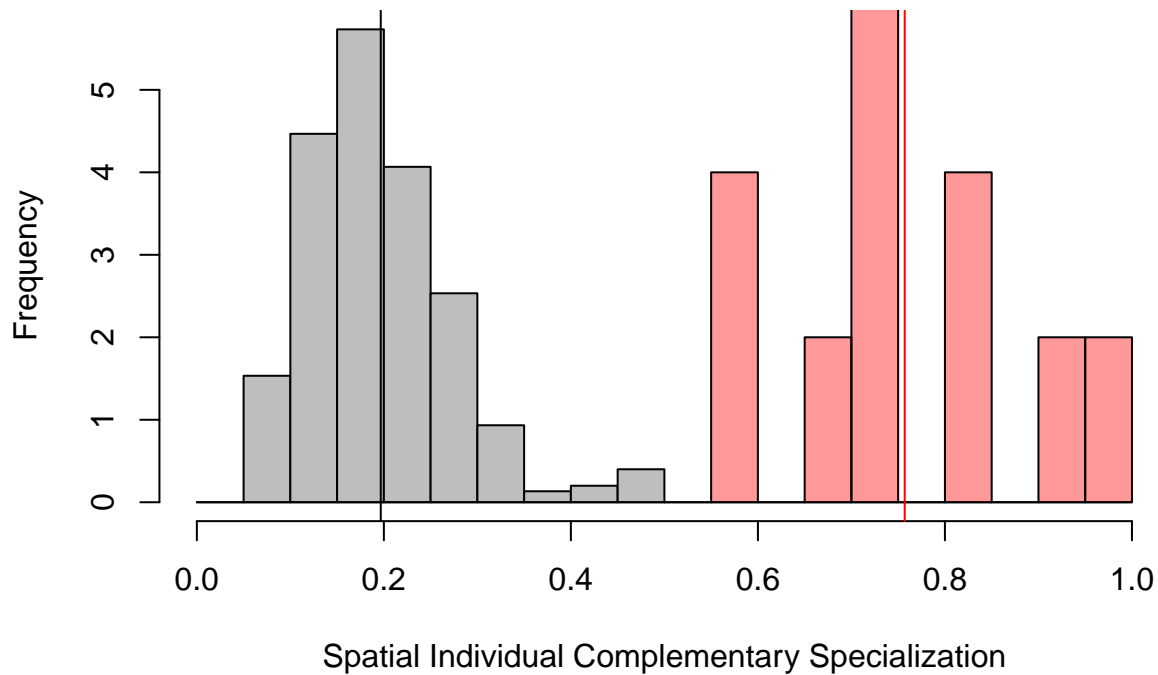
```
##  mean of x  mean of y
## 0.20670280 0.02290142
```

```
# For VI
randomized.VI <- try(SpatIS.randomize(out.list$VI, not.randomize.col = "nest",
                                       not.randomize.val = 1, iterations = 30))
```

Spatial Individual Complementary Specialization

```
# VI, significance for SpatIS
randomized.VI[[1]]$SpatIS.significance
```

```
##
##  Welch Two Sample t-test
##
## data:  observed and expected.polled
## t = 8.5019, df = 9.1282, p-value = 6.203e-06
## alternative hypothesis: true difference in means is greater than 0
## 5 percent confidence interval:
##  0.5233912       Inf
## sample estimates:
## mean of x mean of y
## 0.6964447 0.2657650
```
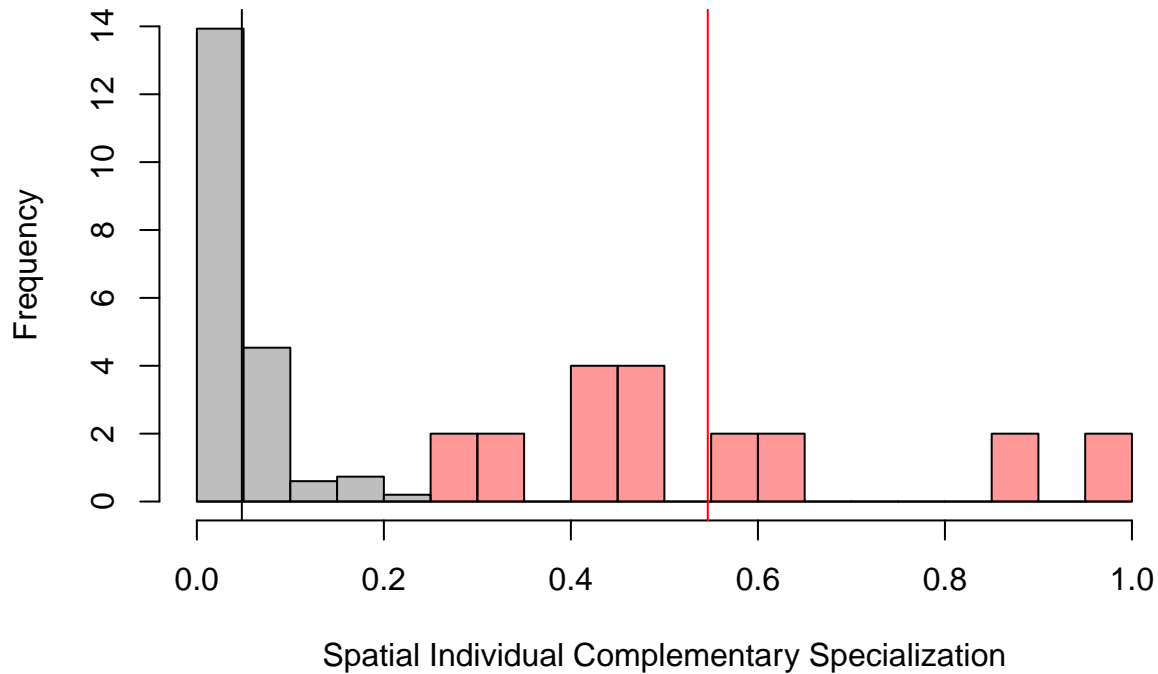
```
# VI, significance for SpatICS
randomized.VI[[2]]$SpatICS.significance
```

```
##
##  Welch Two Sample t-test
##
## data:  observed.C and expected.polled.C
## t = 12.119, df = 9.1875, p-value = 2.935e-07
## alternative hypothesis: true difference in means is greater than 0
## 5 percent confidence interval:
##  0.6441391       Inf
## sample estimates:
```

```
## mean of x mean of y
## 0.7569617 0.1972823
```

```r
# For BA
randomized.BA <- try(SpatIS.randomize(out.list$BA, not.randomize.col = "nest",
                                      not.randomize.val = 1, iterations = 30))
```



```r
# BA, significance for SpatICS
randomized.BA[[2]]$SpatICS.significance
```

```
##
##  Welch Two Sample t-test
##
## data:  observed.C and expected.polled.C
## t = 7.2076, df = 9.018, p-value = 2.495e-05
## alternative hypothesis: true difference in means is greater than 0
## 5 percent confidence interval:
##  0.6248482       Inf
## sample estimates:
##  mean of x  mean of y
## 0.54640790 0.04823274
```
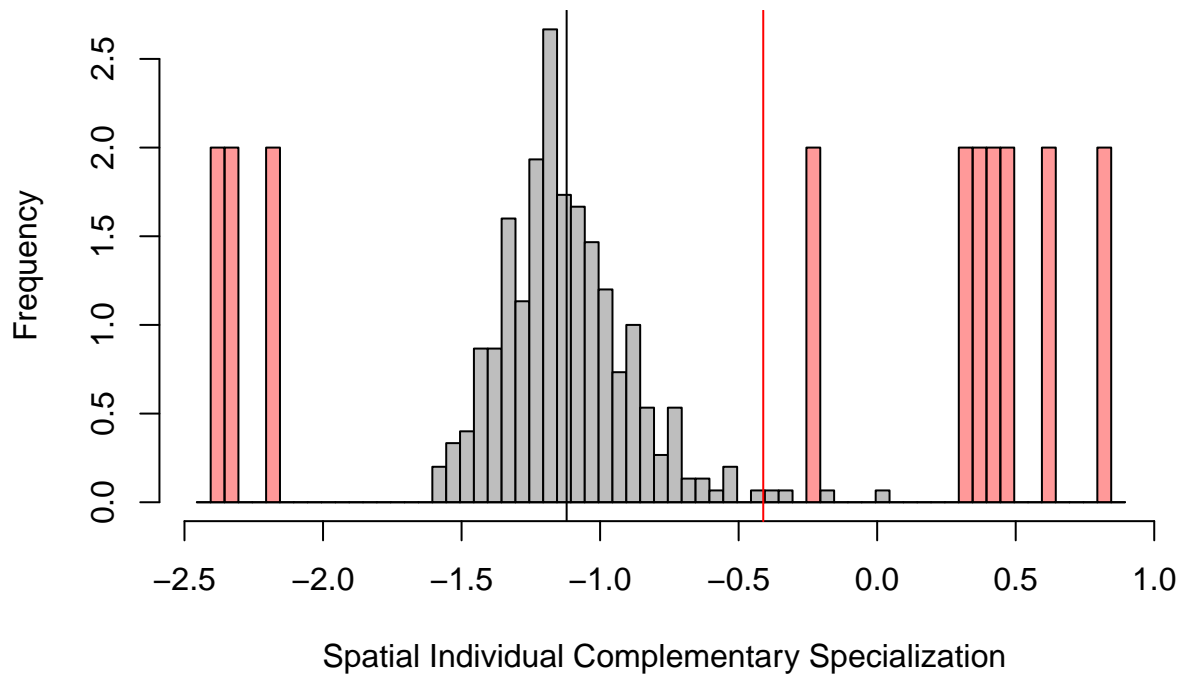
```r
# For UDOI
randomized.UDOI <- try(SpatIS.randomize(out.list$UDOI, not.randomize.col = "nest",
                                        not.randomize.val = 1, iterations = 30))
```

Spatial Individual Complementary Specialization

```
# UDOI, significance for SpatICS
randomized.UDOI[[2]]$SpatICS.significance
```

Citation

If you need more information or use *SpatIS* and *SpatICS*, please refer to

Kerches-Rogeri, P.; Niebuhr, B. B.; Muylaert, R. L., Mello, M. A. R. Individual specialization in the space use of frugivorous bats. *Journal of Animal Ecology.*

Additional references

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197, 516-519.

Fieberg, J. & Kochanny, C.O. (2005) Quantifying Home-Range Overlap: the Importance of the Utilization Distribution. Journal of Wildlife Management, 69, 1346–1359. doi: 10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Hurlbert, S.H. 1978. The measurement of niche over-lap and some relatives. Ecology, 59, 67–77.