Downscaling species occupancy: an introduction and tutorial

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1 Introduction to downscaling

In order to assess and manage the status of a species we need to know the abundance of individuals in the population(s) and their changes over time. For the vast majority of species this information is unobtainable, however one important proxy of true abundance and extinction risk is the area occupied by the species. For example, the area of occupancy (AOO) is a little-used measure of conservation status in the IUCN red list (IUCN 2014). Although easier to estimate than true abundance, the difficulty in estimating AOO lies in the extensive sampling required across the full range of the species at a grain size sufficiently fine to give meaningful estimates (and this grain size may vary with taxa, habitat or region). For the majority of species this is still impractical or unfeasible at these grain sizes. However, as we estimate occupancy at increasing grain sizes we increase our confidence in our presence-absence predictions. Such coarse-grain atlas data, generally generated from opportunistic recording over extended periods of time are much more widely available, however, at such coarse grain sizes we also lose resolution in our status estimates as occupancy rates at large grain sizes are less closely correlated with true abundance (Hartley and Kunin 2003).

A solution is to employ the occupancy-area relationship (OAR), that is the increase in the area occupied by a species increases as grain size increases (Kunin 1998). If the relationship can be described for occupancy at these coarser grain sizes, where confidence is high, then we can extrapolate the occupancy predictions to the fine grain sizes necessary for conservation assessments that are more closely related to the true abundance, distribution and conservation status.

Many models have been proposed to model this geometric relationship, and it appears that no one model consistently provides the best predictions (Azaele et al. 2012, Barwell et al. 2014). This package provides functions for ten commonly applied models, along with functions for preparing coarse-scale data, plotting results, and an ensemble method for running multiple models and averaging their predictions.

2 Using the downscale package

The general flow of the downscale package is presented in fig. 1. Ten downscaling models are available (Nachman, power law, logistic, poisson, negative binomial,

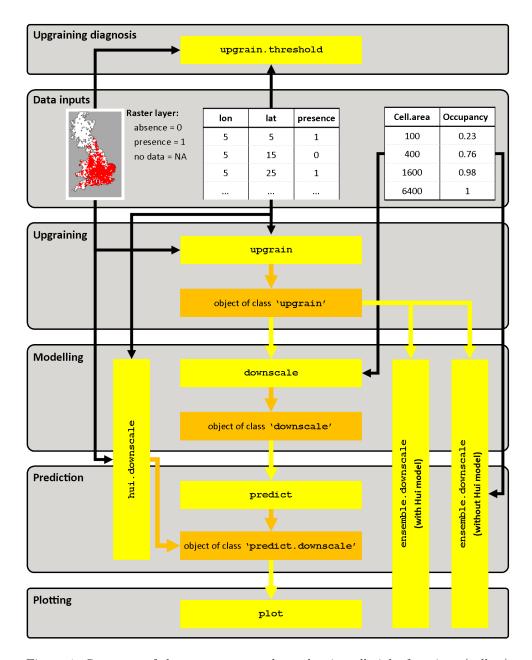


Figure 1: Structure of the downscale package showing all eight functions (yellow) and the three output object classes (orange).

generalised negative binomial, improved negative binomial, finite negative binomial, Thomas and Hui models). Details of all models can be found in the help files, and in the supplementary information of Barwell et al. 2014.

The user may input three types of data:

- 1) A data frame of grain sizes (cell area) and occupancies in that order;
- 2) A data frame of sample (cell) coordinates and presence-absence data (presence

- = 1; absence = 0). Column names must be "lon", "lat", and "presence";
- 3) A raster layer of presence-absence data (presence = 1; absence = 0; no data = NA).

If the user wishes to carry out downscaling with the Hui model (Hui et al. 2006, 2009) or upgraining of atlas data (and exploration of upgraining thresholds) then the input data must be of type 2 or 3. Table 1 shows the functions to use to achieve desired objectives with regards to input data.

Input data type	Objective	Function flow	
Data frame of cell areas	Downscale (excluding	${\tt downscale}{\Rightarrow}$	
and occcupancies	Hui model)	$ exttt{predict} \Rightarrow$	
		plot	
Data frame of cell co-	Downscale (excluding	$ ext{upgrain.threshold} \Rightarrow$	
ordinates and presence-	Hui model)	$\mathtt{upgrain} \Rightarrow$	
absence data		$\texttt{downscale} \Rightarrow$	
		$ exttt{predict} \Rightarrow$	
		plot	
Raster layer of presence-	Downscale (excluding	$\texttt{upgrain.threshold} {\Rightarrow}$	
absence data	Hui model)	$\mathtt{upgrain} \Rightarrow$	
		$\texttt{downscale} \Rightarrow$	
		$ exttt{predict} \Rightarrow$	
		plot	
Data frame of cell co-	Downscale (including	$\verb hui.downscale \Rightarrow$	
ordinates and presence-	Hui model)	plot	
absence data			
Raster layer of presence-	Downscale (including	hui.downscale⇒	
absence data	Hui model)	plot	
Data frame of cell co-	Ensemble modelling	ensemble.downscale	
ordinates and presence-	(excluding Hui model)		
absence data	,		
Raster layer of presence-	Ensemble modelling	$\texttt{upgrain.threshold} {\Rightarrow}$	
absence data	(with or without Hui upgrain		
	model)	ensemble.downscale	

Table 1: Flow of functions for different objectives depending on data input type.

For downscale modelling it is important they check their data for the scale of saturation and endemism. The scale of saturation is the grain size where all cells are occupied (fig. 2a). The scale of endemism is the grain size where the entire distribution occurs in a single cell (2b). All occupancies above these grain sizes should be set to NA, as they are providing no information for the occupancy-area curve. The downscale functions will automatically set these occupancies to NA for modelling purposes, which can lead to not enough scales remaining for downscaling.

3 Package tutorial

First, we must download the downscale package from CRAN.

> install.packages("downscale")

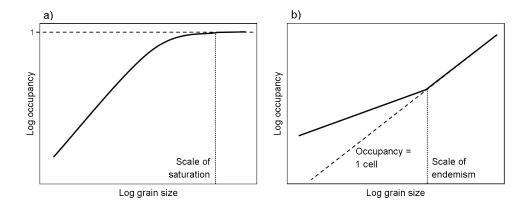


Figure 2: Occupancy-area relationships for two species showing a) the scale of saturation (the grain size at which all cells are occupied – ie occupancy = 1) and b) the scale of endemism (the scale at which only one cell is occupied). Occupancies of all grain sizes above these points should be set to NA.

Then load in the library

> library("downscale")

3.1 A quick example

We will start with the simplest example of using the downscaling package, where we already have occupancy data across a number of spatial scales (grain size). In this tutorial, we'll create some dummy data; a data frame where the first column are the cell areas (grain size) and the proportion of occupancy as the second column:

```
> occupancy <- data.frame(Cell.area = c(100, 400, 1600, 6400),
+ Occupancy = c(0.23, 0.56, 0.87, 1))
```

Now we use downscale to estimate the model parameters for the logistic model to the data (note: for this type of data input we must also specify the total extent):

```
2 400 0.56
3 1600 0.87
4 6400 1.00
$extent
[1] 320000
```

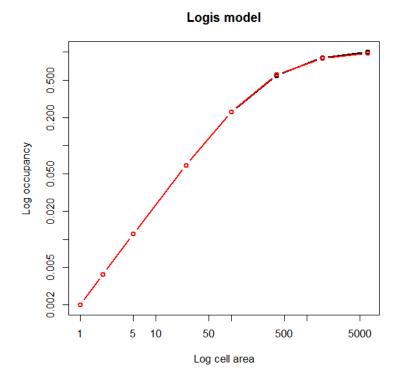
attr(,"class")

[1] "downscale"

Using the modelled parameters from the 'downscale' object we can predict occupancies at finer grain sizes. We will first create a vector of cell sizes (area) to predict. If we include the original cell sizes used for modelling we can also observe the model fit.

```
Cell.area
             Occupancy
                               A00
         1 0.002010876
                          643.4802
1
2
         2 0.004252482 1360.7942
3
         5 0.011396541
                         3646.8932
4
        25 0.061873397 19799.4871
5
       100 0.228564935 73140.7793
       400 0.570999511 182719.8435
6
7
       1600 0.856717834 274149.7068
8
       6400 0.964106833 308514.1867
```

- > ## now we can plot the predictions
- > plot(logis.pred)



3.2 Using atlas data

For the majority of cases we will only have atlas data that first needs to be upgrained. Read in example atlas data for the UK (in this case a data frame of sample cell coordinates and presence-absence data):

```
> ## if it is not already loaded, load in the package
> library(downscale)
> data.file <- system.file("extdata", "atlas_data.txt", package = "downscale")
> atlas.data <- read.table(data.file, header = TRUE)</pre>
```

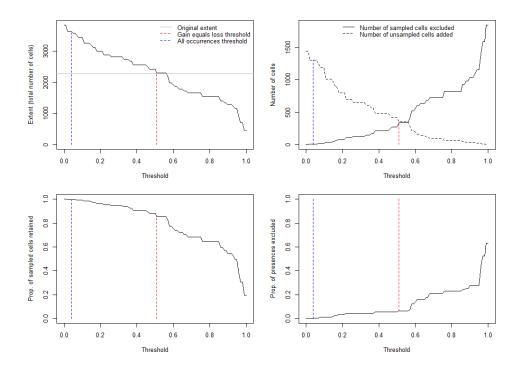
The data frame must have the column names "lon", "lat" and "presence":

> head(atlas.data)

lon	lat	presence
8170	10	0
8130	20	0
8140	20	0
8160	20	0
8170	20	0
8140	30	0
	8170 8130 8140 8160 8170	8170 10 8130 20 8140 20 8160 20 8170 20

The first step is to upgrain the atlas data to calculate occupancy at larger grain sizes than the atlas data – this provides the proportion of occupancy data points to fit the different downscaling models to. Therefore it is important that we fix the extent

for all grain sizes, but this means compromising between assigning unsampled cells as absences or excluding sampled cells as No Data. We can explore this trade-off with upgrain.threshold:

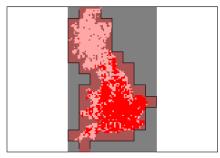


This gives two sets of plots (hit return or click on the plot window to see the second set). The first are a set of four plots that explore the trade-offs, and the second set are the standardised atlas data generated after applying four different threshold criteria ("All Sampled", "All Presences", "Gain Equals Loss" and "Sampled Only"). It is highly recommended to read the vignette "Upgraining atlas data for downscaling: threshold selection using upgrain.threshold" for more detail on creating your cross-scale standardised atlas data:

> vignette("Upgraining", package = "downscale")

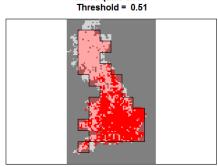
The user can input any threshold they wish, but for now we'll use one of the predefined options "All Presences" which ensures that all presence records are maintained:

All Interior Threshold = 0



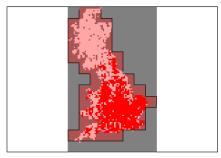
Prop. interior cells retained = 1; Prop. presences excluded = 0 Interior cells excuded = 0; Exterior cells added = 1439

Gain Equals Loss



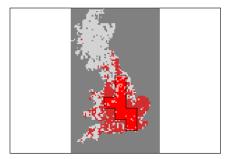
Prop. interior cells retained = 0.853; Prop. presences excluded = 0.06 Interior cells excuded = 336; Exterior cells added = 351 Prop. interior cells excuded = 1841; Exterior cells added = 0

All Occurrences Threshold = 0.04



Prop. interior cells retained = 0.999; Prop. presences excluded = 0 Interior cells excuded = 3; Exterior cells added = 1306

Interior Only Threshold = 1



- > ## upgrain data (using All Presences threshold)
- > occupancy <- upgrain(atlas.data,</pre>
- cell.width = 10,
- scales = 3,
- method = "All_Presences")

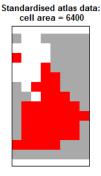
Original atlas data: cell area = 100

Standardised atlas data: cell area = 100

cell area = 400

Standardised atlas data:

Standardised atlas data: cell area = 1600



This creates an object of class 'upgrain' which can then be used directly as an input for downscaling.

3.3 Downscaling - more detailed examples

Fitting the downscaling models is as before, except that we no longer require to input the extent, which is passed directly from 'upgrain'. Let's try the improved negative binomial model (INB):

```
3 1600 0.5219298
4 6400 0.7017544
$extent
[1] 364800
attr(,"class")
[1] "downscale"
```

The downscaling functions use an optimisation procedure to fit the models to the upgrained occupancy data. Suitable starting values for model parameters are automatically inputted, however if the models aren't converging then it is possible to specify user-specific parameters. They must be in the form of a list with the same parameter names (take particular note of capitals) as the original starting parameters:

```
> ## Specifying the starting parameters
> params.new <- list("C" = 0.1, "r" = 0.00001, "b" = 0.1)
> (inb.new <- downscale(occupancies = occupancy,
                        model = "INB",
                        starting_params = params.new))
$model
[1] "INB"
$pars
            С
                          r
1.161747e-28 1.669658e-05 -3.712604e-01
$observed
 Cell.area Occupancy
       100 0.2713542
1
2
       400 0.4122807
3
       1600 0.5219298
4
       6400 0.7017544
$extent
[1] 364800
attr(,"class")
[1] "downscale"
```

Table 2 shows the default starting parameters implemented.

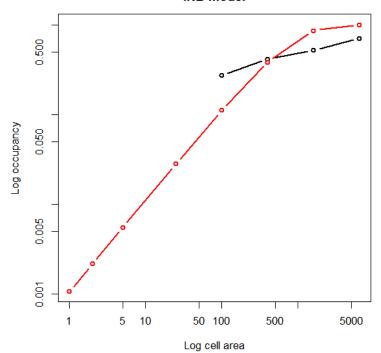
We can visually compare the two to see which has a better fit (plotting can be called directly from predict or through plot):

```
> ## plot the predictions of two FNB models using predict.downscale
> ind.pred <- predict(inb,
+ new.areas = c(1, 2, 5, 25, 100, 400, 1600, 6400),
+ plot = TRUE)
> inb.pred.new <- predict(inb.new,</pre>
```

Model	Parameter 1	Parameter 2	Parameter 3
Nachman	"C" = 0.01	"z" = 0.01	
PL	"C" = 0.01	"z" = 0.01	
Logis	"C" = 0.01	"z" = 0.01	
Poisson	"lambda" = $1e-8$		
NB	"C" = 0.01	"k" = 0.01	
GNB	"C" = 0.00001	"z" = 1	"k" = 0.01
INB	"C" = 1	"r" = 0.01	"b" = 0.1
FNB	"W" = 10	"k" = 10	
Thomas	"rho" = $1e-8$	"mu" = 10	"sigma" = 1

```
new.areas = c(1, 2, 5, 25, 100, 400, 1600, 6400),
plot = TRUE)
```

INB model

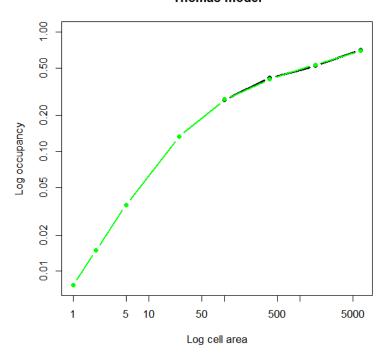


The Thomas model involves an integration process that can be time-consuming to run. For this reason the user may select tolerance during integration – the finer the tolerance, the more accurate the prediction. It can therefore be a good idea to initially try a larger tolerance value in order to ascertain if the starting parameters are likely to be correct.

```
new.areas = c(1, 2, 5, 25, 100, 400, 1600, 6400),
tolerance = 1e-6)

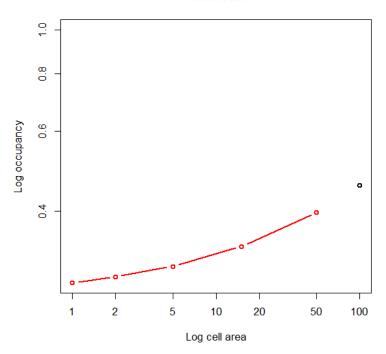
## When plotting the results we can change the graphics
plot(thomas.pred,
col.pred = "green",
pch = 16,
lwd.obs = 3)
```

Thomas model



The Hui model is slightly different from the other downscaling models in that it does not need occupancy from multiple scales. Instead, it only takes the data from the atlas scale and uses this to calculate occupancy at finer grain sizes – in effect the hui.downscale function runs downscale and predict.downscale in one step. Therefore the input data must either be a presence-absence raster layer of the atlas data, or a data frame of cell coordinates and presence-absence data. Additionally the function requires the cell widths of the input data, along with the grain size (cell area) for which we wish to predict occupancy. These must be smaller than the cell area of the input data. Additionally, like the Thomas model, the tolerance can be specified if the results appear inaccurate (set tolerance to a smaller number) or takes extensive programming time (set tolerance to a larger number).

Hui model



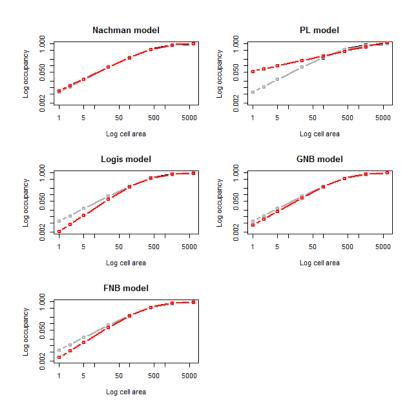
3.4 Ensemble modelling

It is probable that the user won't know which model will provide the most accurate predictions. Therefore there is an ensemble function that will model and predict occupancy for multiple models simultaneously. It also applies a simple model averaged prediction (the means of the log occupancies). Some or all of the models can be selected. If we don't wish to run the Hui model input data can be a data frame of occupancies and cell areas, along with the grain sizes we wish to predict and the total extent:

```
> ## if it is not already loaded load in the package
> library(downscale)
 ## hypothetical occupancy data
 occupancy <- data.frame(Cell.area = c(100, 400, 1600, 6400),
                          Occupancy = c(0.23, 0.56, 0.87, 1)
 ## grain sizes (cell areas) to predict
> areas.pred <- c(1, 2, 5, 25, 100, 400, 1600, 6400)
 ensemble <- ensemble.downscale(occupancy,</pre>
+
                                  new.areas = areas.pred,
                                  extent = 320000,
                                  models = c("Nachman",
+
                                             "PL",
                                             "Logis",
                                             "GNB",
```

```
+ "FNB"),
+ plot = TRUE)
```

Nachman model is running... complete
PL model is running... complete
Logis model is running... complete
GNB model is running... complete
FNB model is running... complete



- > ## the model averaged predictions are in grey
- > ## predicted proportion of occupancies
- > ensemble \$0ccupancy

3 0.014068055 0.023300961 4 0.067107408 0.085204625

-	oneometevecupancy						
	Cell.area	Nachman	PL	Logis	GNB		
1	1	0.007084977	0.05581996	0.002010876	0.004059485		
2	2	0.012179638	0.07113722	0.004252482	0.007645696		
3	5	0.024851808	0.09801796	0.011396541	0.017587267		
4	25	0.085220244	0.17211624	0.061873397	0.073735530		
5	100	0.232474679	0.27953528	0.228564935	0.230188967		
6	400	0.544305709	0.45399534	0.570999511	0.558122075		
7	1600	0.903148404	0.73733723	0.856717834	0.877387332		
8	6400	0.999026625	1.19751493	0.964106833	0.984486991		
	FI	NB Mean	ns				
1	0.00284089	94 0.00620137	73				
2	2 0.005668054 0.010981077						

```
5 0.228575983 0.239104306
6 0.566654658 0.536927362
7 0.870161429 0.846858509
8 0.976325167 1.020839639
```

> ## predicted area of occupancies (AOO)

> ensemble\$A00

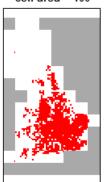
```
Cell.area
            Nachman
                            PL
                                                 GNB
                                     Logis
        1 2267.193 17862.39
                                  643.4802
                                            1299.035
1
            3897.484 22763.91
2
         2
                                 1360.7942
                                            2446.623
3
        5
            7952.579 31365.75 3646.8932 5627.925
4
        25 27270.478 55077.20 19799.4871 23595.370
5
       100 74391.897 89451.29 73140.7793 73660.469
6
       400 174177.827 145278.51 182719.8435 178599.064
7
      1600 289007.489 235947.91 274149.7068 280763.946
8
      6400 319688.520 383204.78 308514.1867 315035.837
         FNB
                 Means
1
    909.0862
               1984.439
2
   1813.7772 3513.945
3
   4501.7776 7456.307
4 21474.3707 27265.480
5 73144.3146 76513.378
6 181329.4907 171816.756
7 278451.6571 270994.723
8 312424.0534 326668.684
```

Alternatively, the input data may be an object of class 'upgrain', which also allows us to run the Hui model as long as we specify the cell width:

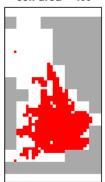
Original atlas data: cell area = 100



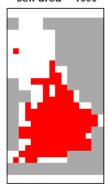
Standardised atlas data: cell area = 100



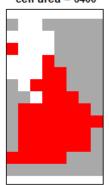
Standardised atlas data: cell area = 400



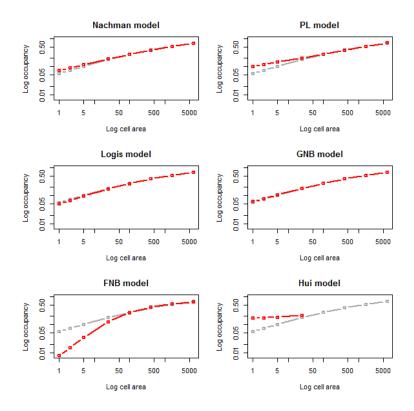
Standardised atlas data: cell area = 1600



Standardised atlas data: cell area = 6400

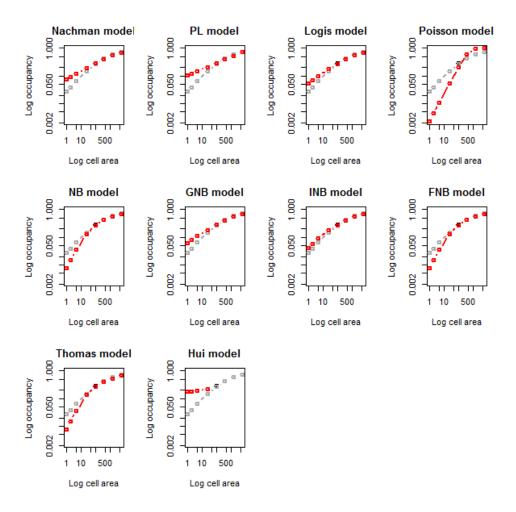


Nachman model is running... complete
PL model is running... complete
Logis model is running... complete
GNB model is running... complete
FNB model is running... complete
Hui model is running... complete



If we want to run all ten models we can specify models = "all". Once again, we can set the tolerance values for the modelling (tolerance_mod) and prediction (tolerance_pred) of the Thomas model and the Hui model (tolerance_hui) to improve processing times or accuracy.

```
ensemble <- ensemble.downscale(occupancy,</pre>
                                 new.areas = areas.pred,
                                 cell.width = 10,
                                 models = "all",
                                 tolerance_mod = 1e-3,
                                 plot = TRUE)
Nachman model is running...
                             complete
PL model is running... complete
Logis model is running... complete
Poisson model is running... complete
NB model is running... complete
GNB model is running... complete
INB model is running... complete
FNB model is running... complete
Thomas model is running...
                            complete
Hui model is running... complete
```



We can also specify the starting parameters for specific models. For each model the starting parameters should be in the form of a list as before, and each model list is an item in a combined list:

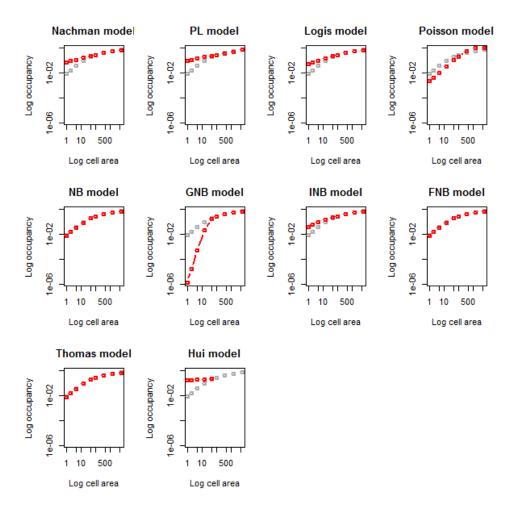
```
> ## Specifying starting parameters for Nachman and GNB models
> new.params <- list(Nachman = list("C" = 0.1, "z" = 0.01),
+ GNB = list("C" = 0.1, "z" = 1, "k" = 0.01))
> new.params
$Nachman
$Nachman$C
[1] 0.1
$Nachman$z
[1] 0.01
```

[1] 0.1

```
$GNB$k
[1] 0.01
> ensemble <- ensemble.downscale(occupancies = occupancy,
                                new.areas = c(1, 2, 5, 15, 50, 100, 400, 1600,
                                              6400),
                                cell.width = 10,
                                models = "all",
                                tolerance_mod = 1e-3,
                                starting_params = new.params,
                                plot = TRUE)
Nachman model is running... complete
PL model is running... complete
Logis model is running... complete
Poisson model is running... complete
NB model is running... complete
GNB model is running... complete
INB model is running... complete
```

\$GNB\$z [1] 1

FNB model is running... complete
Thomas model is running... complete
Hui model is running... complete



3.5 Creating atlas data from point records

It may be that instead of having pre-existing atlas data, we may need to create our own coarse-scale data from point records (for example herbarium records or GBIF data).

The grain size (cell width) needs to be carefully chosen so that we can best meet the assumption that all cells have been sampled. If there are cells or regions where we do not expect this to be the case it is best to change these to NA's rather than assign them as absences.

The library **spocc** will automatically harvest GBIF data for a desired species for a specified region.

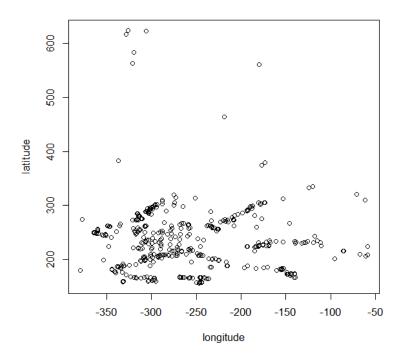
- > library(spocc)
- > library(downscale)

We'll get the records for the chalkhill blue (Polyommatus coridon), a species with a patchy breeding distribution in the UK.

> records <- occ(query = "Polyommatus coridon",

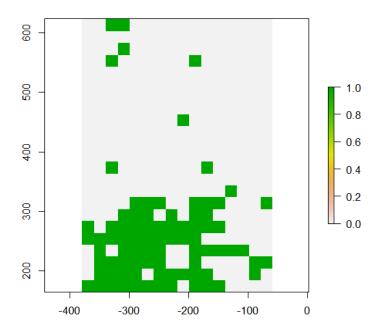
We can have a quick look at the point records if we like.

- > records.coords <- records@coords
- > plot(records.coords)



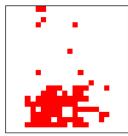
Now we have to convert these points in to a coarse-scale raster. The simplest method is to bound our raster by the limits of the location coordinates. Careful thought must also be put in to the grain size. It must be large enough that we are confident it is an accurate representation of presence-absence, but also small enough to allow upgraining to give at least three spatial scales worth of occupancy data. Here, as the UK is generally well-sampled, we will set a grain size of 20 km width $(400 \ km^2)$, which will still comfortably allow us to upgrain to give three scales $(400, 1600, 6400 \ km^2)$.

```
> gbif_raster <- raster(xmn = min(records.coords[, "longitude"]),
+ xmx = max(records.coords[, "longitude"]),</pre>
```

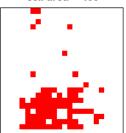


As our area is rectangular we should not be too worried about setting our thresholds for upgraining, and so we can choose the "All Sampled" option to maintain all data.

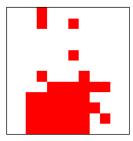
Original atlas data: cell area = 400



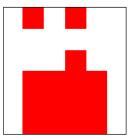
Standardised atlas data: cell area = 400



Standardised atlas data: cell area = 1600



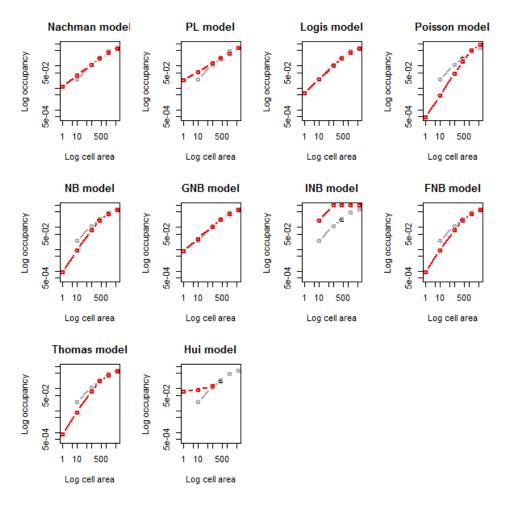
Standardised atlas data: cell area = 6400



- > ## We can see there has not been much increase in extent
 > occupancy\$occupancy.orig[1, 2]
- [1] 147200
- > occupancy\$extent.stand
- [1] 153600

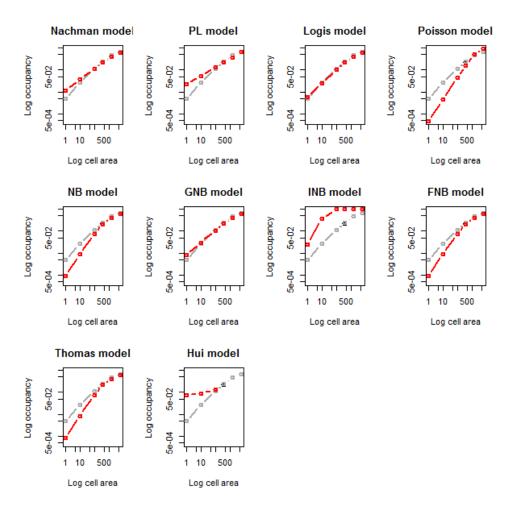
Now we can run our ensemble downscaling models:

Nachman model is running... complete
PL model is running... complete
Logis model is running... complete
Poisson model is running... complete
NB model is running... complete
GNB model is running... complete
INB model is running... complete
FNB model is running... complete
Thomas model is running... complete
Hui model is running... complete



The INB model has not converged satisfactorily and thrown up a warning message (it has predicted a 0 at the finest grain size which we know to be impossible). We can try tweaking it's starting parameters to see if we can get a better fit:

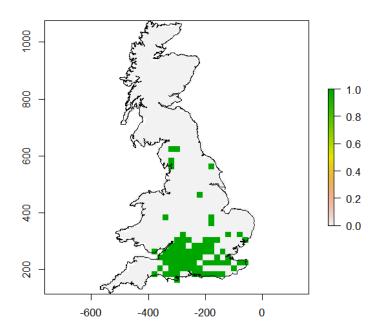
Nachman model is running... complete
PL model is running... complete
Logis model is running... complete
Poisson model is running... complete
NB model is running... complete
GNB model is running... complete
INB model is running... complete
FNB model is running... complete
Thomas model is running... complete



In this case we have simply drawn a rectangle around our points, but perhaps we have a better idea of the possible range limits of the species. In our case, it is probably sensible to set the extent as mainland UK. There is a shapefile which we can load in and set as our extent.



Now, we make our raster to be the same extent as the UK polygon, and then mask the raster file with the UK polygon so that any cells outside this polygon are assigned as NA (unsampled cells):

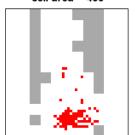


Now, we just upgrain and downscale as before:

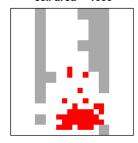
Original atlas data: cell area = 400



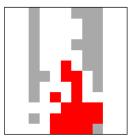
Standardised atlas data: cell area = 400



Standardised atlas data: cell area = 1600



Standardised atlas data: cell area = 6400

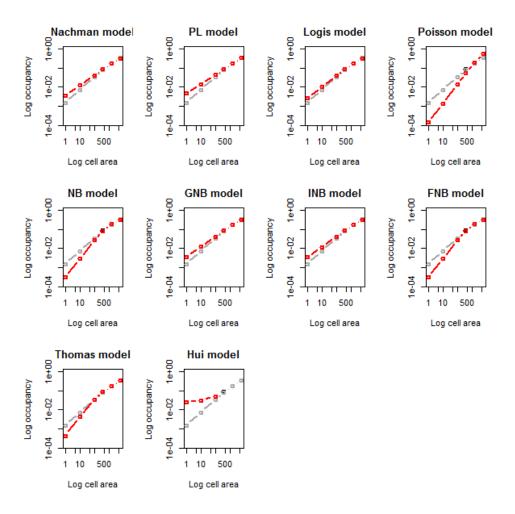


Nachman model is running... complete
PL model is running... complete
Logis model is running... complete
Poisson model is running... complete
NB model is running... complete
GNB model is running... complete
INB model is running... complete
FNB model is running... complete
Hui model is running... complete
Hui model is running... complete
SOccupancy

Cell.area Nachman PLPoisson Logis 1 0.003574872 0.004720191 0.00268301 0.0001365129 1 2 10 0.012295747 0.014454274 0.01042208 0.0013642906 3 100 0.041839989 0.044262197 0.03959798 0.0135594518 4 400 0.086210319 0.086827282 0.08573215 0.0531445930 5 1600 0.173180215 0.170325414 0.17577808 0.1962247036 6 6400 0.330438881 0.334120174 0.32661407 0.5826132897

```
GNB
                                INB
                                            FNB
1 0.0003038185 0.003573846 0.003413519 0.0003084653
2 0.0030044948 0.012293650 0.012060053 0.0030488420
3 0.0271216798 0.041837325 0.041665287 0.0274028922
4 0.0835920937 0.086209204 0.086227000 0.0838010248
5 0.1882913465 0.173182594 0.173436297 0.1874537560
6 0.3128847147 0.330437696 0.330522529 0.3131943391
       Thomas
                    Hui
                             Means
1 0.0004386724 0.02611997 0.001551775
2 0.0042863249 0.03144745 0.007353972
3 0.0349979327 0.05133530 0.034391011
4 0.0889687100
                     NA 0.081463488
5 0.1740512870
                     NA 0.178902245
                    NA 0.348818071
6 0.3400108394
$A00
 Cell.area
            Nachman
                           PL
                                  Logis
                                              Poisson
       1 1281.234 1691.716
                                  961.5907
                                              48.92622
           4406.796 5180.412 3735.2743
                                            488.96174
2
        10
       100 14995.452 15863.571 14191.9169
3
                                           4859.70751
4
       400 30897.778 31118.898 30726.4033 19047.02212
      1600 62067.789 61044.628 62998.8645 70326.93378
5
6
      6400 118429.295 119748.671 117058.4813 208808.60301
          NB GNB INB FNB Thomas
1
   108.8886 1280.866 1223.405
                                  110.554
                                            157.2202
             4406.044
                       4322.323
                                            1536.2188
2
   1076.8109
                                   1092.705
3 9720.4100 14994.497 14932.839 9821.197 12543.2591
4 29959.4064 30897.379 30903.757 30034.287 31886.3857
5 67483.6186 62068.642 62159.569 67183.426 62379.9813
6 112137.8818 118428.870 118459.274 112248.851 121859.8849
       Hui
                Means
1 9361.398
             556.1562
2 11270.767 2635.6635
3 18398.570 12325.7384
       NA 29196.5141
4
5
       NA 64118.5645
```

NA 125016.3965



If we want to compare occupancy between the two raster extents we must compare the converted area of occupancies (AOO), no proportion of occupancy (which are the proportions for different extents). In this case the estimates for grain sizes of 1 km and 10 km from the bounded rectangle (AOO = 627 km^2 and 3052 km^2) are larger than the estimates using the full mainland UK (AOO = 556 km^2 and 2635 km^2) highlighting the importance of this decision.

4 Bibliography

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