Ecological signals of plant-microbe associations are consistent across eDNA and vegetation surveys in northeast Greenland

Supplementary information 1

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Table S1. Summary of the taxonomic assignment for different loci. Each entry identifies the number of sequences achieving a plausible (probability of correct assignment >0.5; top) or reliable (probability of correct assignment >0.9; bottom) assignment at the respective taxonomic level for the locus in question. Column "% reads assigned" represents the percentage of sequences identified to a given taxonomic rank, as a proportion of the original, "raw" number of reads. ITS2 and rbcLa correspond to the loci used to identify plants, ITSF the locus for identifying fungi and 16S bacteria.

	Plant					
Plausible (P>0.5)	**ITS2**			**RBCLA**		
	Total reads	% reads assigned	Number of taxa	Total reads	% reads assigned	Number of taxa
Raw	2.8M			5.1M		
Phylum						
Class	2.7M	96.4	2	3.34M	65.5	2
Order	2.6M	92.9	15	3.29M	64.5	16
Family	2.6M	92.9	21	3.21M	62.9	25
Genus	2.5M	89.3	52	705K	13.8	52
Species	2M	71.4	102	35K	0.7	37

	Plant					
Reliable (P>0.9)	**ITS2**			**RBCLA**		
	Total reads	% reads assigned	Number of taxa	Total reads	% reads assigned	Number of taxa
Raw	2.8M			5.1M		
Phylum						
Class	2.5M	89.3	2	3.34M	65.5	2
Order	2.5M	89.3	13	3.28M	64.3	16
Family	2.5M	89.3	25	3.21M	62.9	25
Genus	2.28M	81.4	46	656K	12.9	23
Species	1.3M	46.4	82	5K	0.1	25

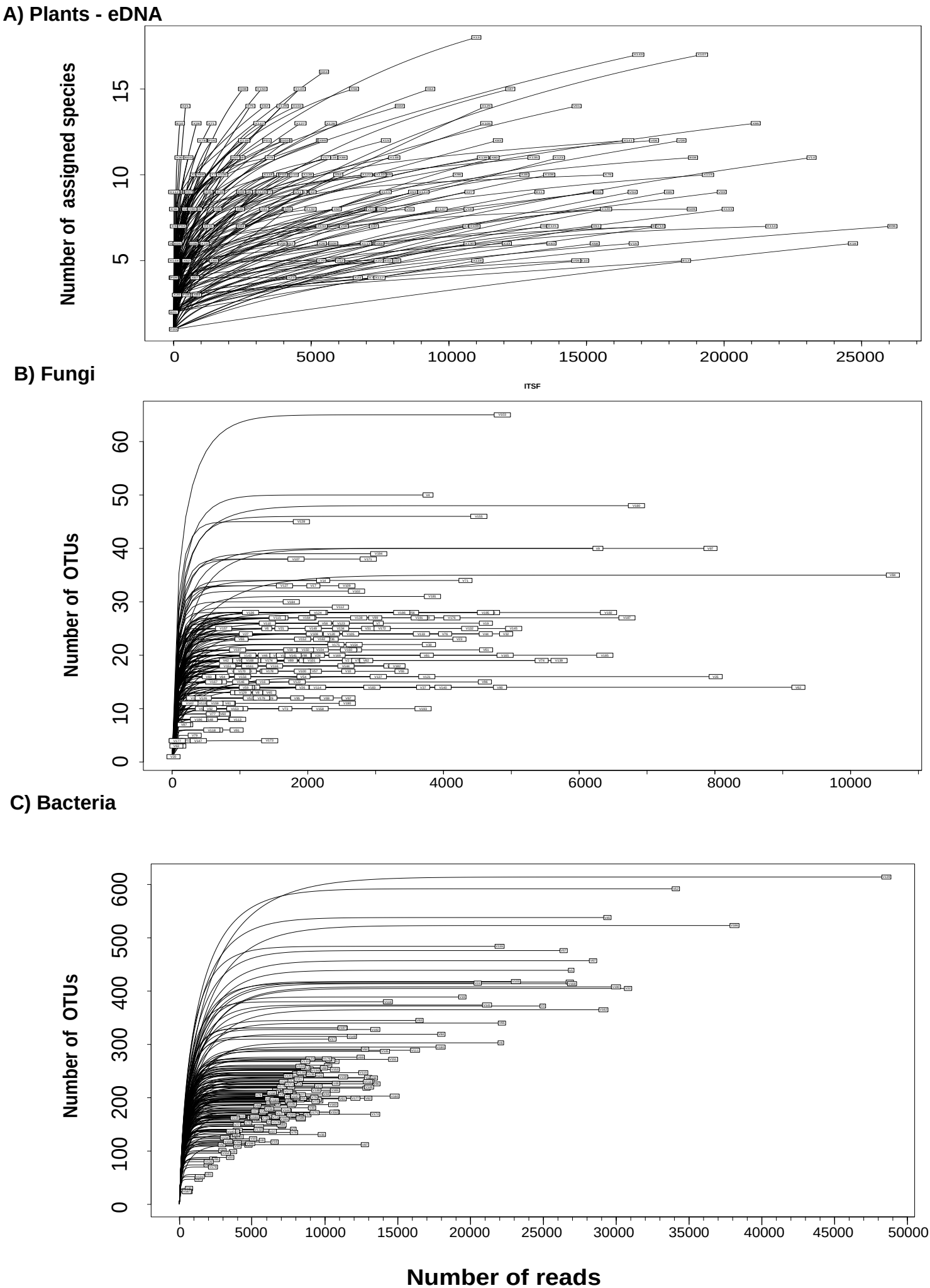


Fig. S1. Rarefaction curves of the number of OTUs per sample as a function of read numbers. Panel (A) shows the number of plant species accumulated per site, panel (B) shows the numberof fungal OTUs, and panel (C) shows the number of bacterial OTUs. Curves produced with the vegan package in R (Oksanen, 2010).

Supplementary text S1: Choice of specific priors for our HMSC model.

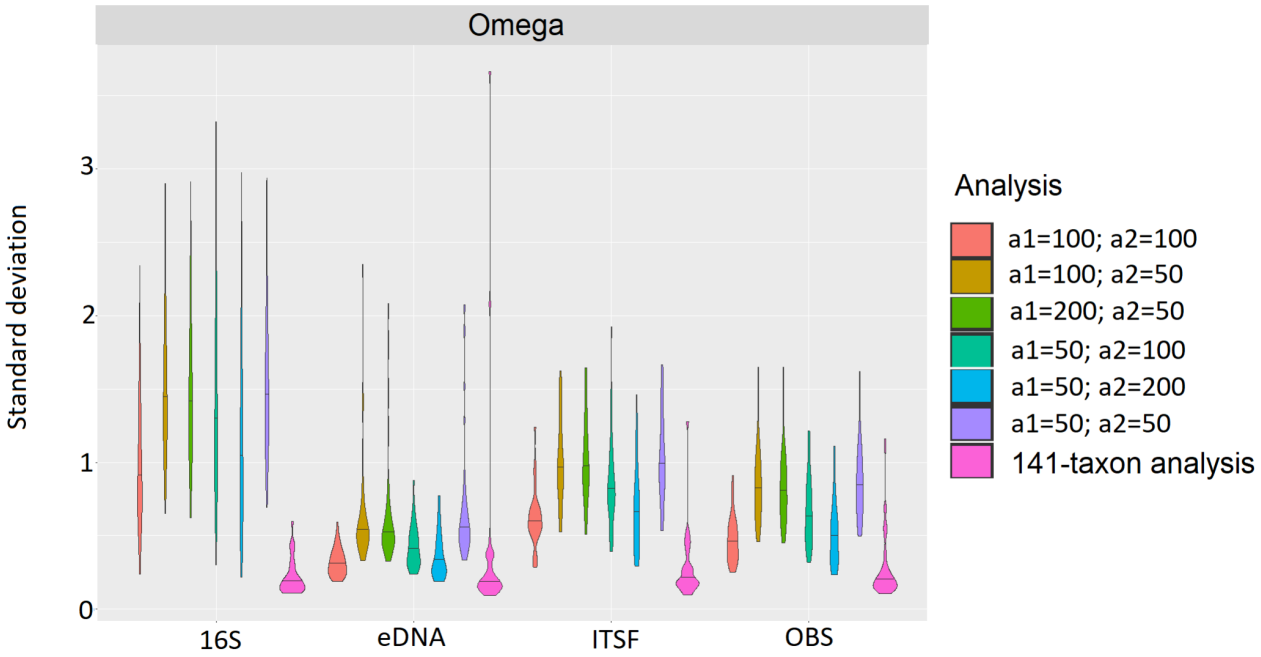
HMSC analyses of two data sets with 141 and 333 taxa, respectively, resulted in some highly different parameter estimates for the plant species, common to both data sets. For the smaller analysis (i.e., including 141 taxa), most of the marginal standard deviation estimates of the site random effect were close to zero, whereas they were much higher in the larger analysis fframed on 333 taxa (Subfig S1, S2). The HMSC model defines the random effects jointly over the species, and consequently the estimates for a single species are affected by the other species in the data set (Ovaskainen & Abrego, 2020). In the smaller data set, there were no clear site effects for almost any of the species, and the estimates were almost uniformly smaller. In the larger data, there was signal of a site effect for many of the microbial species and the variances of the random effects were larger therefore estimated to be larger. As a result, the latter model did not penalize as strongly against higher site variances for the plant species as for the small data set, and their site effect estimates were consequently significantly higher.

The Multiplicative Gamma Process Shrinking Prior in the HMSC model penalizes against overly strong random effects. Without penalization the random effects would not be identifiable with occupancy data and the model might overfit. The prior is defined using several parameters that can be changed to modify the its behaviour. Parameters a1 and a2 control the level of shrinkage for the species association matrix Omega, and their values can have a significant impact on the results (Ovaskainen & Abrego, 2020; Chapter 8.4.2). The first parameter a1 controls the overall strength of the random effect, while the second parameter a2 controls the structure of the association matrix via the effective number of latent factors.

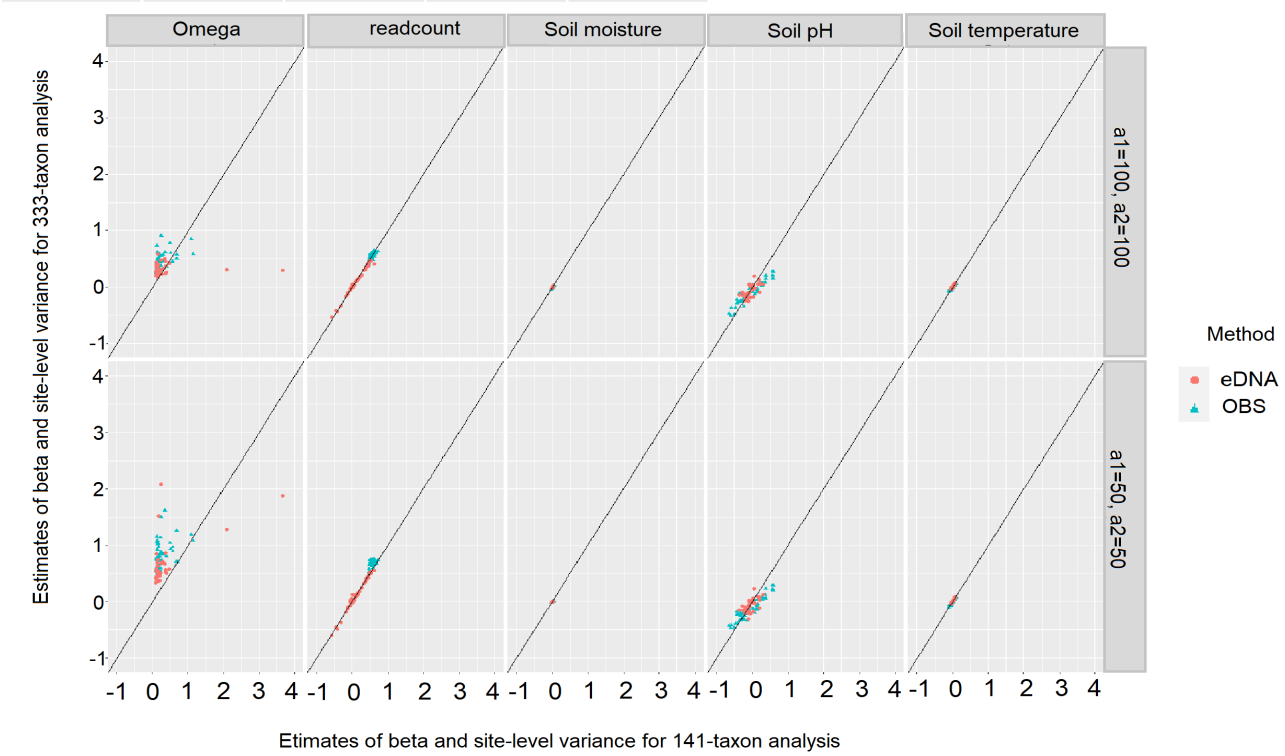
We tested whether using stronger shrinkage resulted in random effect estimates for plants in the larger model that were more similar to those in the original model of the smaller dataset. The default parameter values in the Hmsc R-package are (a1=50,a2=50). We tested five additional prior combinations (a1=100,a2=50), (a1=50,a2=100), (a1=100,a2=100), (a1=200,a2=50) and (a1=50,a2=100).

Systematically changing the values of parameters a1 and a2 had a clear impact on the distributions of the marginal standard deviation estimates of the site random effect over species (Subfig S1). Increasing only the value of a1 resulted in highly similar estimates to those obtained with the default prior. The strongest shrinkage and the most similar estimates for plant species compared to those of the 141 taxa analysis were obtained with the priors (a1=100,a2=100) and (a1=50,a2=100). The prior (a1=50,a2=200) also strongly affected the beta parameter estimates for soil pH for some of the species (Fig S3), while they remained mostly similar with the prior (a1=100,a2=100).

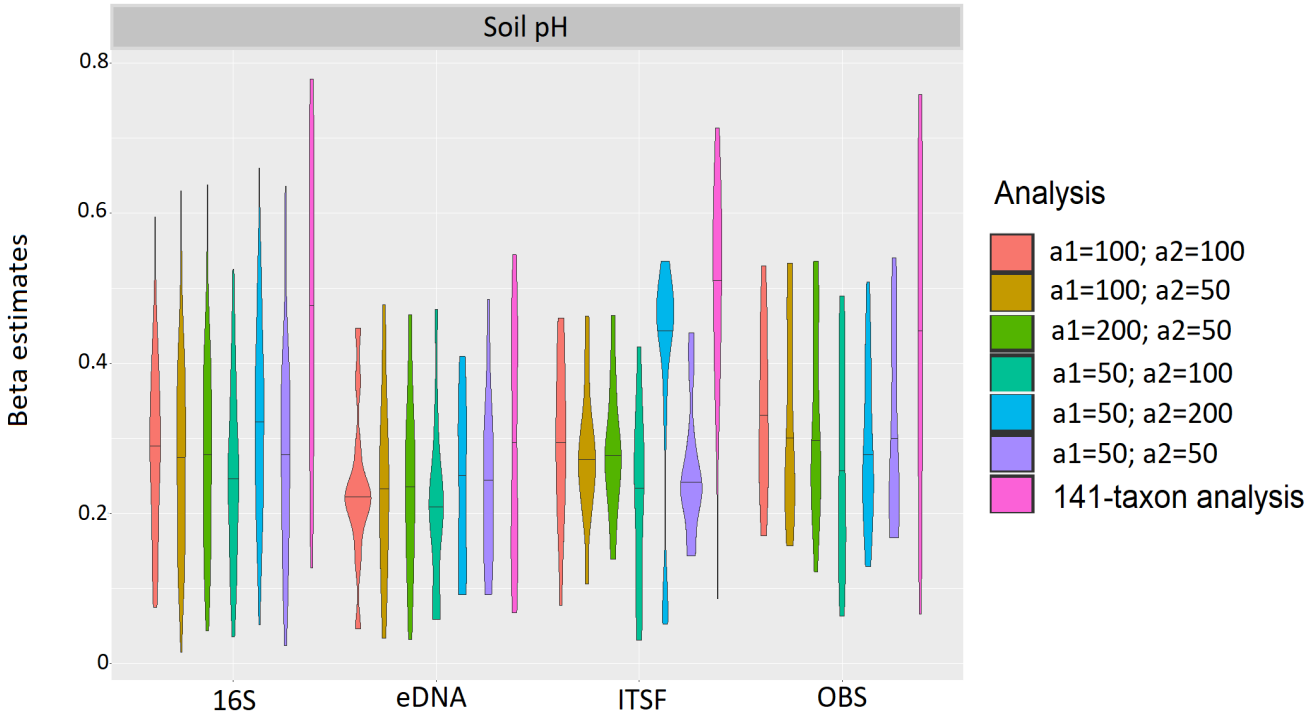
Based on these trials, we chose to use the priors of (a1=100,a2=100) in our analyses. This choice successfully decreased the discrepancy of the random effect parameter estimates for the plant species between the 141 and 333 taxa analyses, without having a strong impact on the other model parameters. Direct comparison of the estimates between these two analyses show that for most of the species, the parameter estimates are more similar with the (a1=100,a2=100) prior than with the default prior (Subfig S2). The stronger shrinkage prior also results in some decreases in the marginal standard deviations for the 16S and ITSF microbial and fungal taxa that are present only in the larger dataset. However, underestimating random effects is usually preferable to overestimating them, because overly high random effect variances can lead to overfitting with this kind of data. The HMSC model used here is complex for the data, and without regularization with the shrinkage prior it would not be identifiable.



Subfigure S1. The distributions of marginal standard deviation estimates of the site random effect over species separately for each taxon group. Each color represents the estimates for a single HMSC analysis: The pink color (i.e., PLMI) refers to an analysis including 141 taxa, whereas the other colors show the results for analyses including 333 taxa with different prior distributions as indicated in the legend. The eDNA and OBS plant species are the same in 141 and 333 taxa analyses, while the 16S and ITSF taxa are not shared between the two analyses.



SubFigure S2. Scatterplots of beta parameter estimates and marginal site random effect variances for the plant species under two analyses. The x-axis shows the parameter estimate in the 141 taxa analysis and the y-axis shows the corresponding estimate in the 333 taxa analysis. The rows show estimates based on different priors in the 333 taxa analysis: top stronger shrinkage prior (a1=100,a2=100), bottom default prior (a1=50,a2=50), and the columns show different parameters with Omega referring to the marginal standard deviation of the site random effect. The different colors indicate whether the plant species was directly observed (OBS, blue) or identified by environmental DNA (eDNA, red). Identity lines are included to facilitate comparison.



Subfigure S3. The distributions of beta parameter estimates for soil pH over species separately for each taxon type. Each color represents the estimates for a single HMSC analysis: PLMI corresponds to an analysis including 141 taxa, whereas the other colors show the results for analyses including 333 taxa with different prior distributions as indicated in the legend. The eDNA and OBS plant species are the same in 141 and 333 taxa analyses, while 16S and ITSF species are not shared between the two analyses.

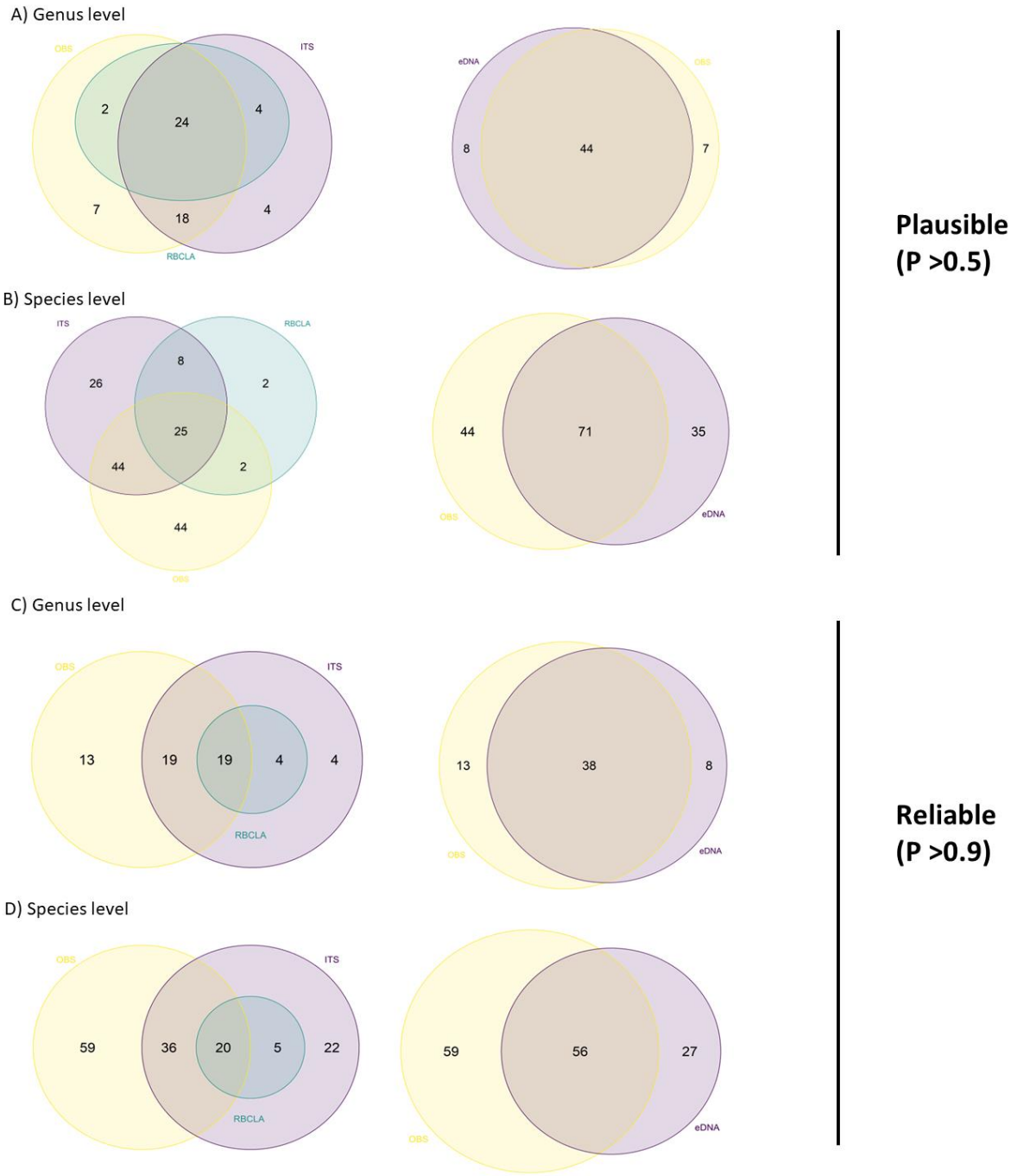
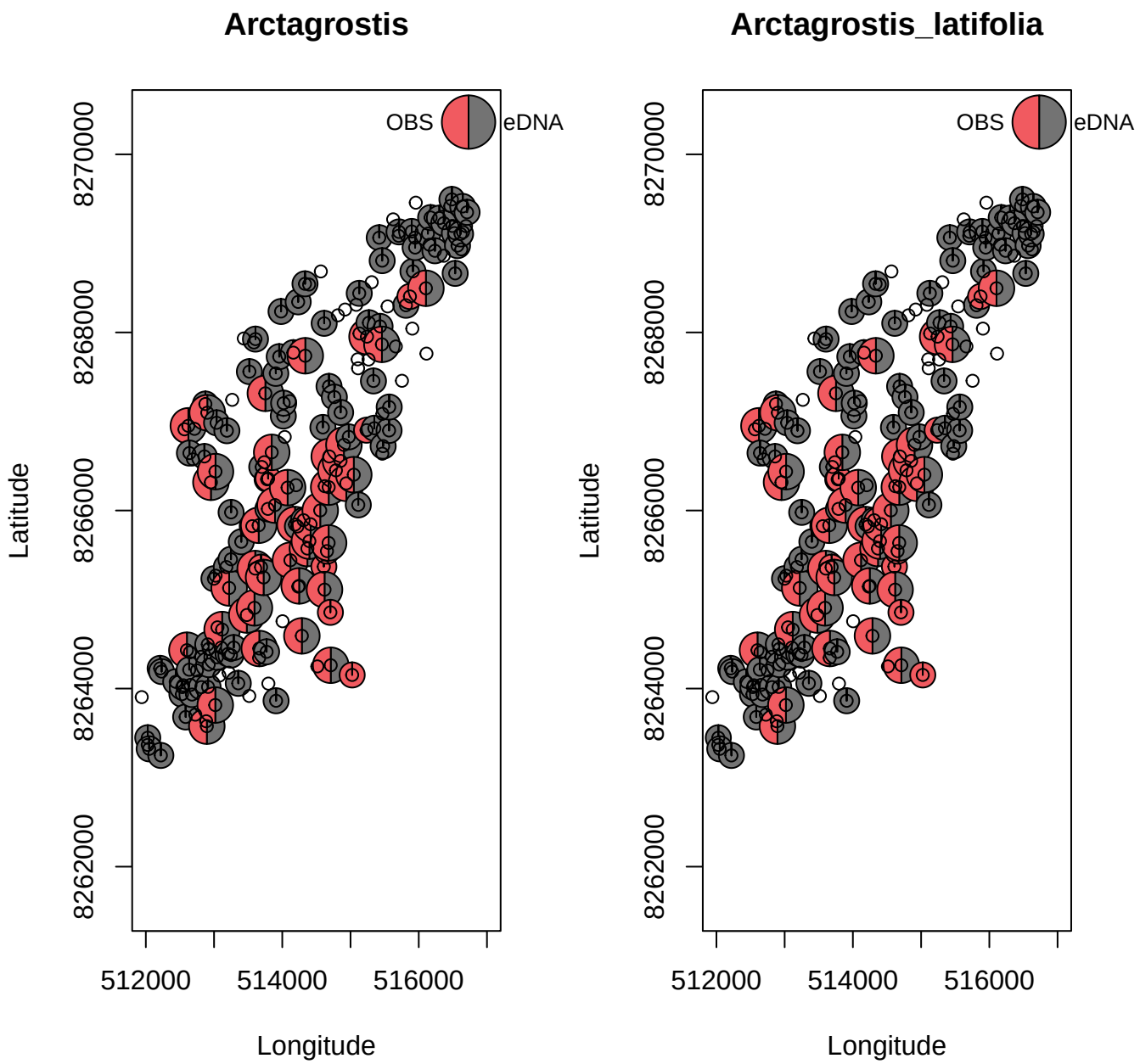
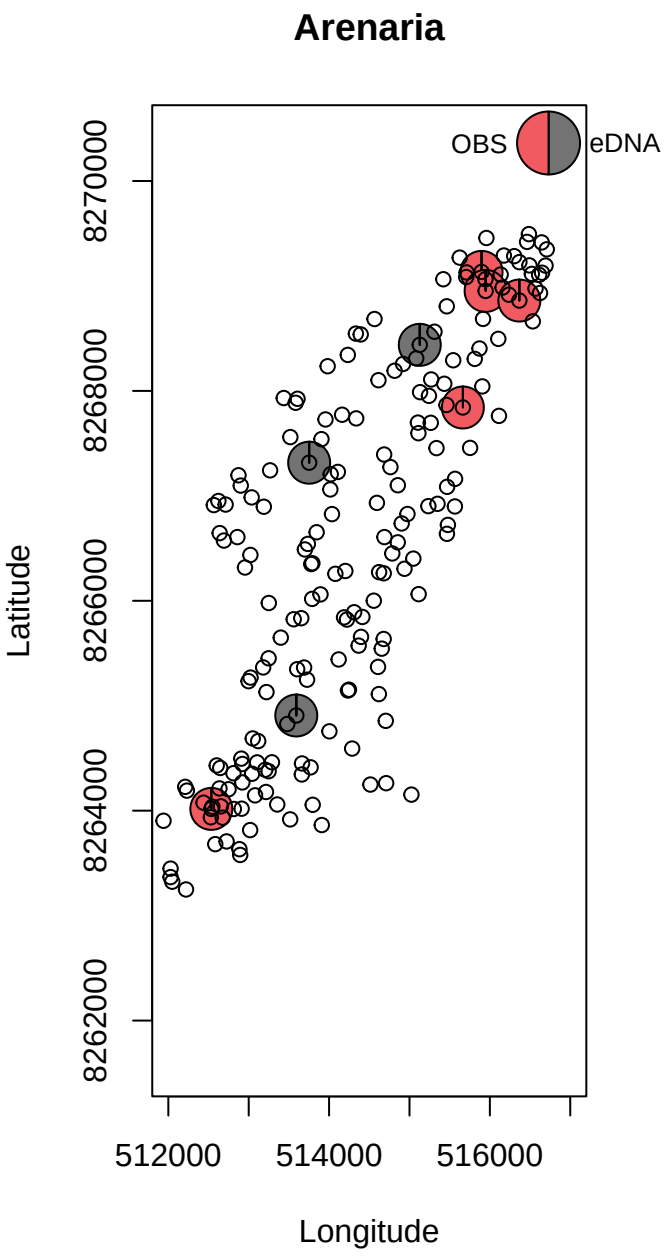


Fig. S2. Venn diagram showing the shared and unique plant taxa detected by different methods of identification. The sizes of the circles represent the total number of plant taxa detected per method, with specific numbers given for each method. Numbers within intersections identify the number of plant taxa detected by all of the respective methods. ITS refers to plants detected using gene region ITS2; rbcLa to plants detected using gene region rbcLa; OBS to plants detected by observation, and eDNA to all plants detected by metabarcoding (as combining evidence from ITS and rbcLa). Results are shown separately at different level of taxonomy (i.e genus vs species) for the two taxonomic assignment threshold used. (i.e,. Plausible, Pr>0.5 and reliable Pr>0.9), as detailed in Table S1.

Supplementary Fig. S3. Pie charts showing spatial patterns in the distribution of plant taxa across the two different methods of scoring. To illustrate differences in detection at different levels of taxonomy we show patterns at two levels: genus (left-hand plot) and species (right-hand plot). The size of the individual pie charts indicates whether the taxon in question was locally detected by both methods (large bicolored circles), by a single method (small unicolored circles) or no method (empty circles). Note that for genera with a single species in the Zackenberg species pool, the two plots will obviously be identical.

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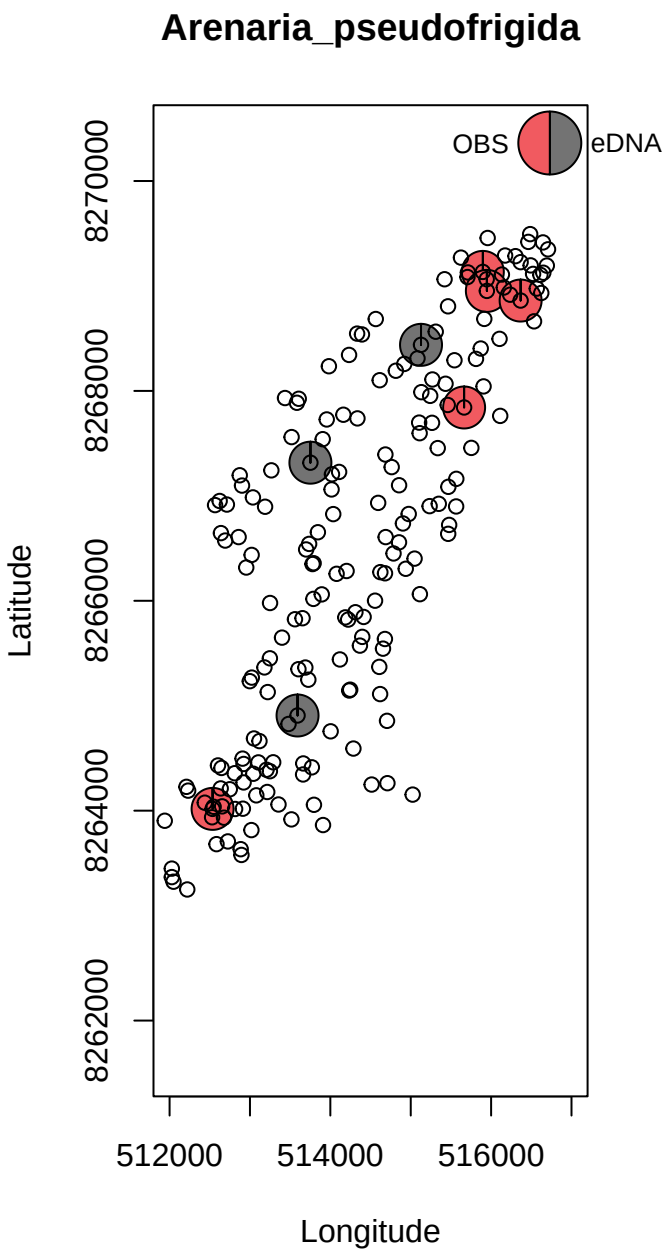
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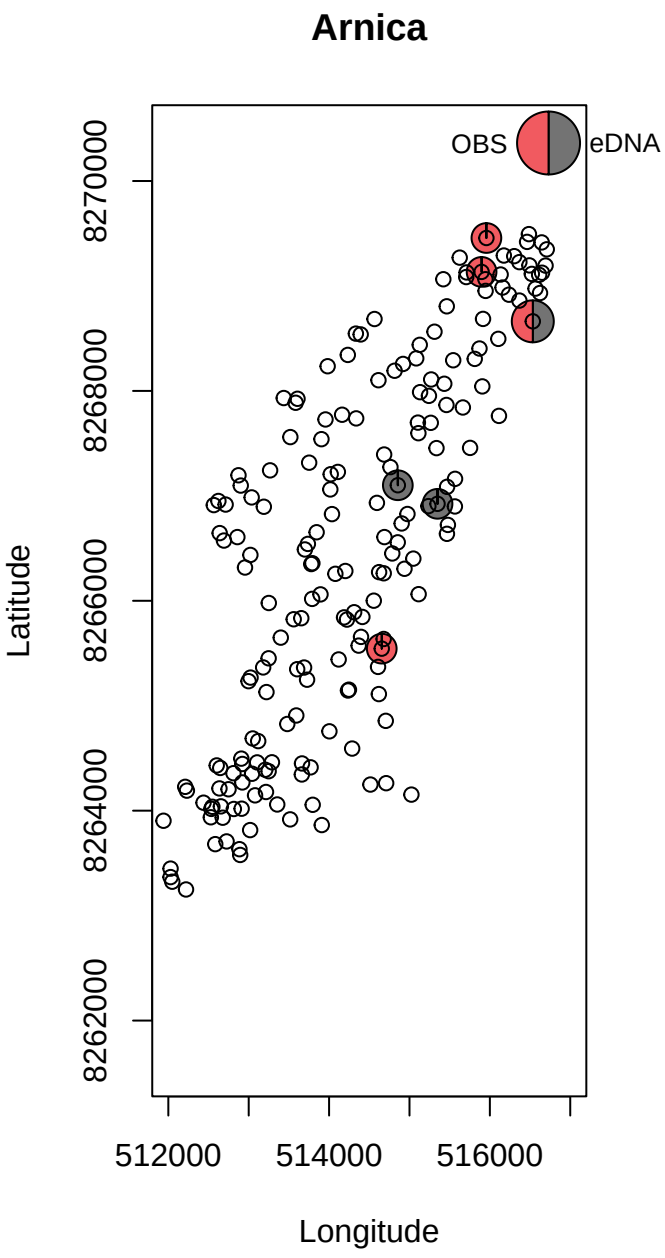
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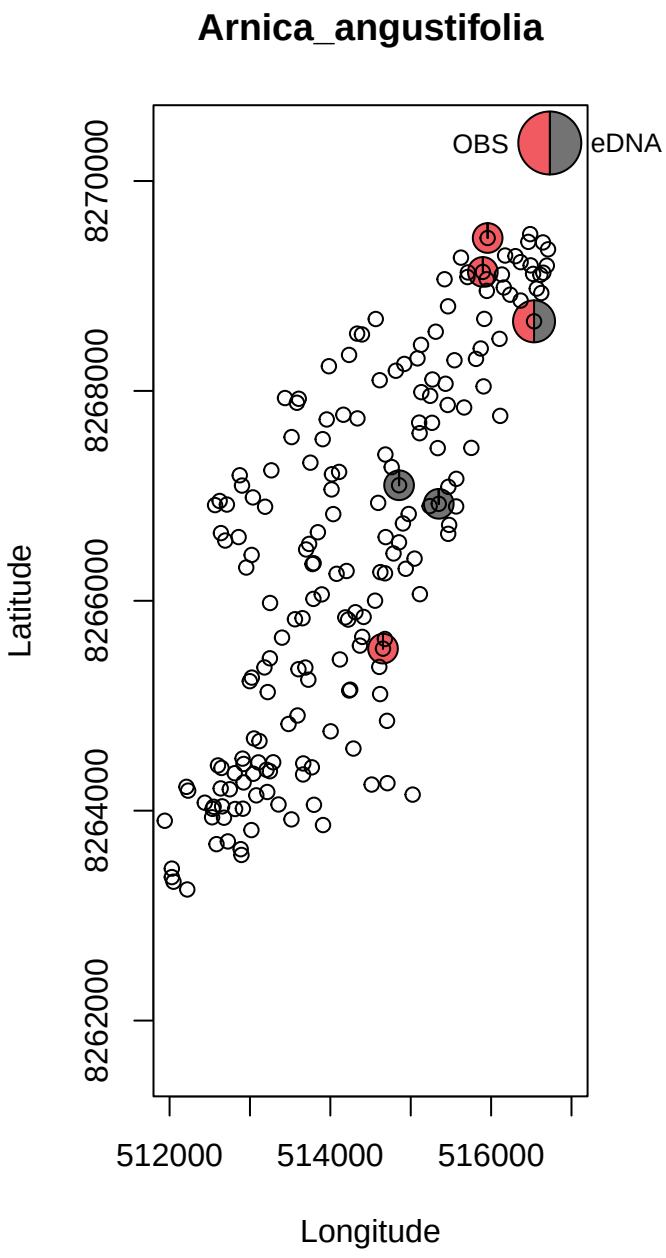
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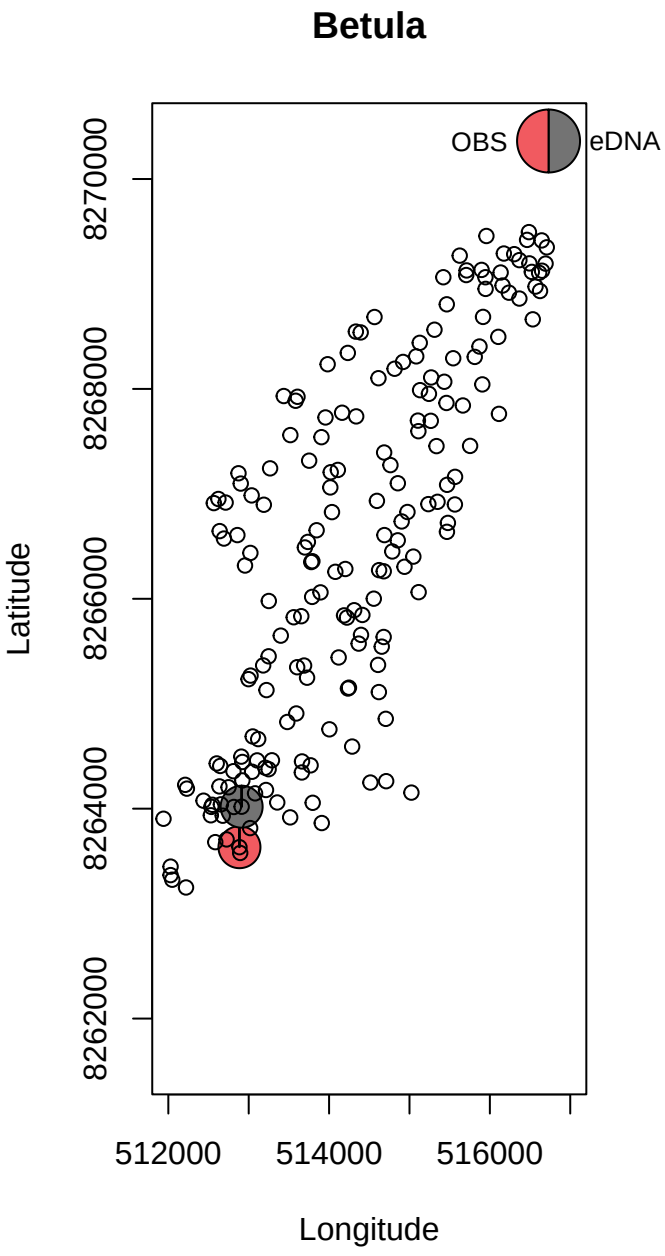
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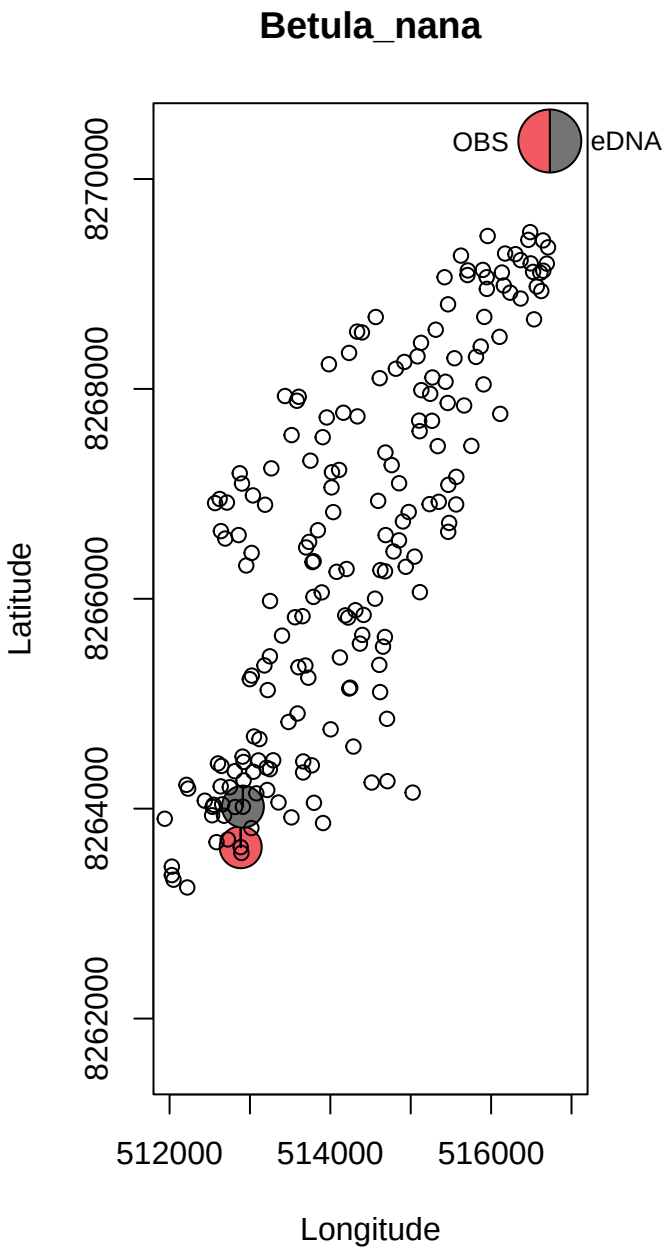
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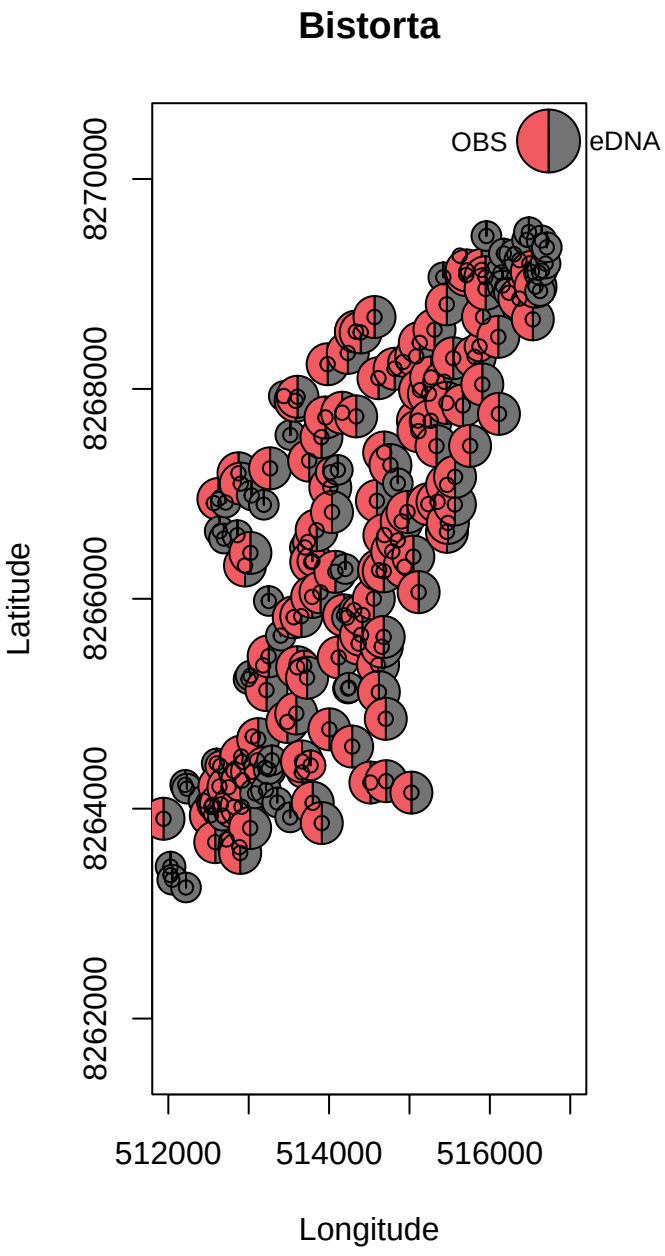
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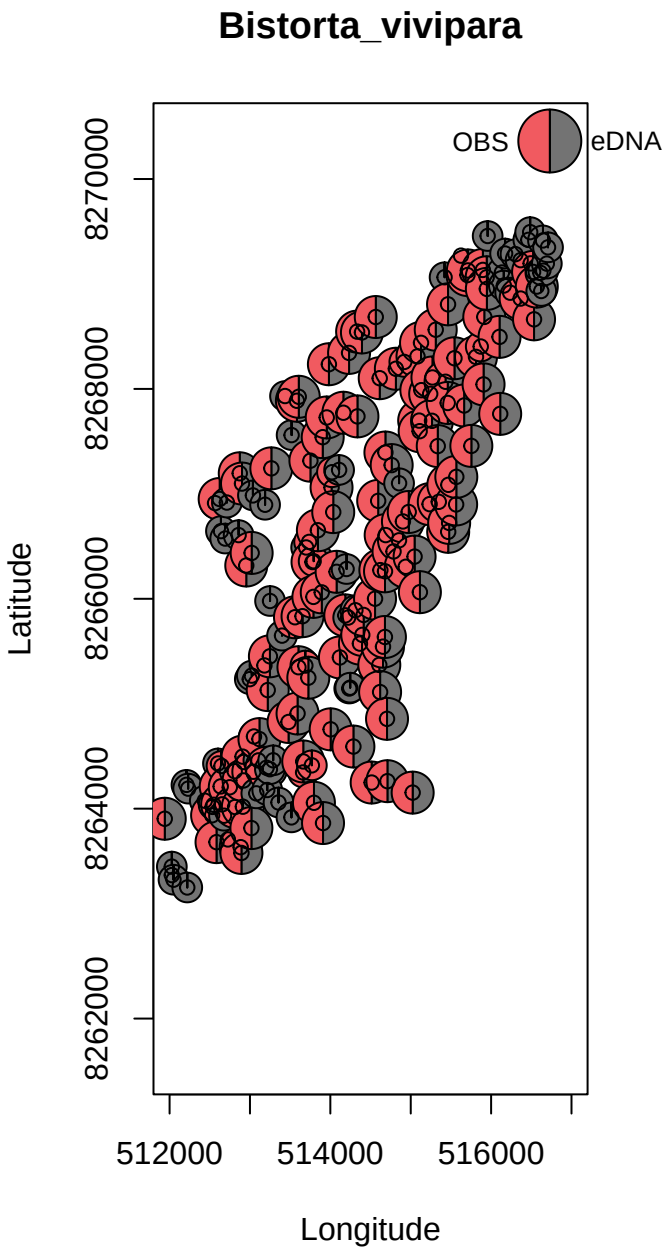
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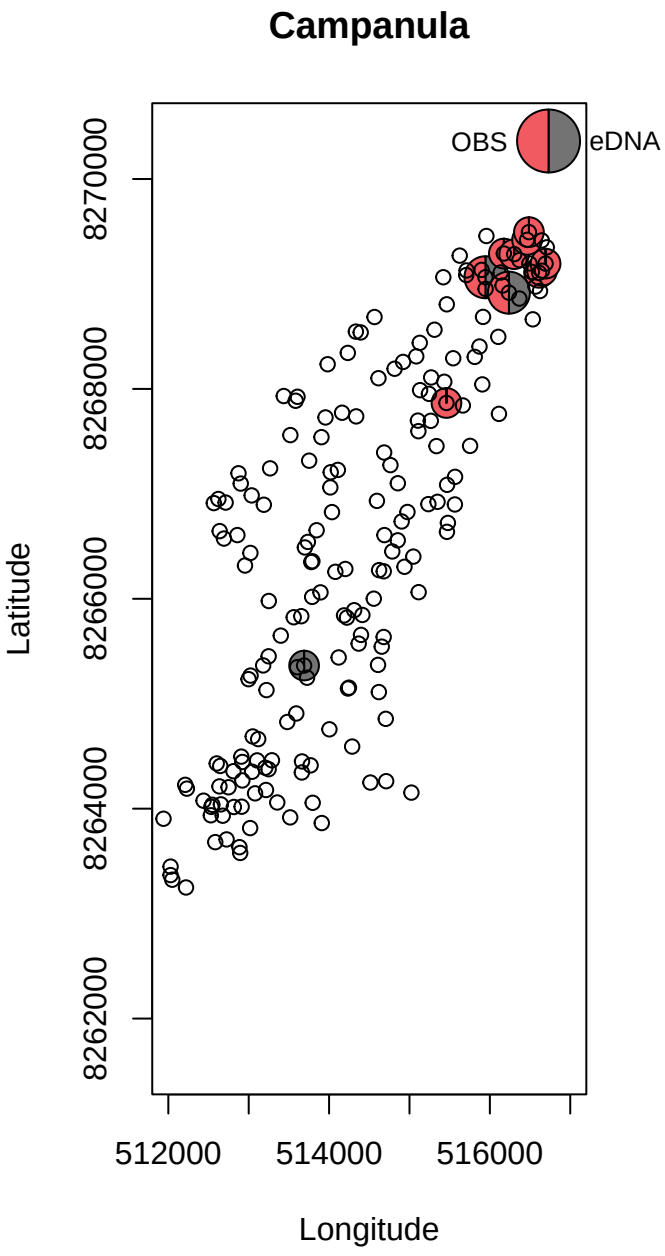
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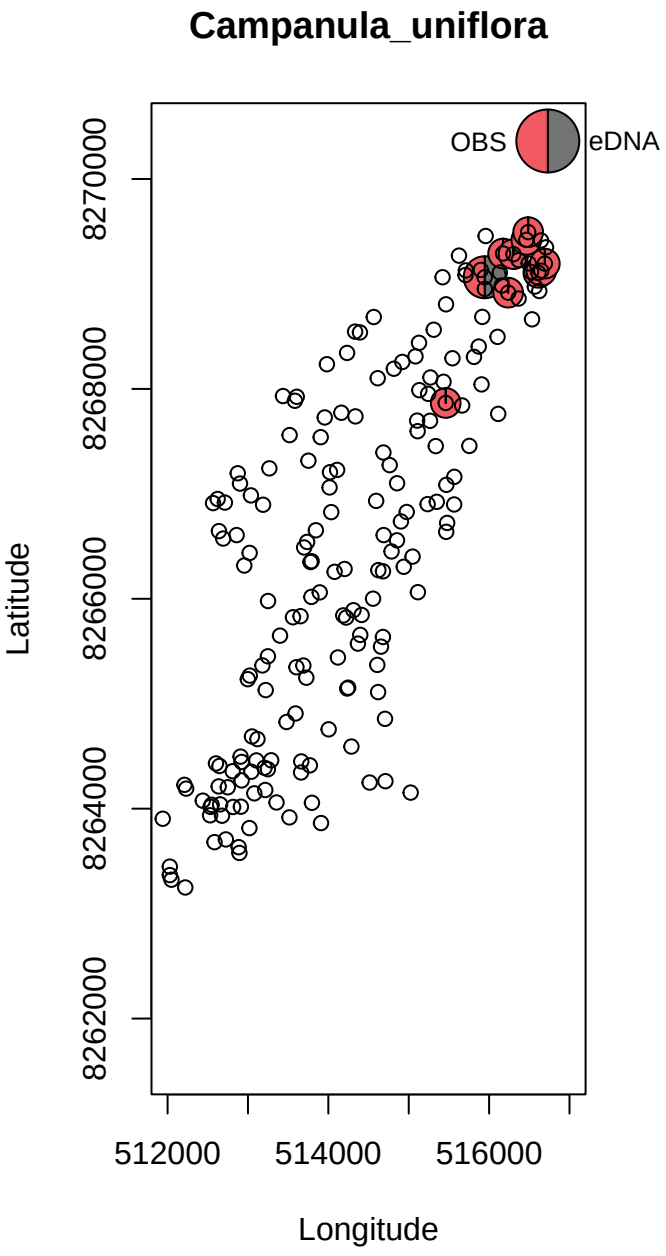
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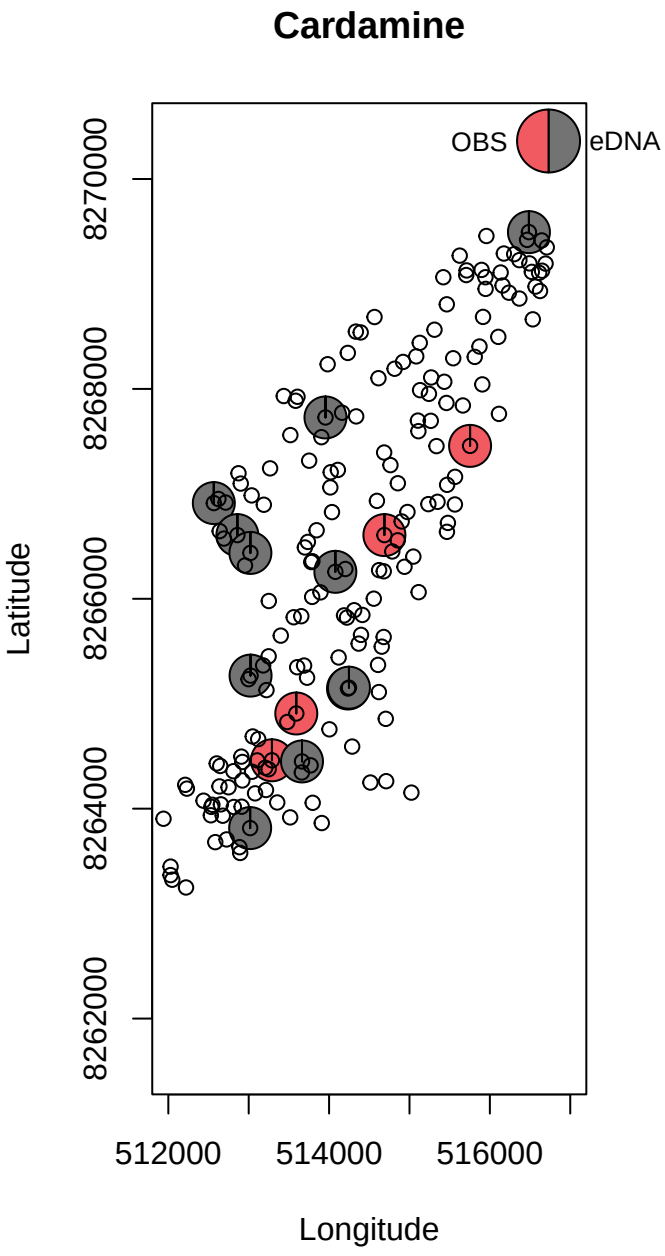
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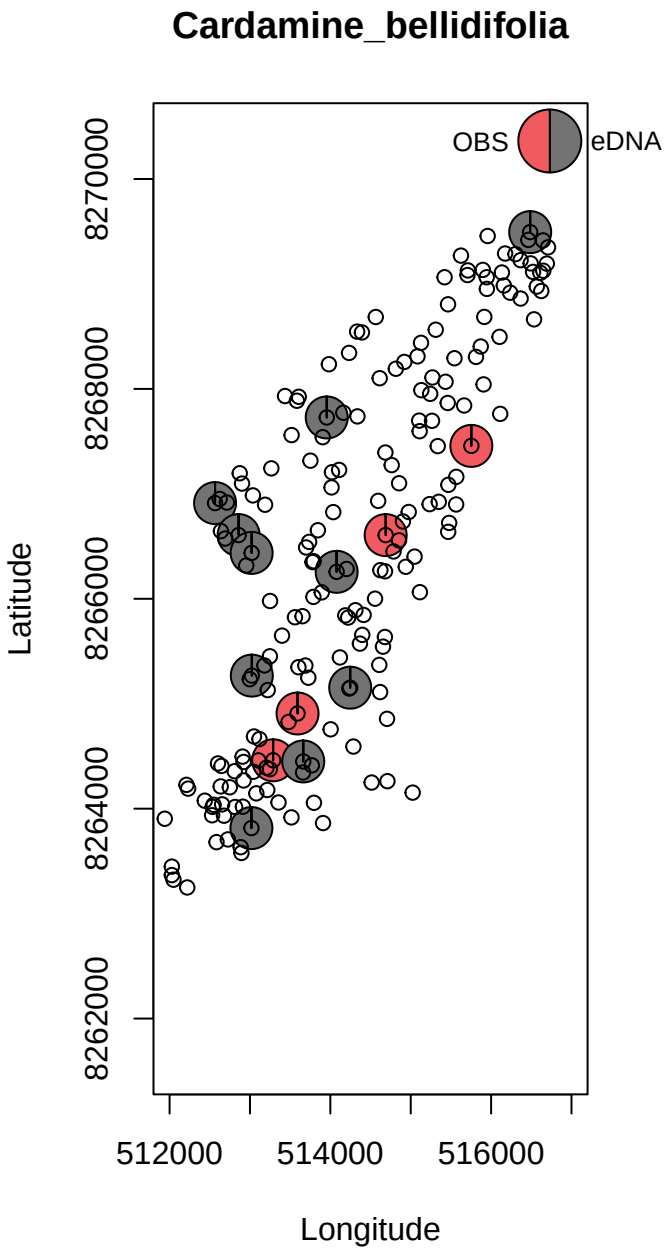
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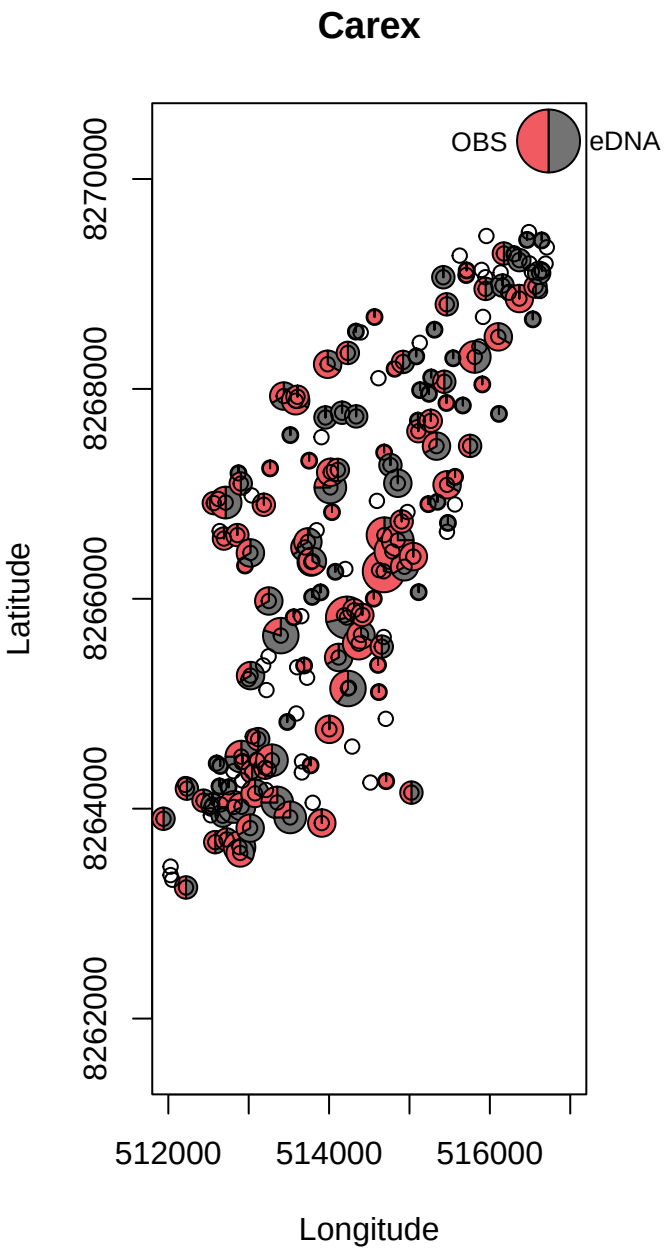
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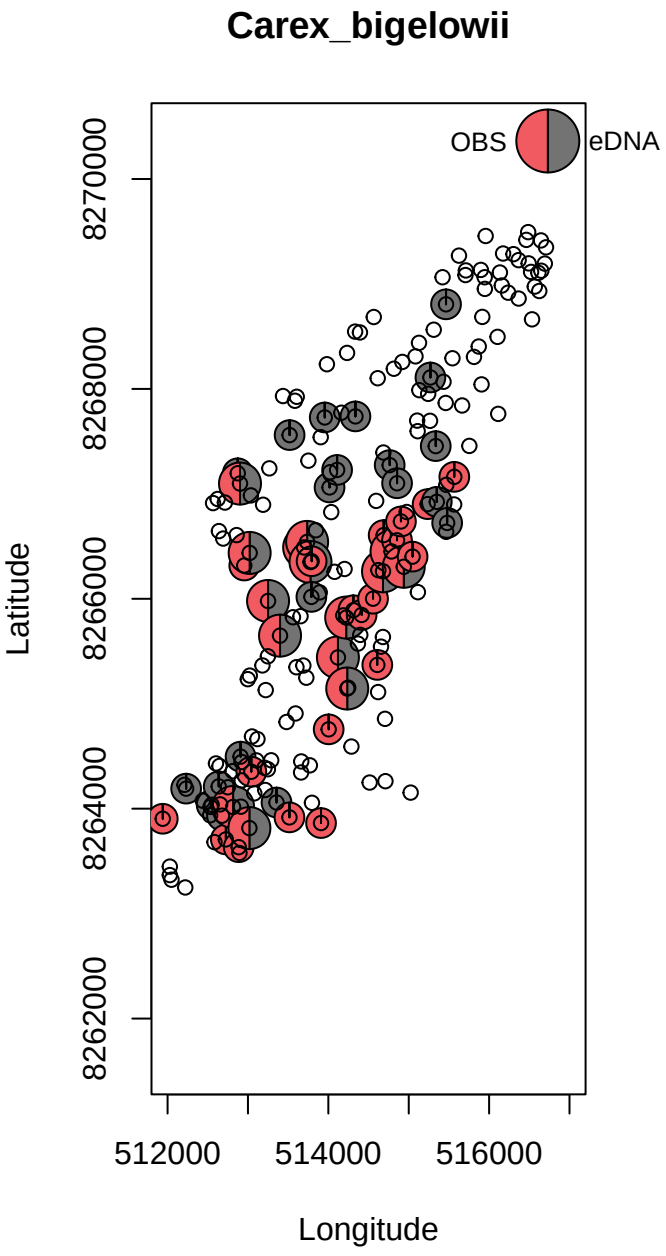
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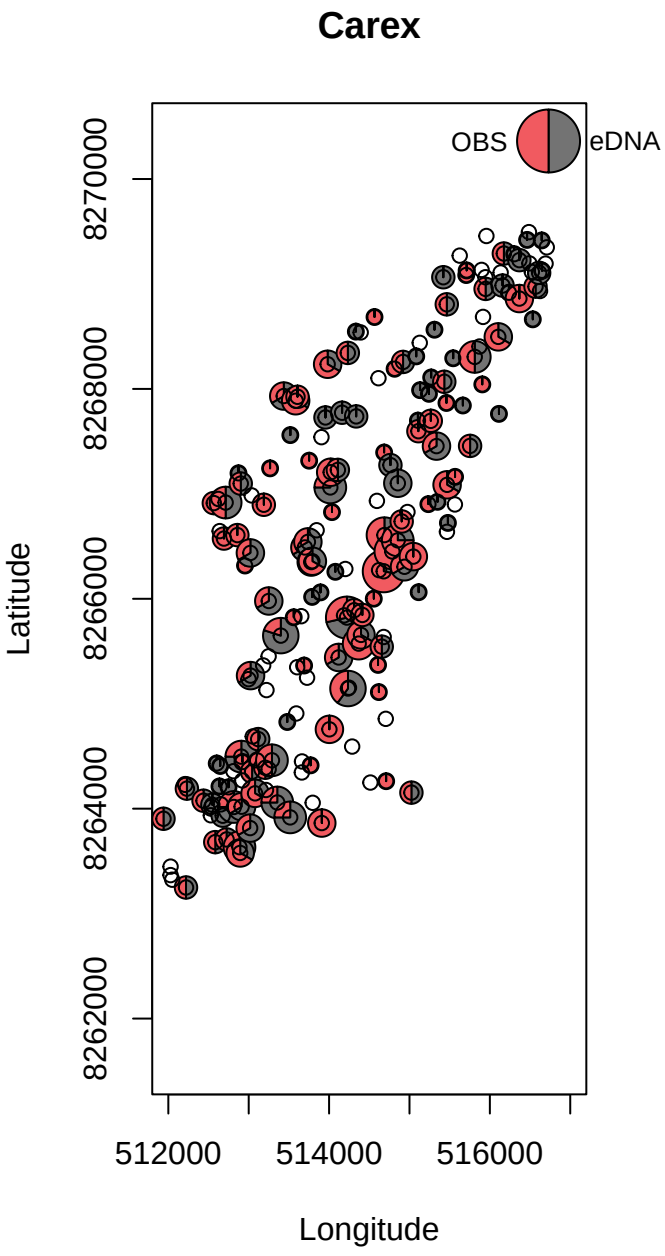
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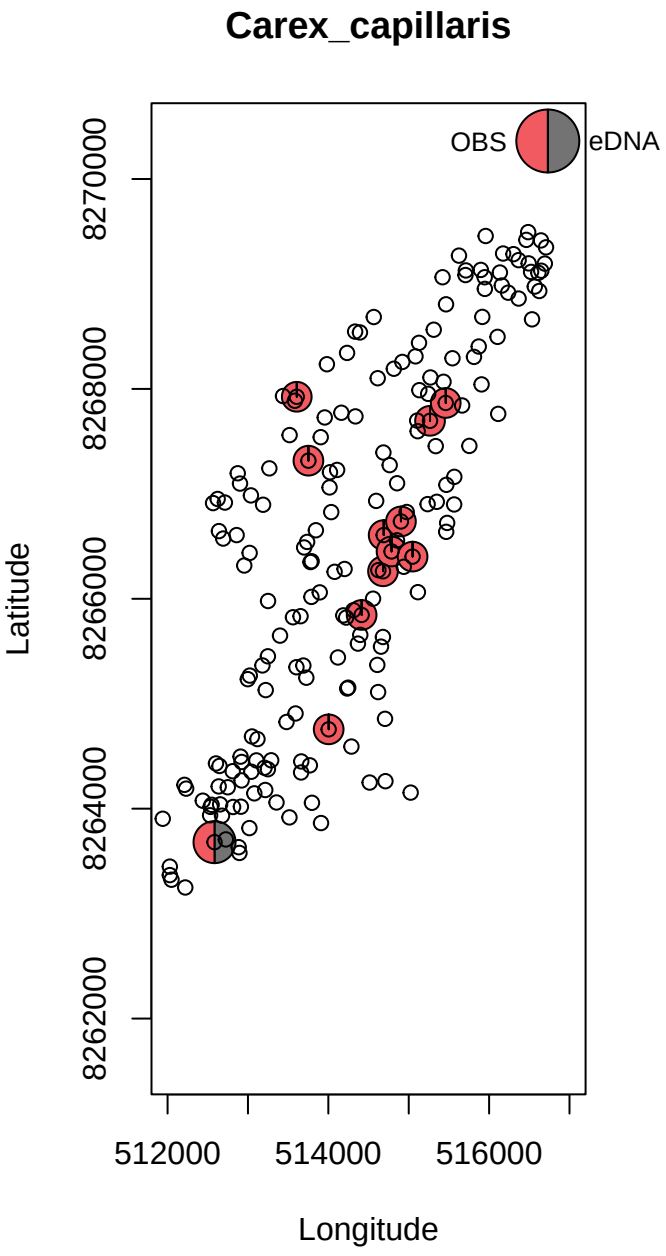
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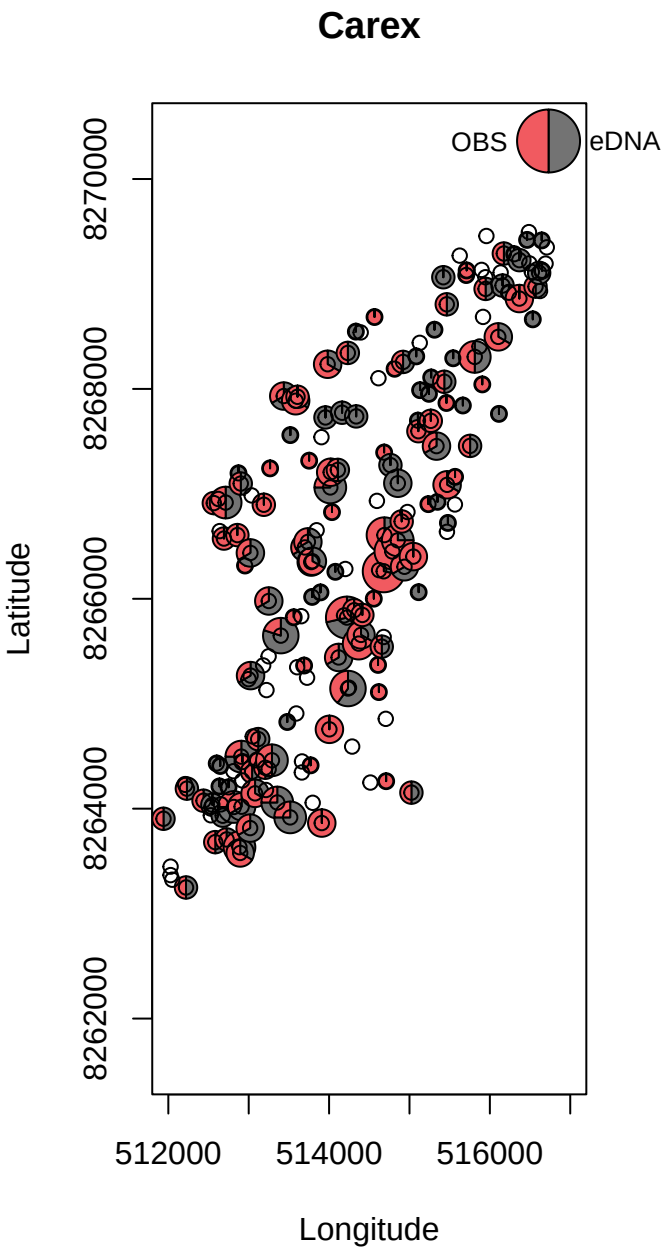
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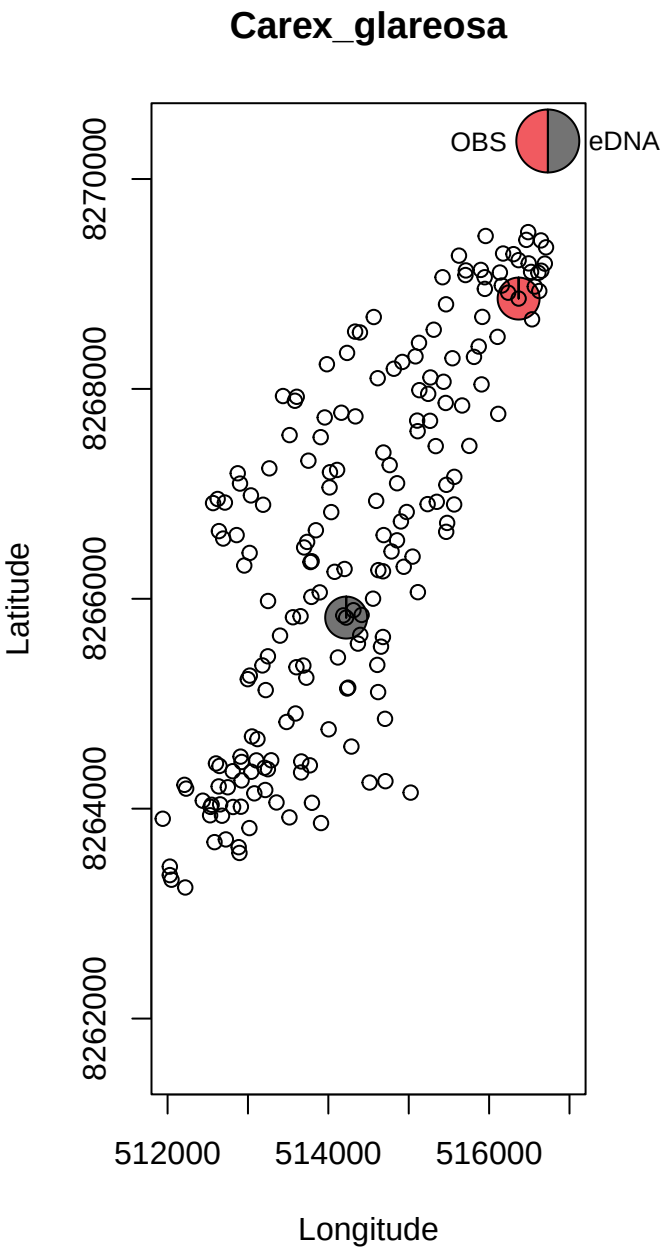
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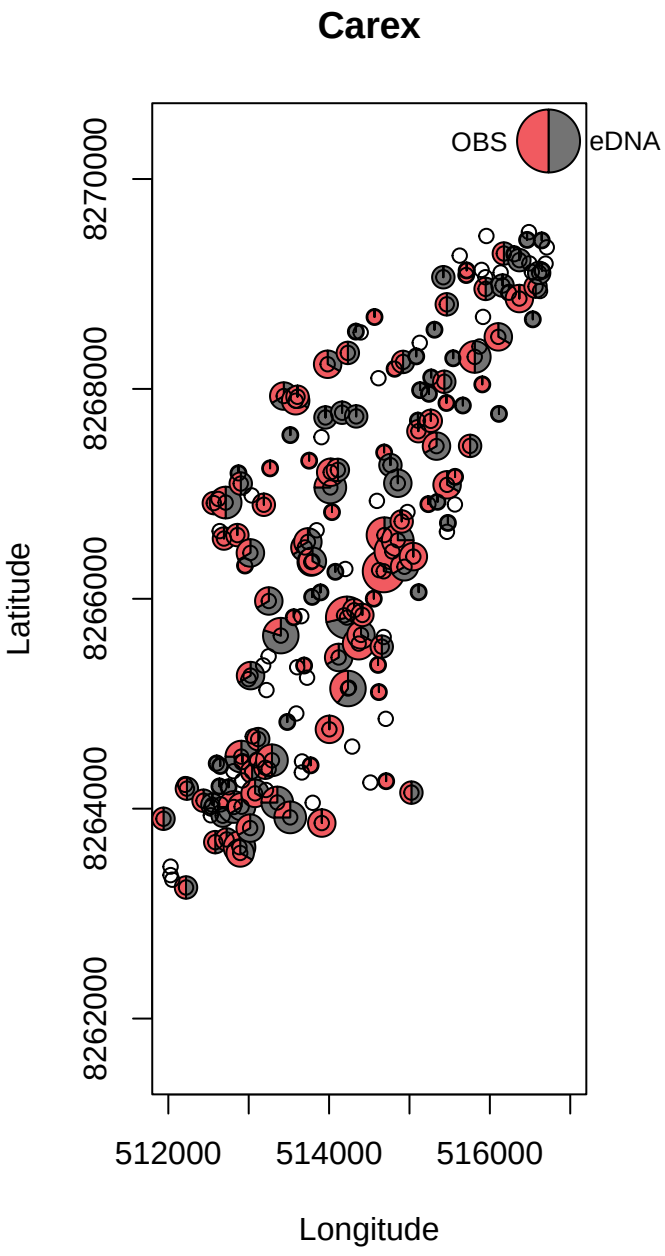
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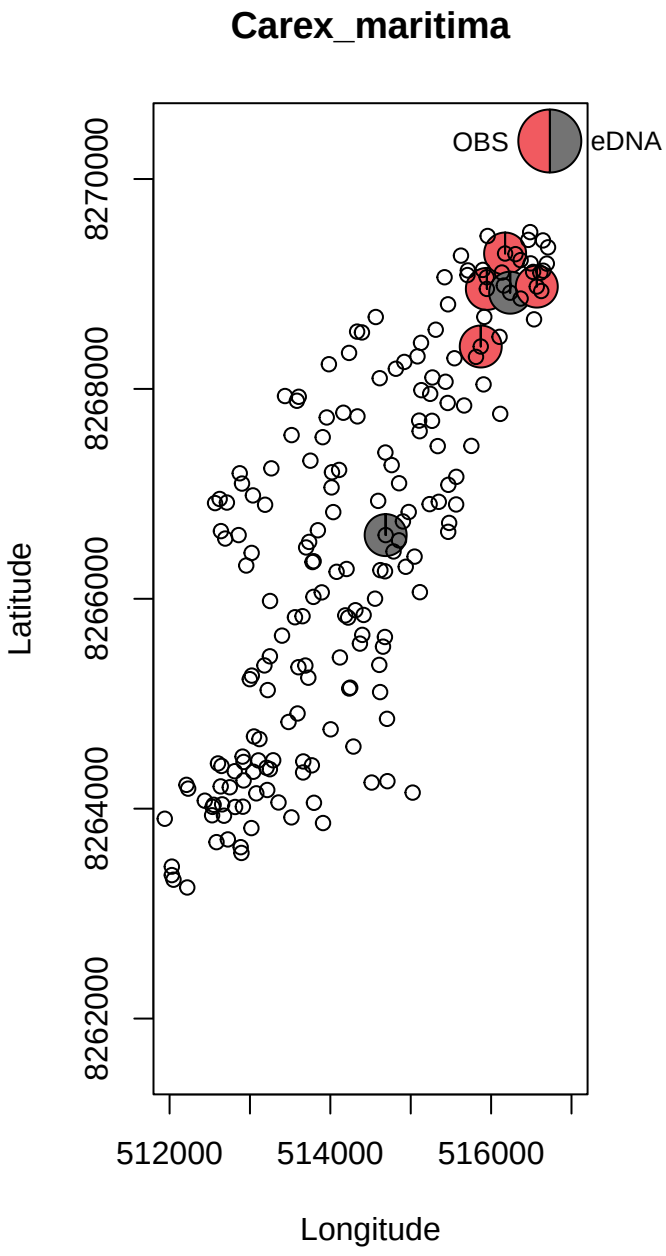
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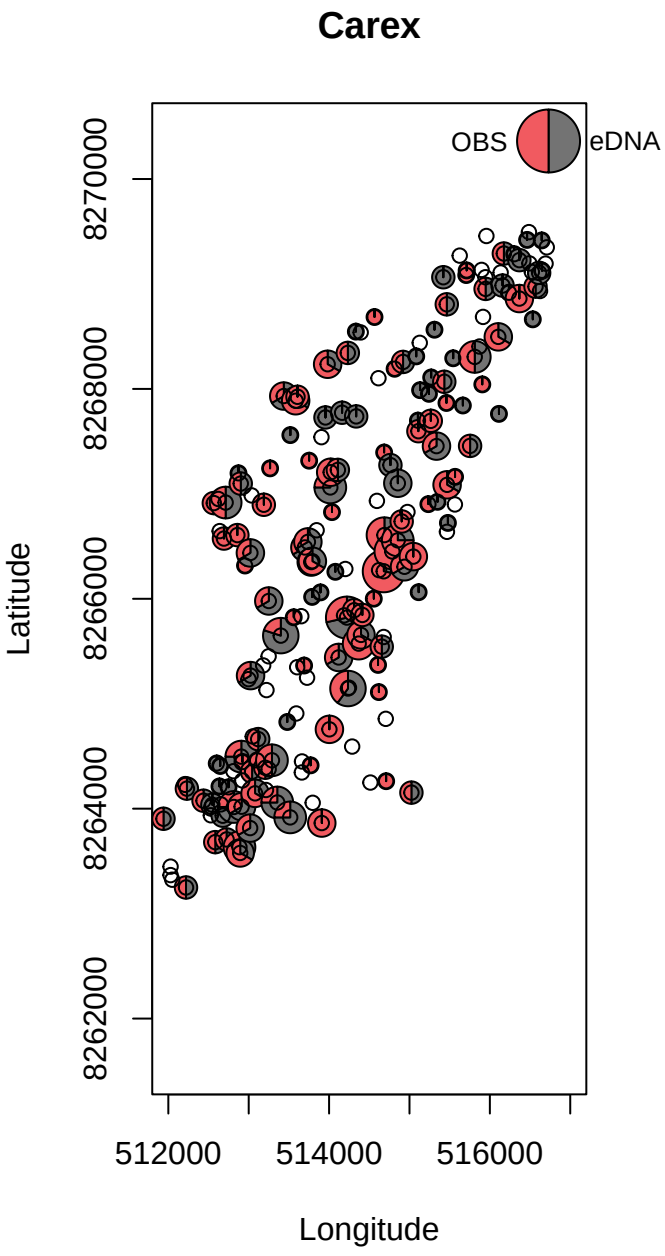
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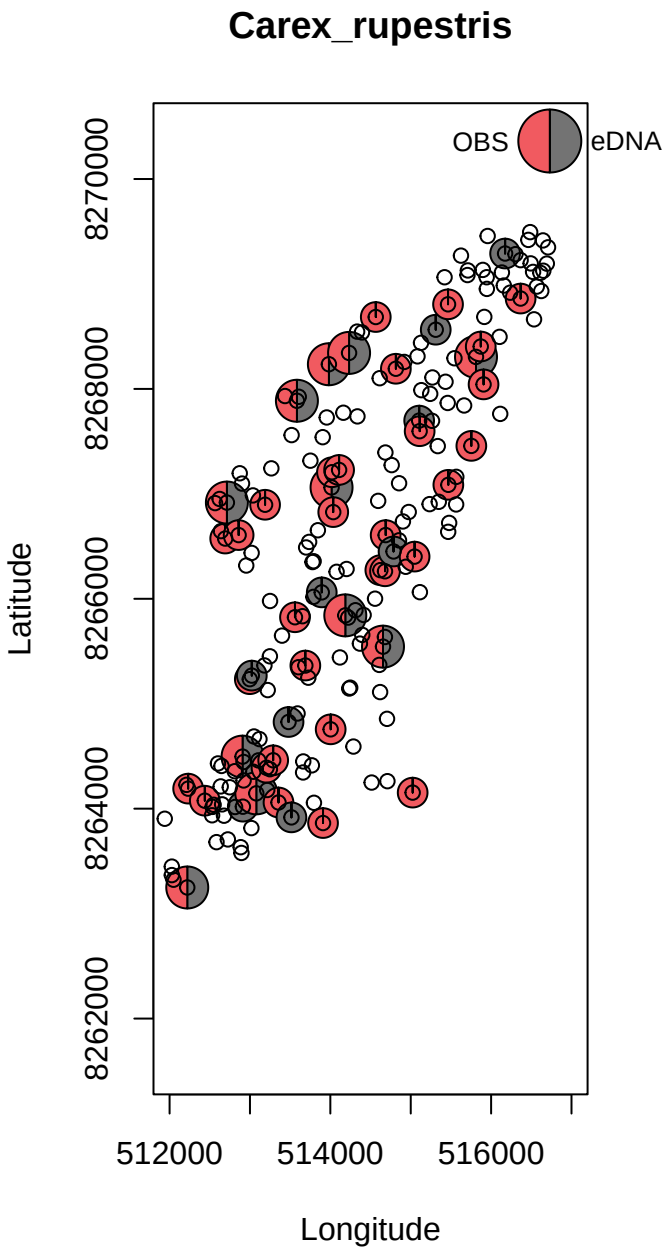
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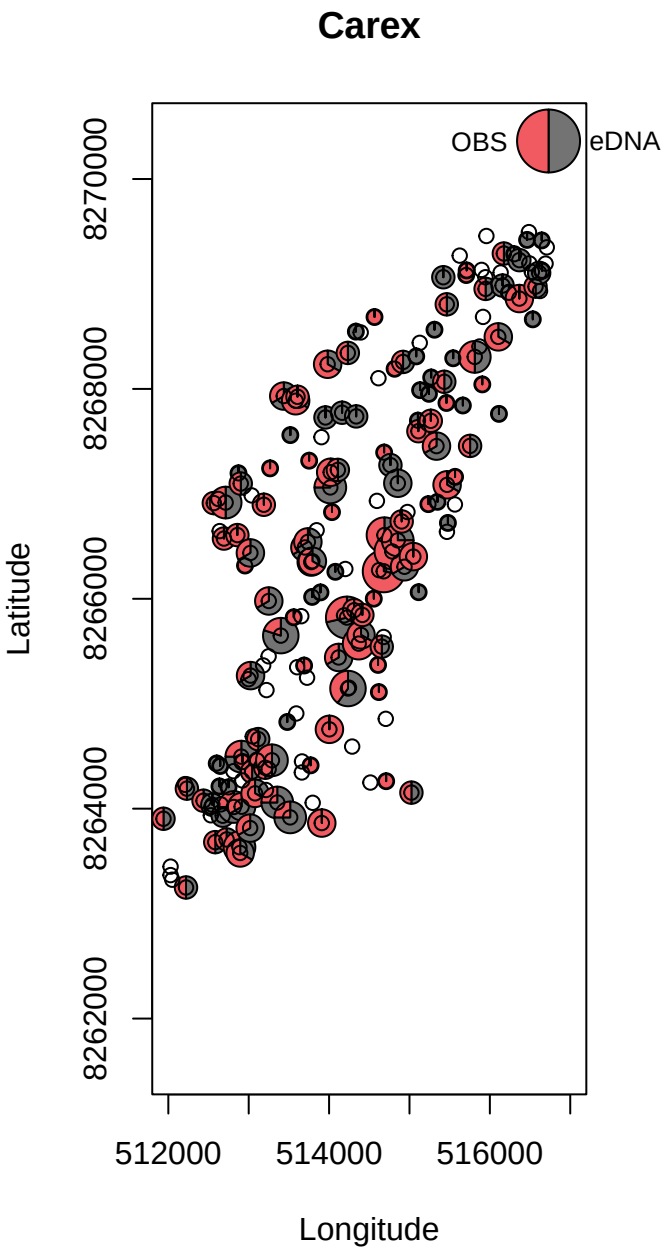
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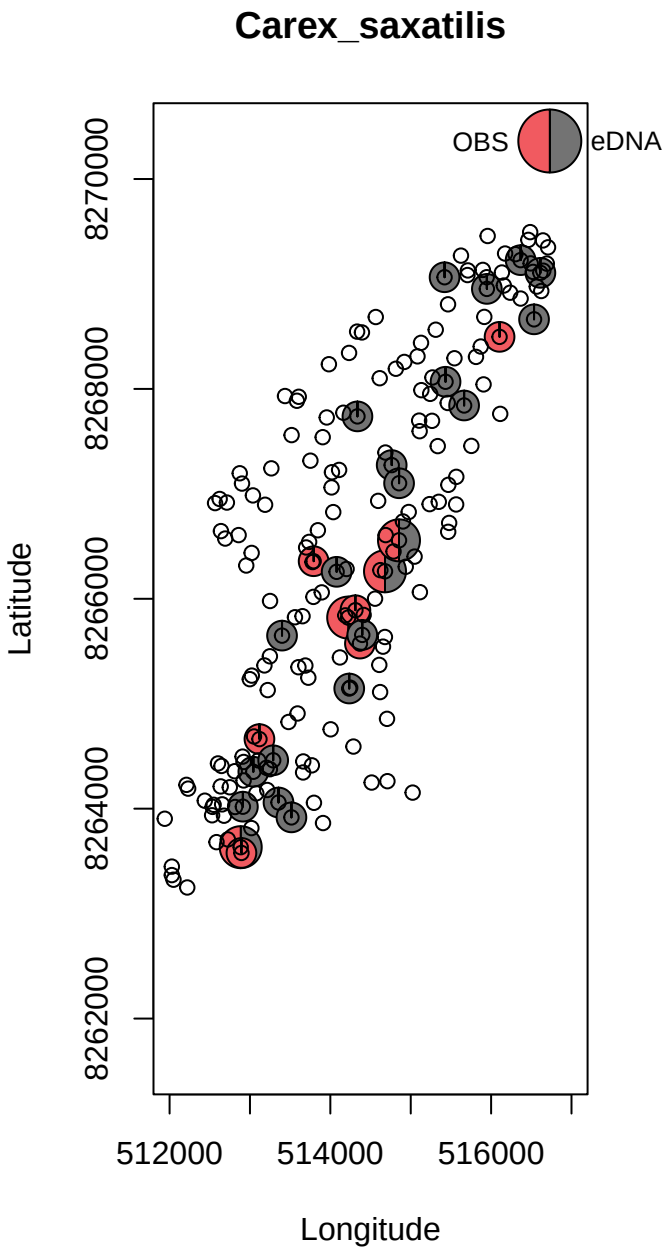
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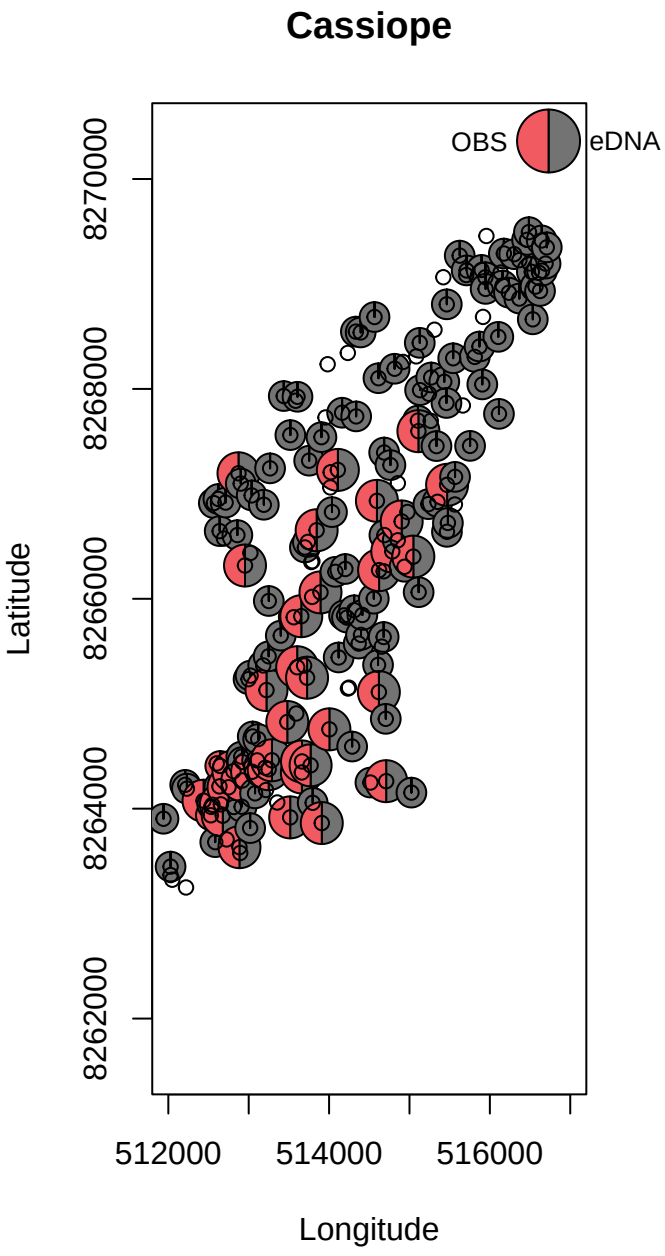
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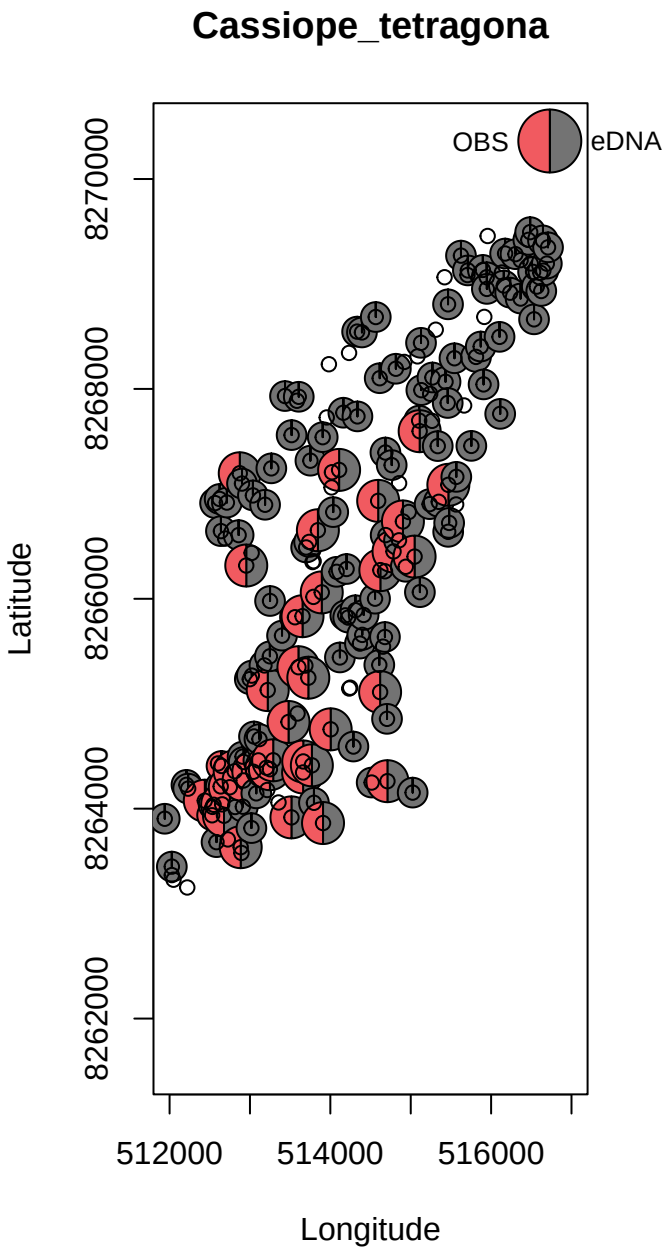
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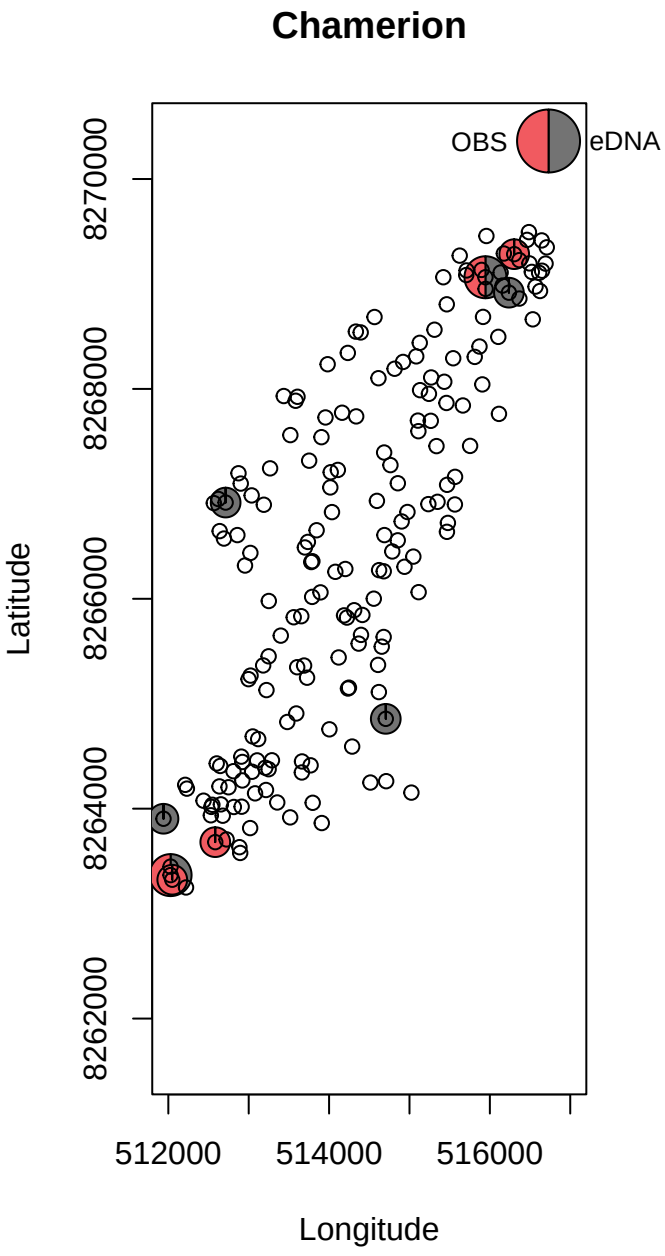
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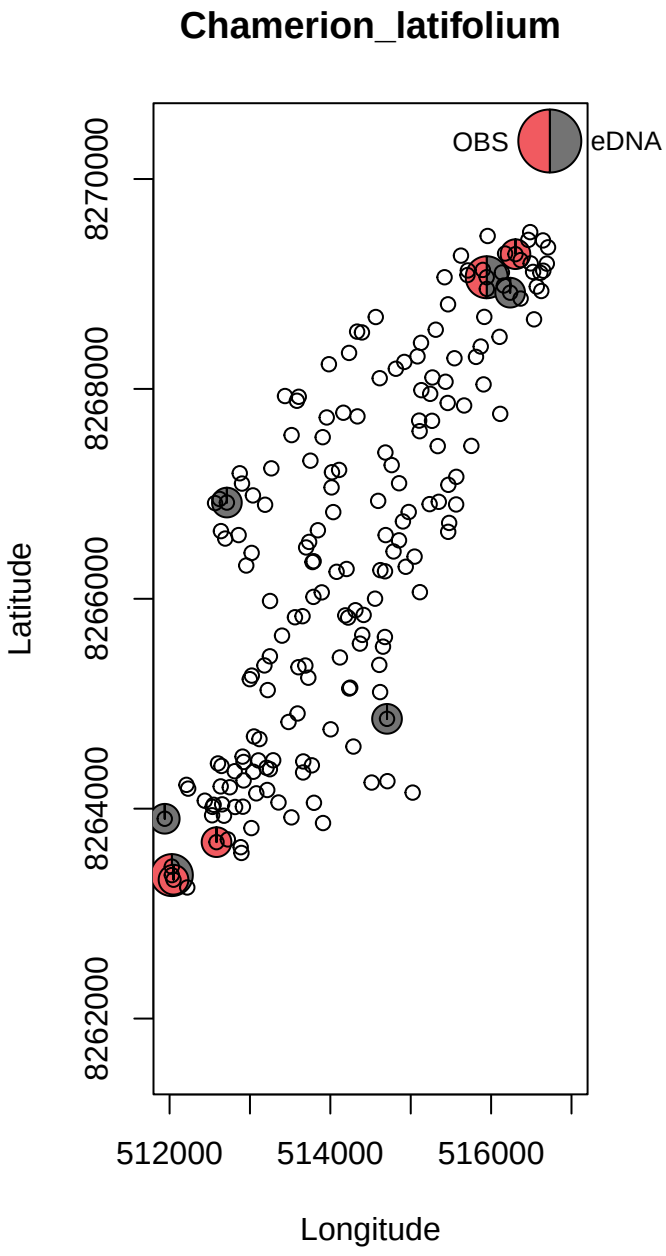
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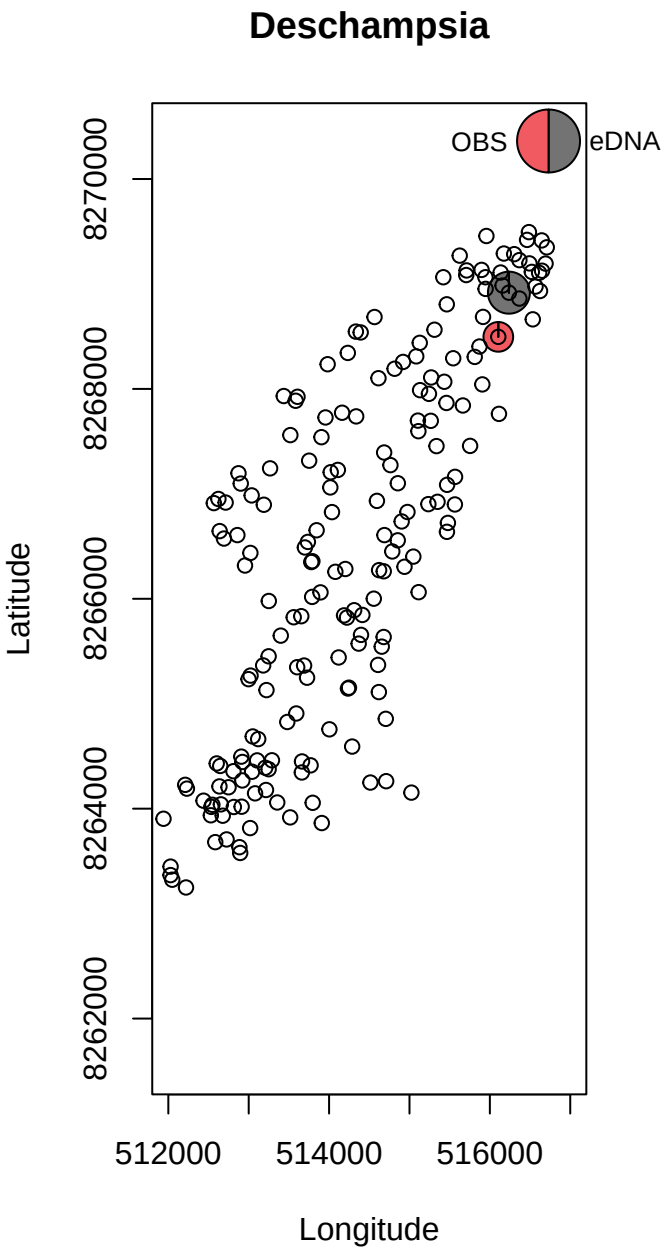
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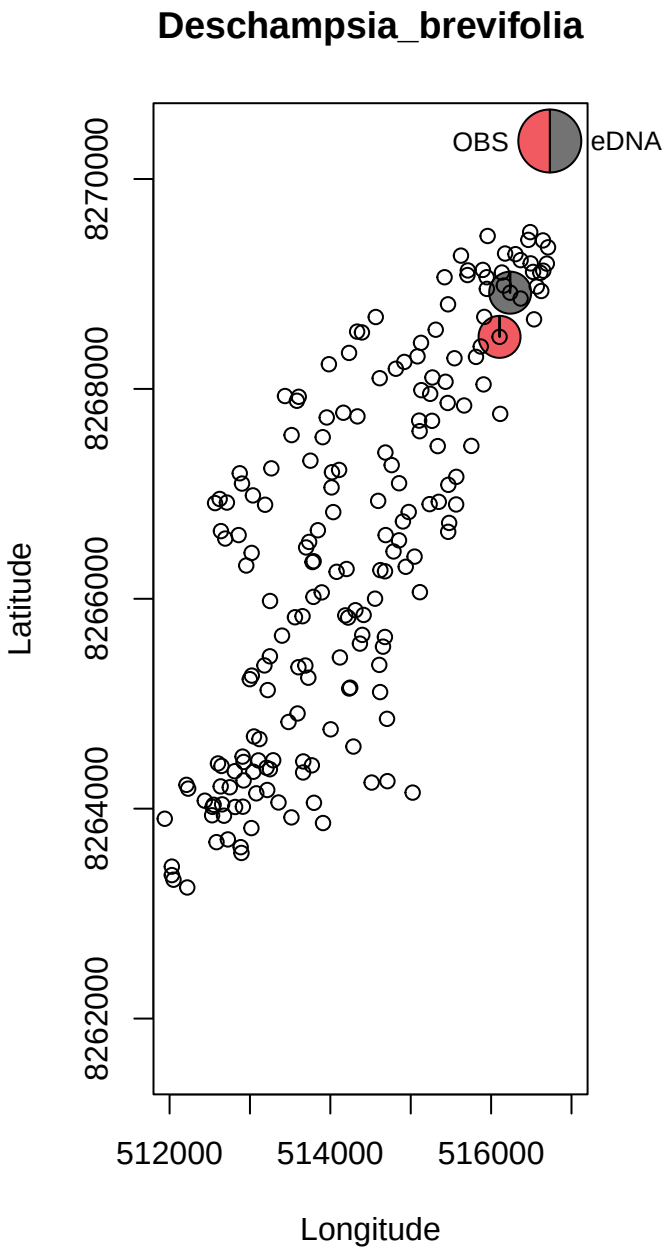
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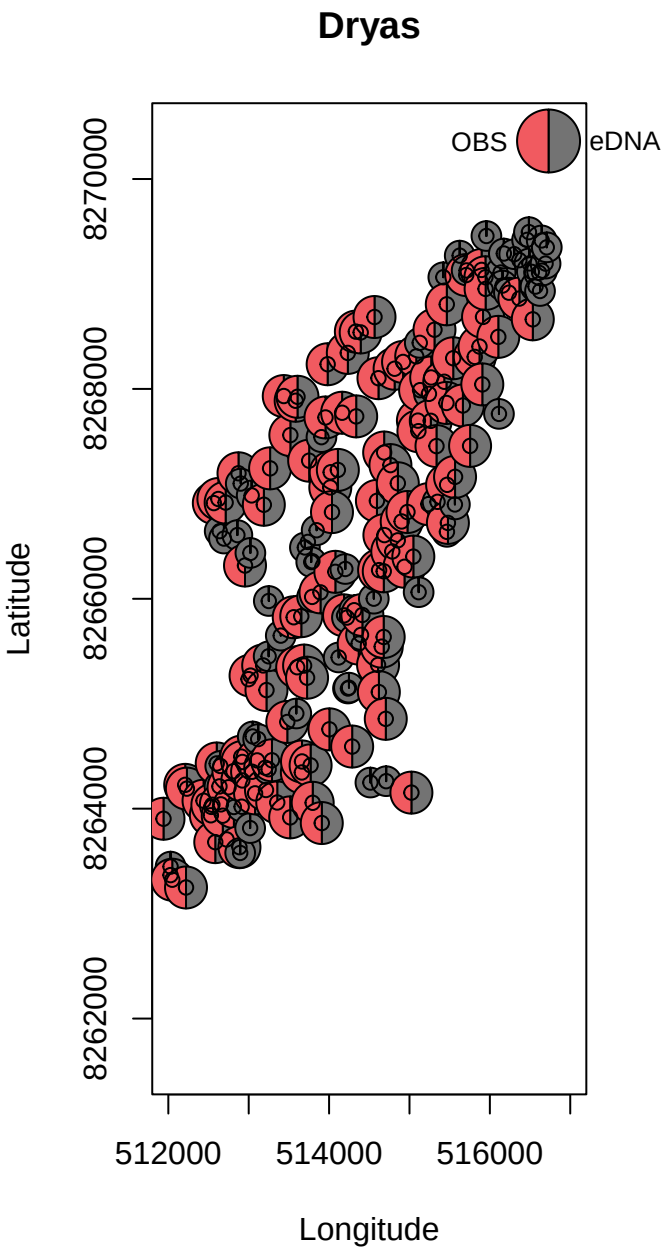
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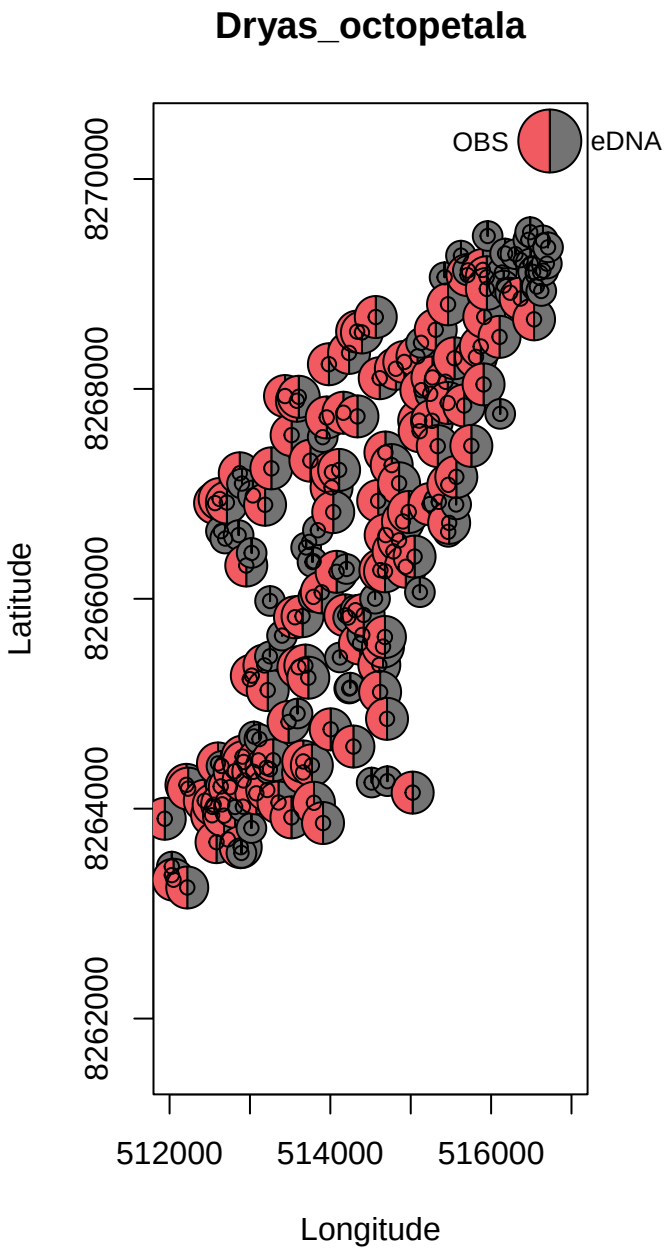
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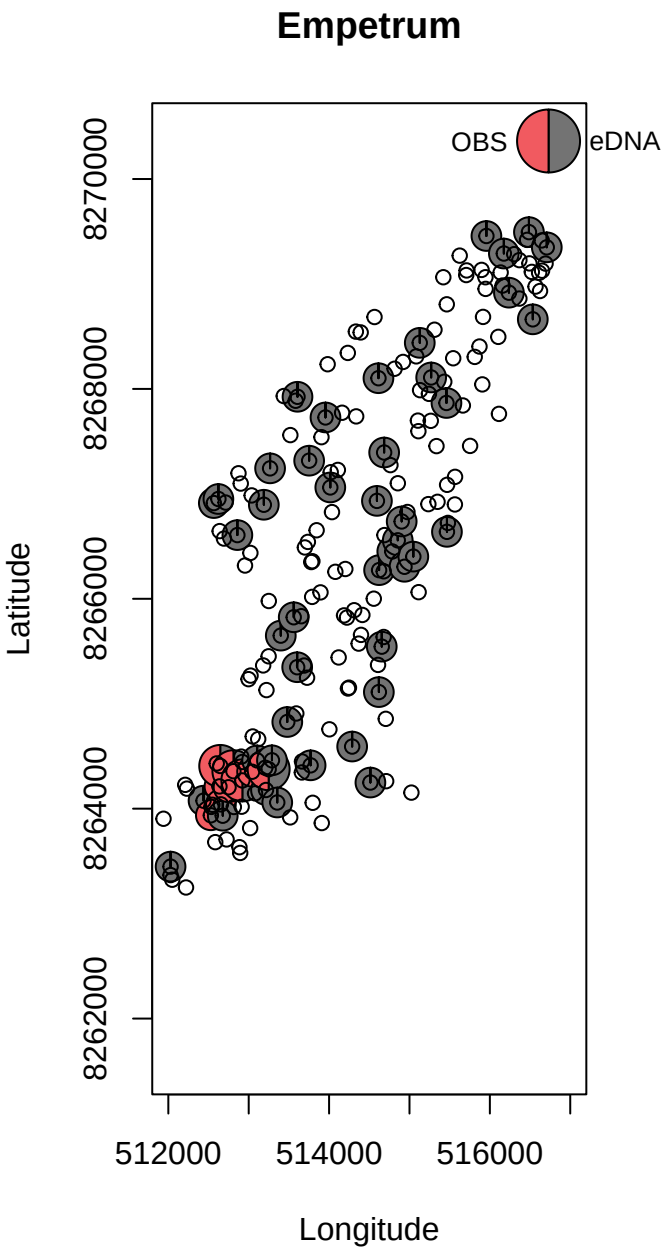
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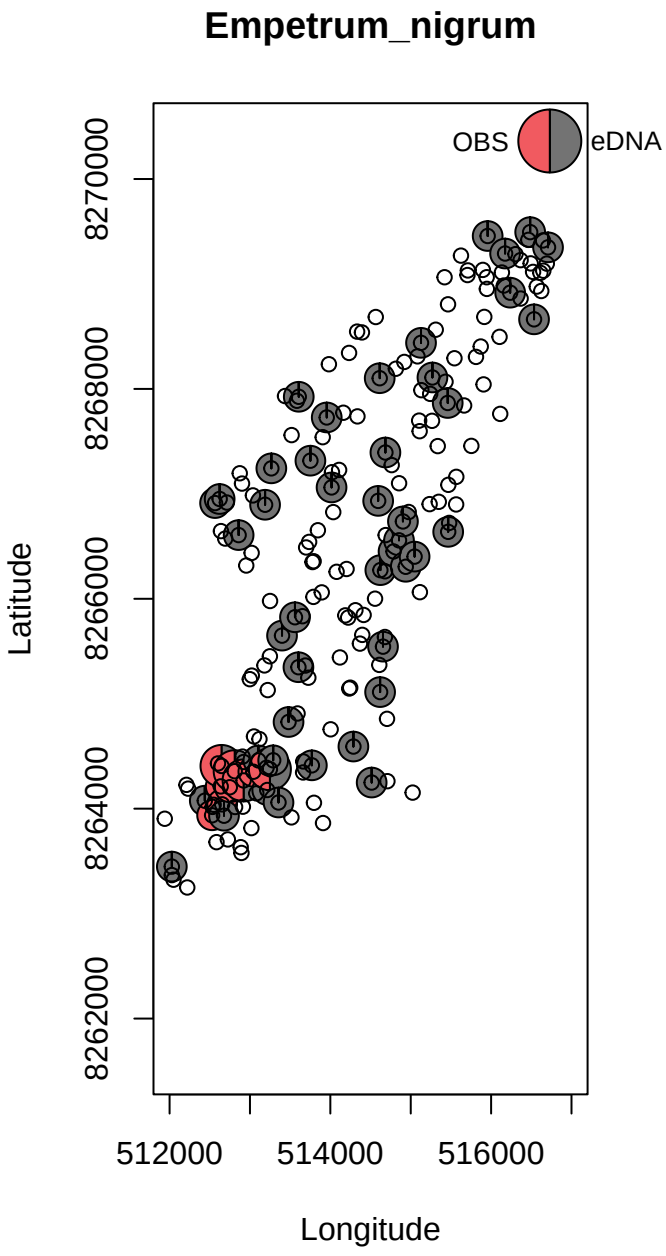
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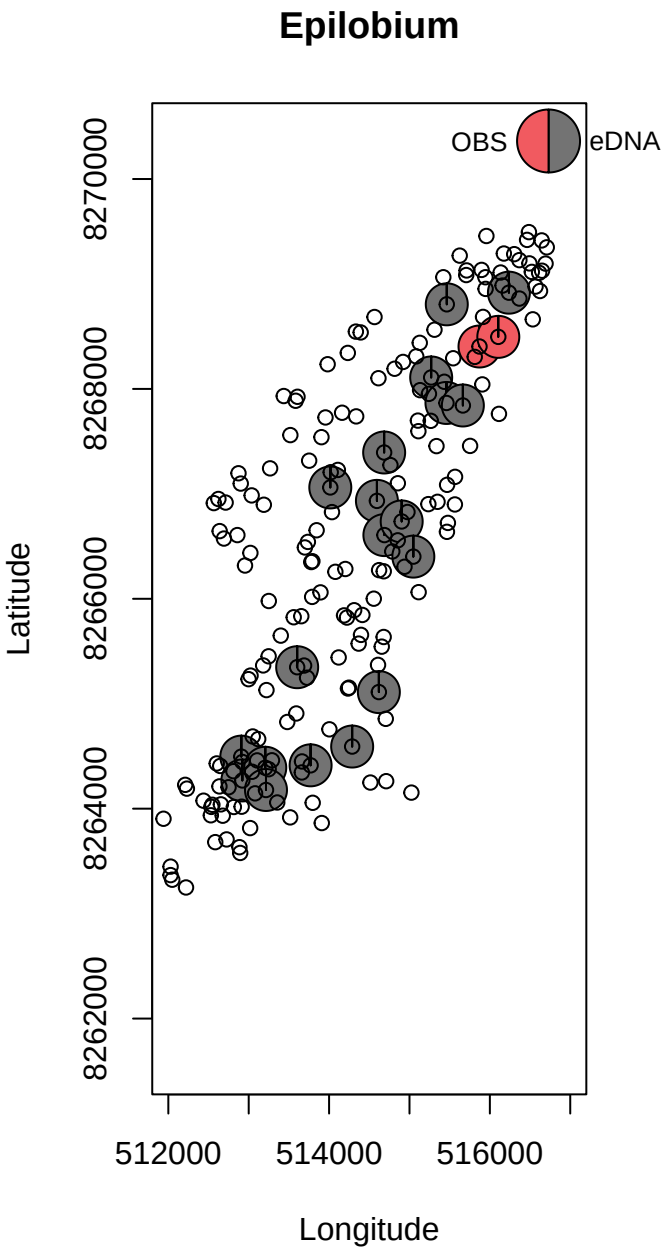
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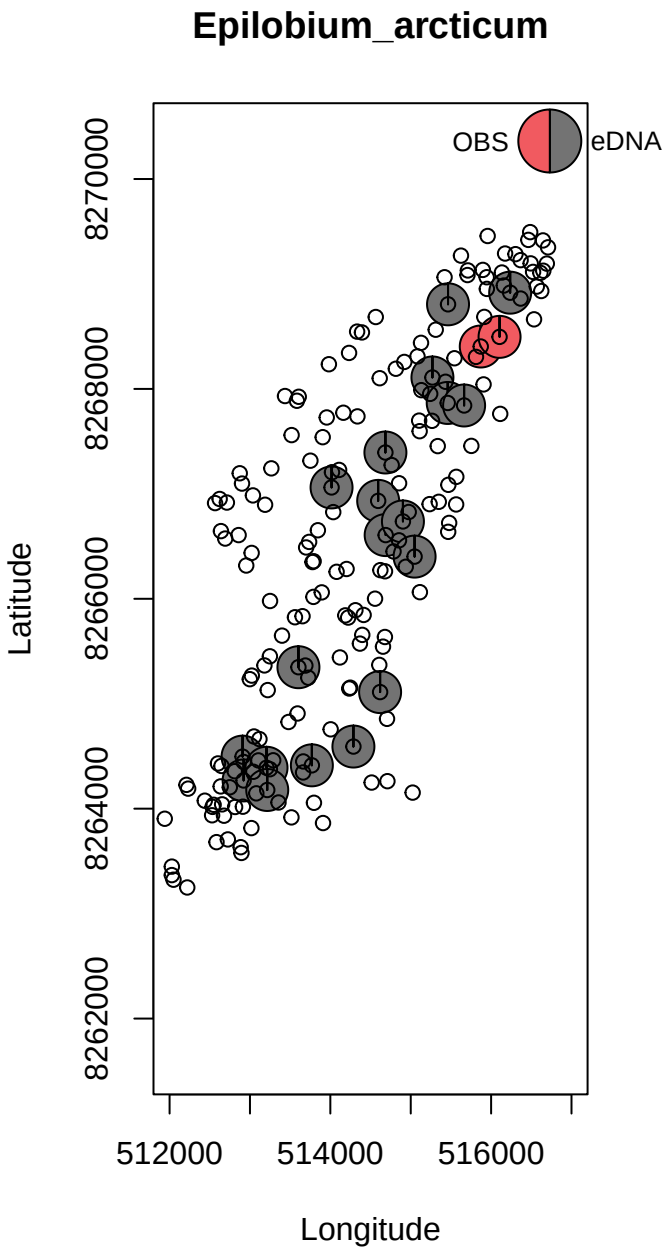
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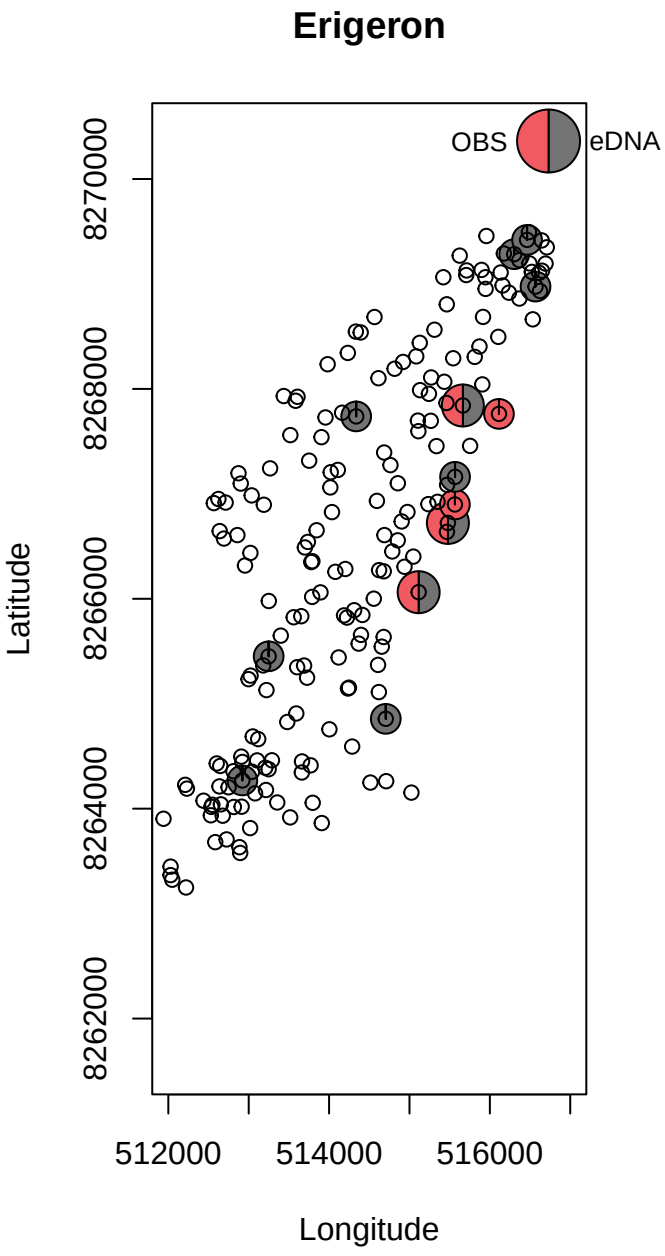
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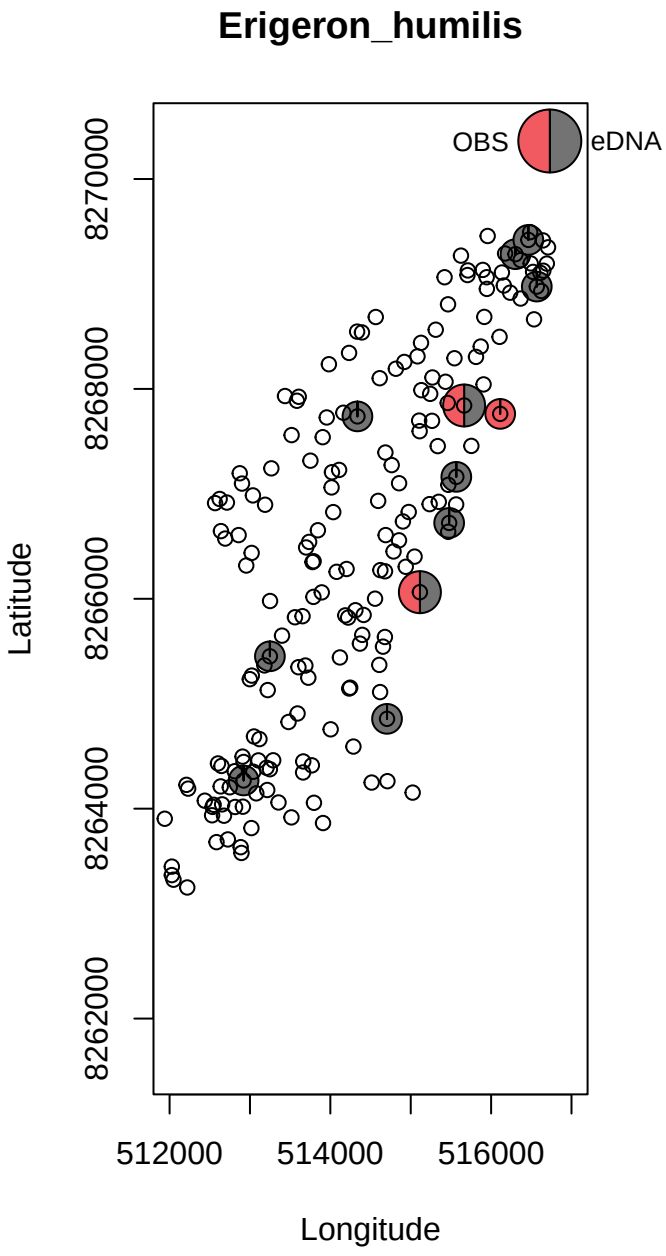
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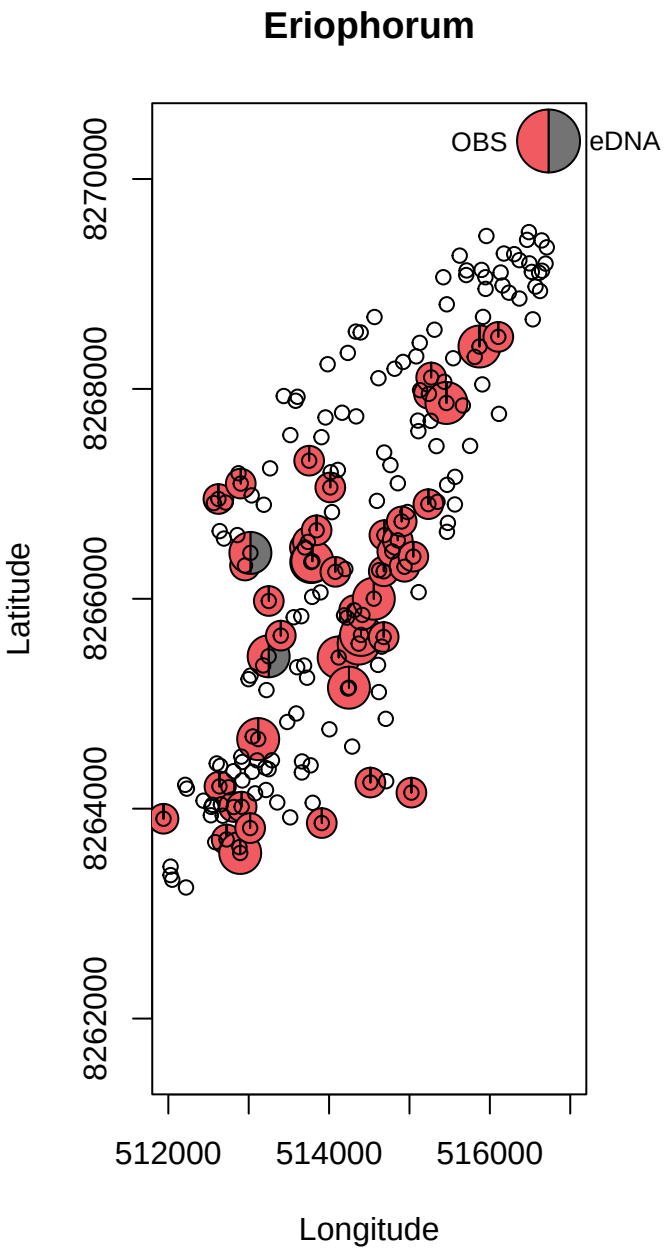
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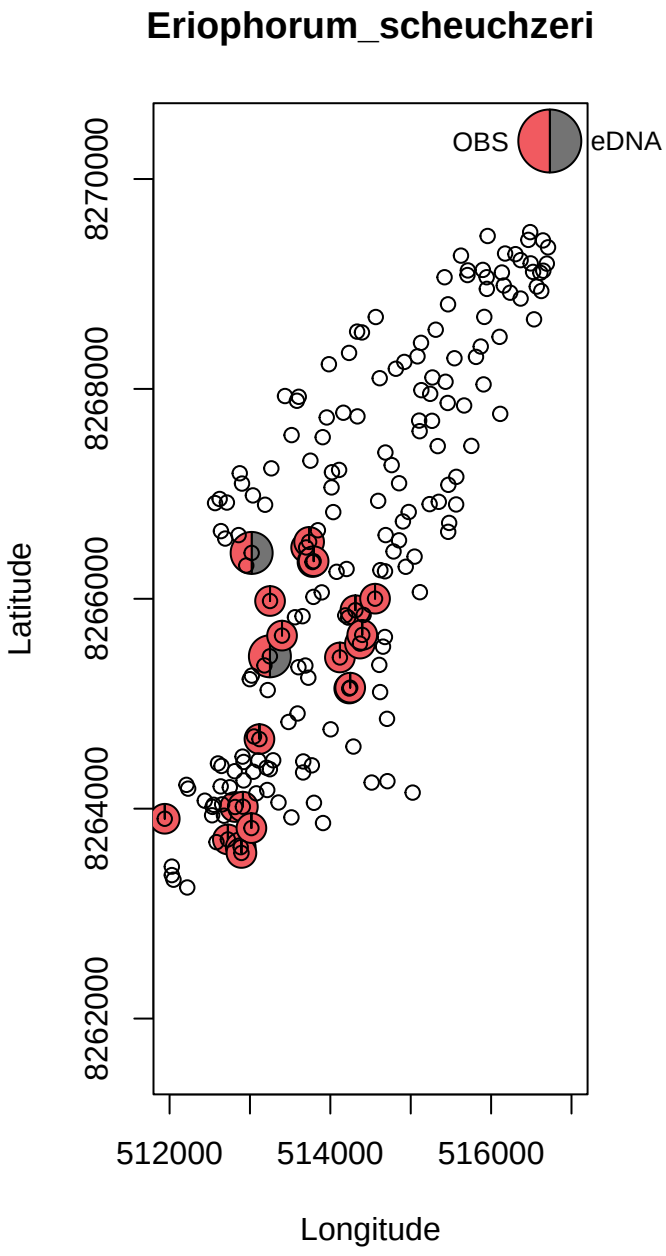
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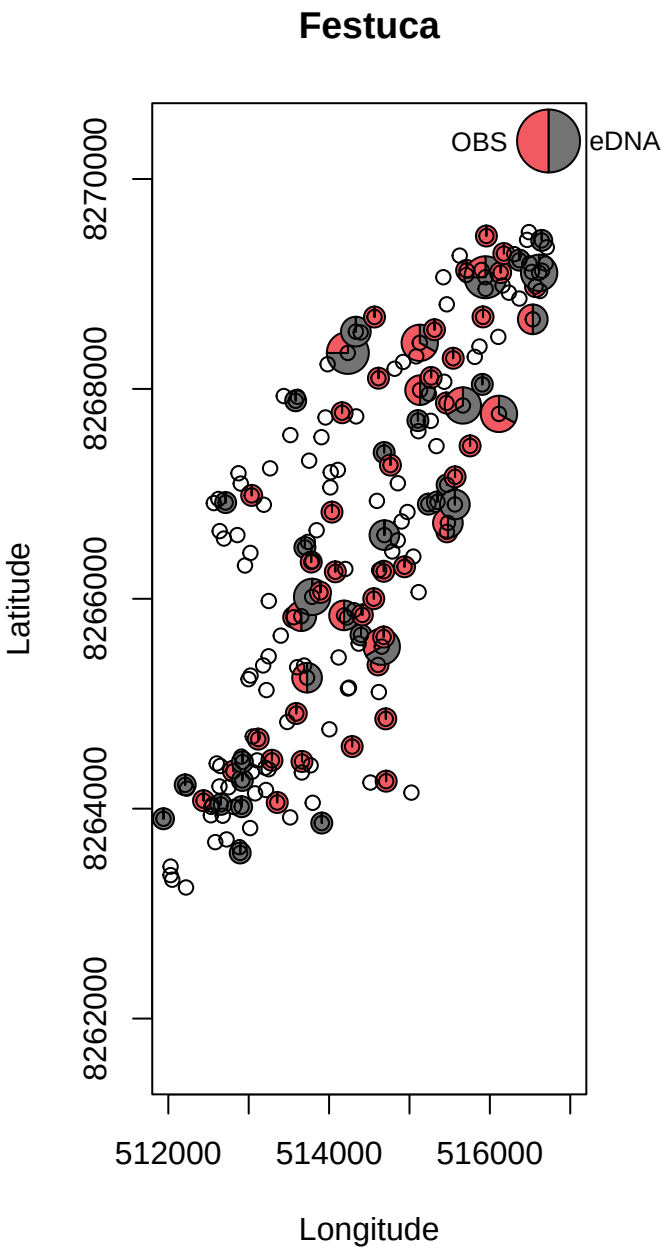
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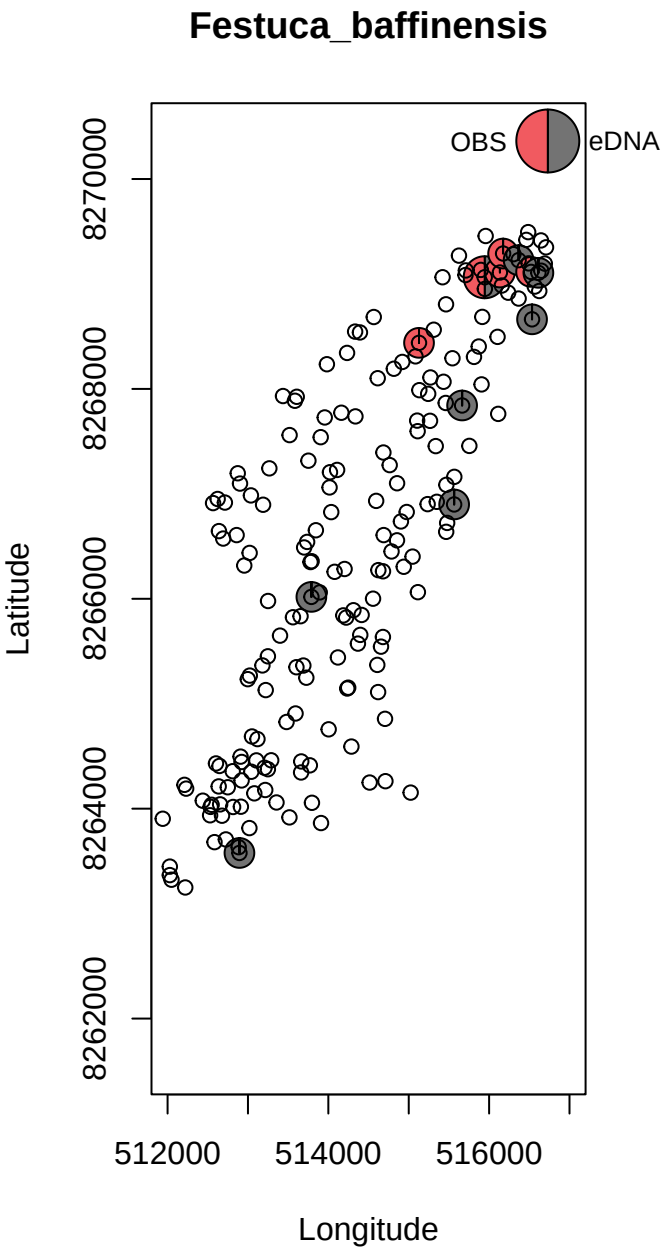
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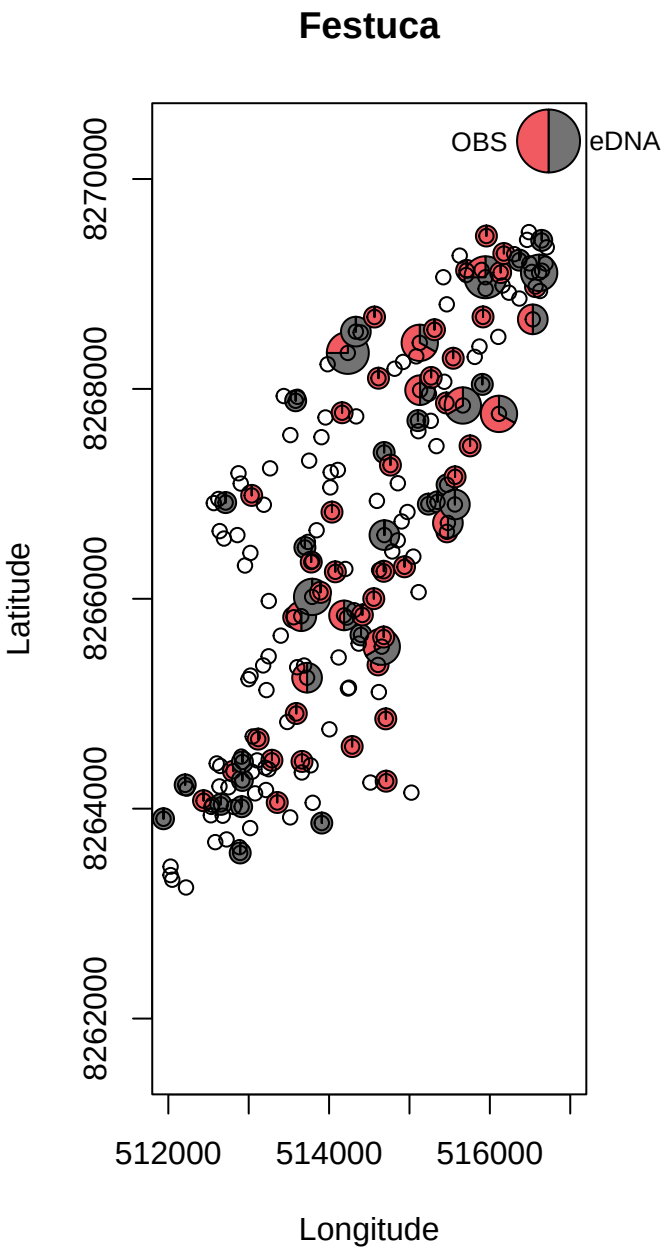
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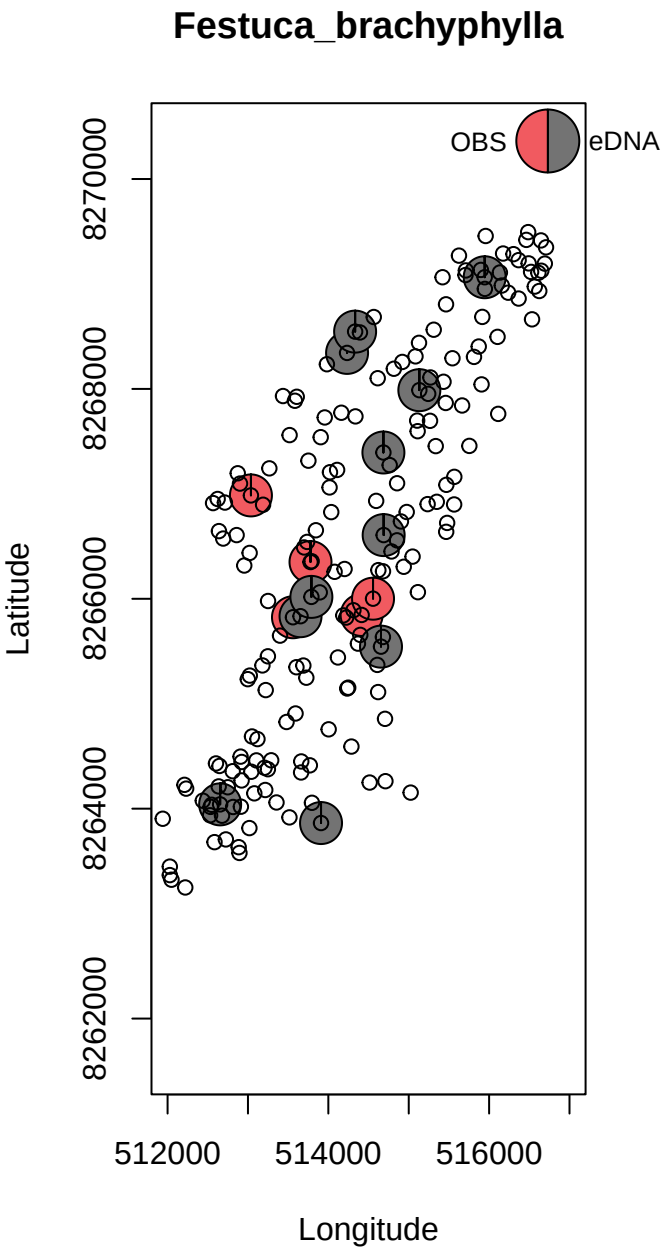
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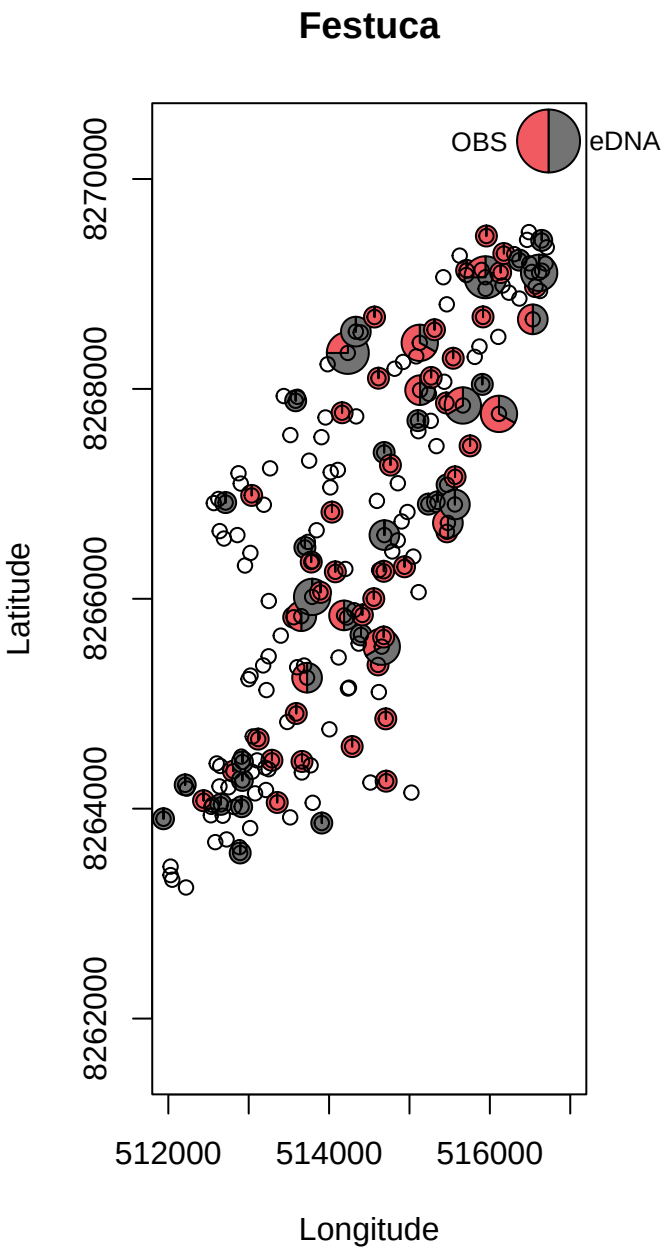
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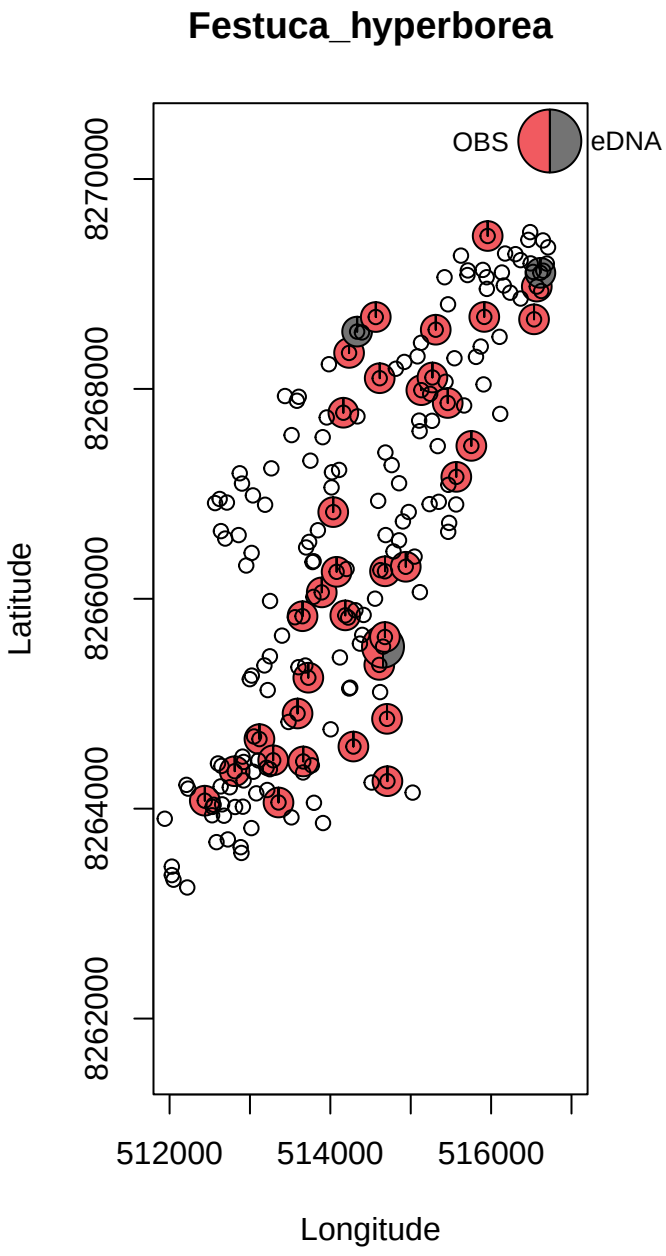
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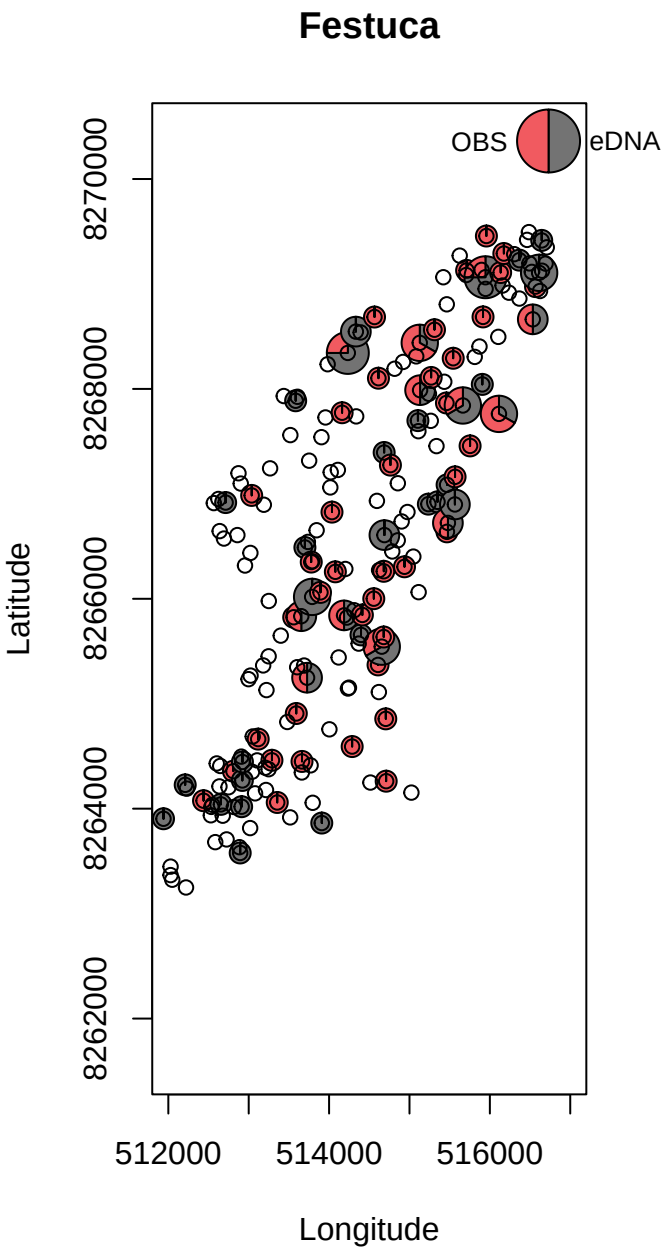
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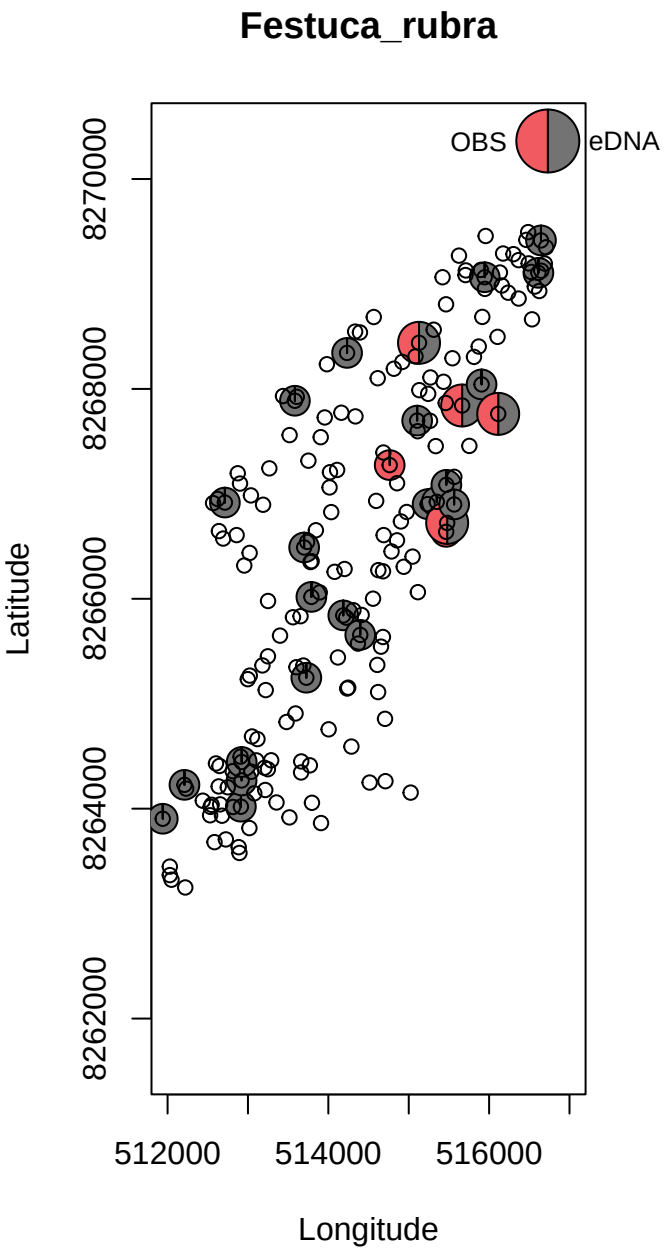
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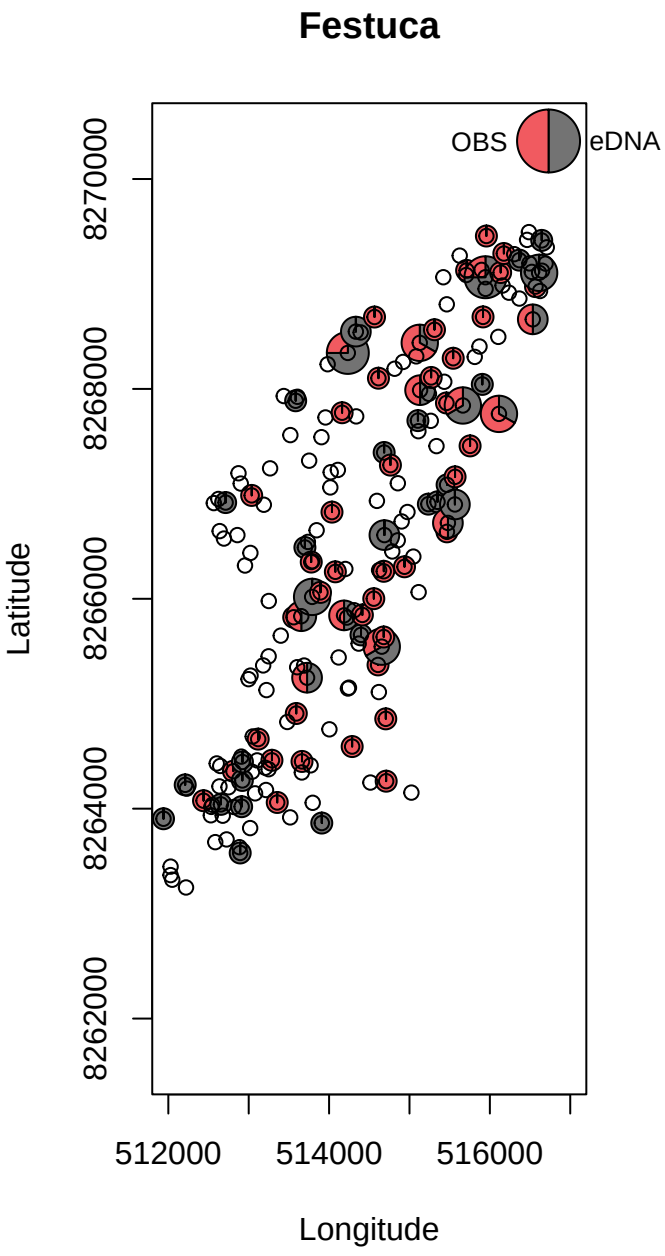
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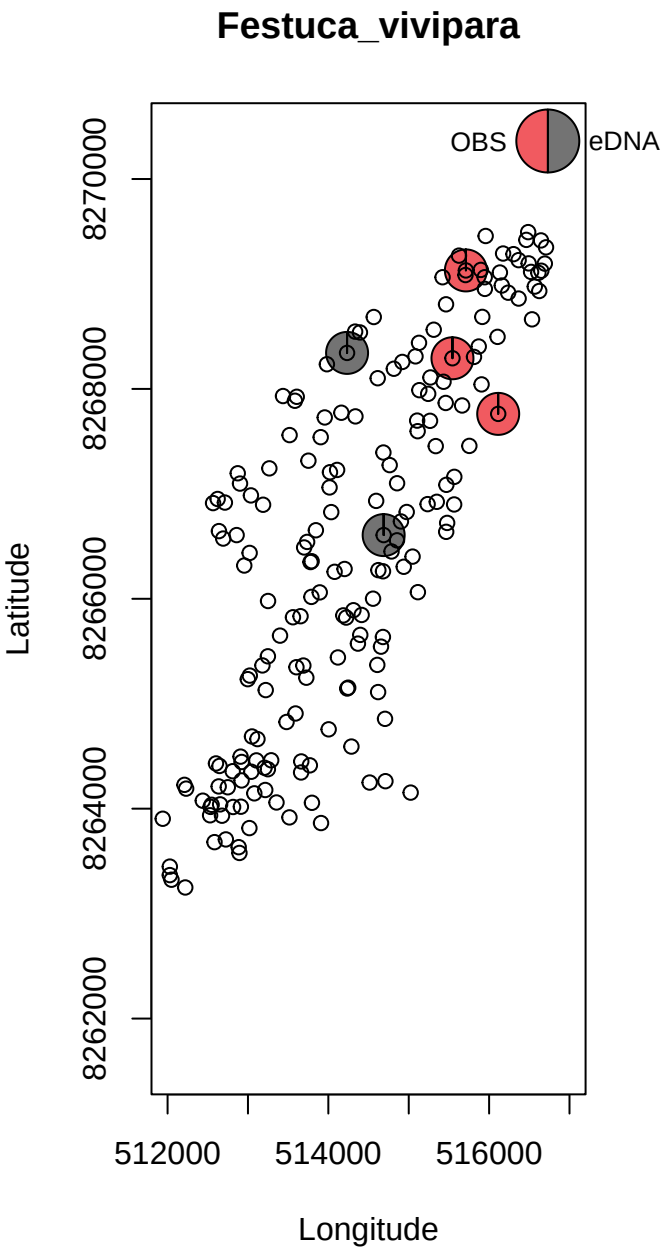
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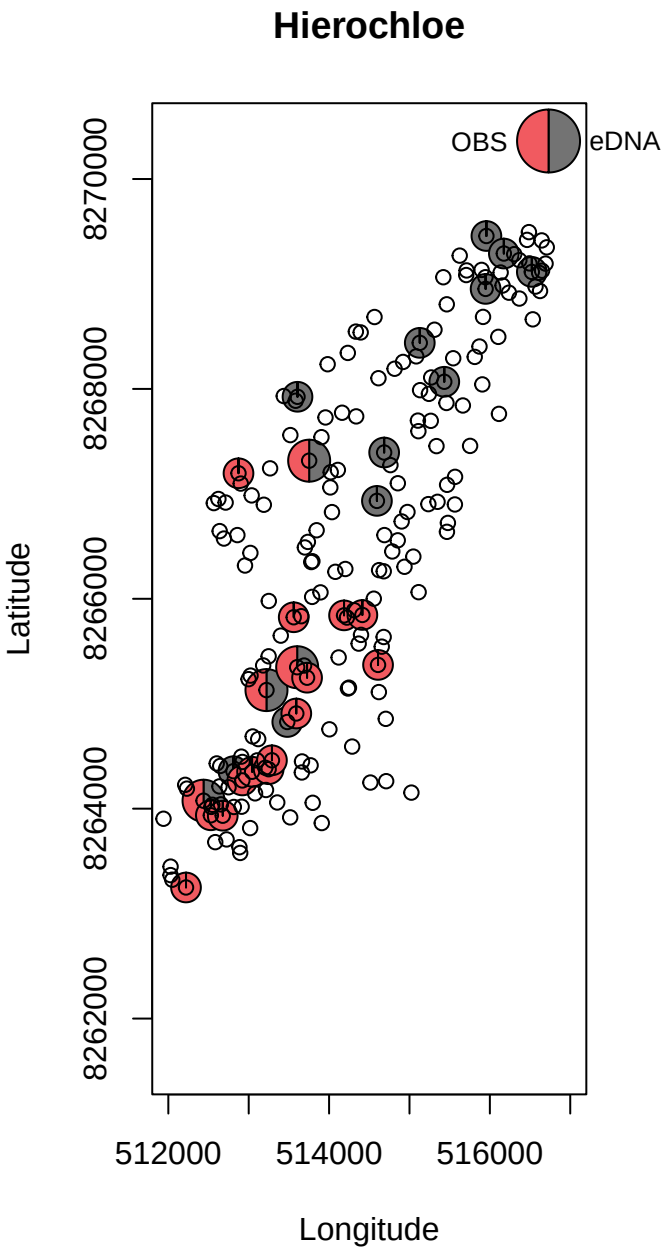
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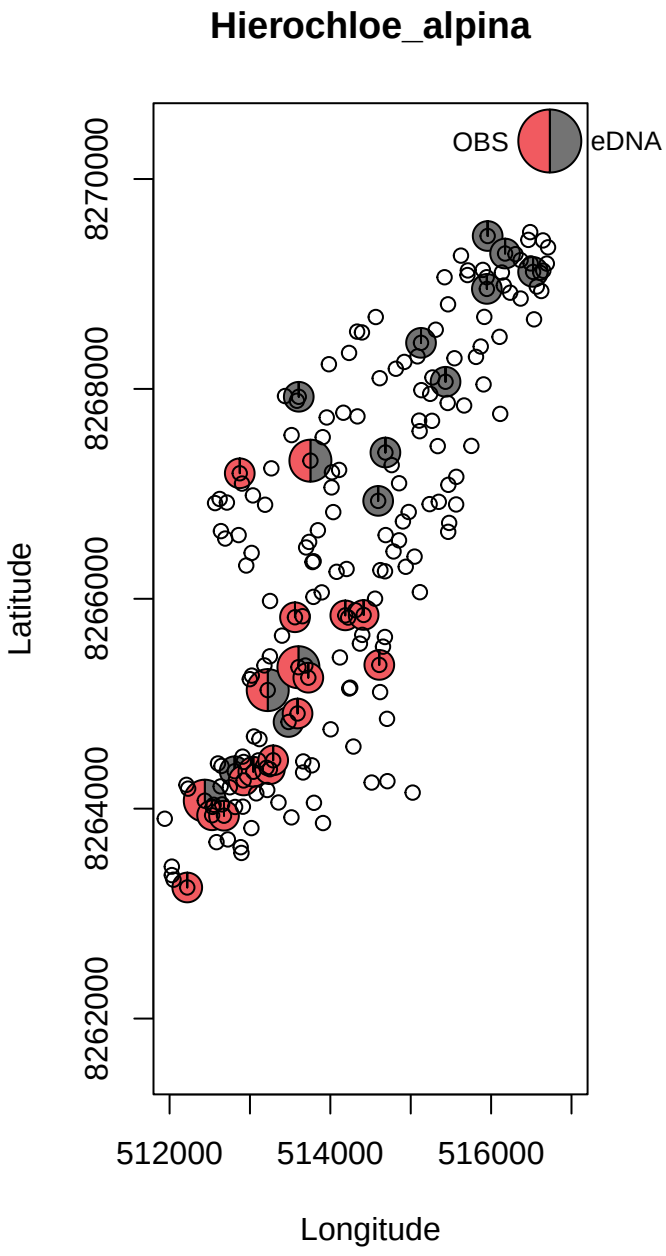
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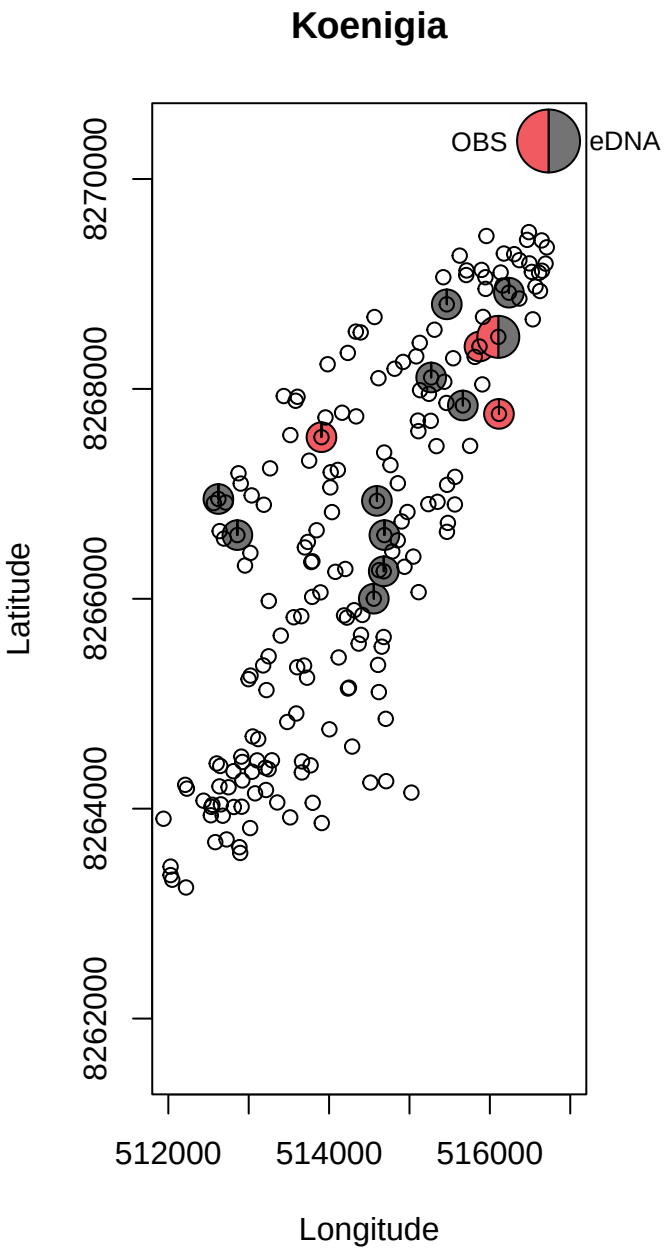
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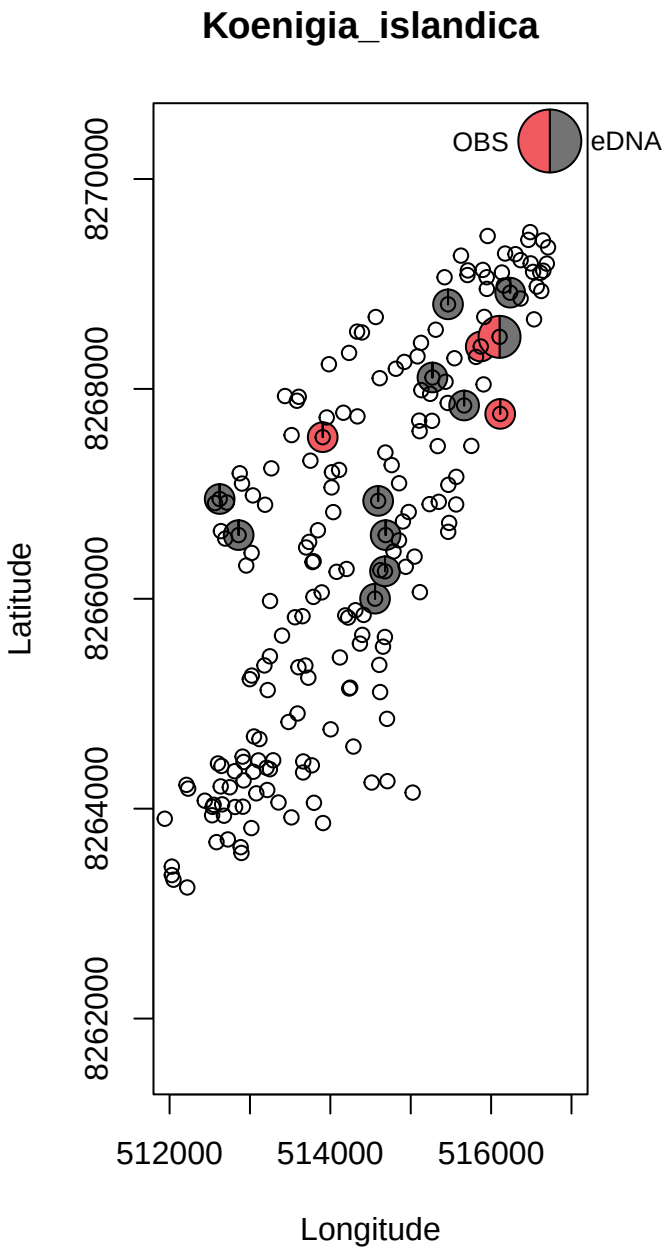
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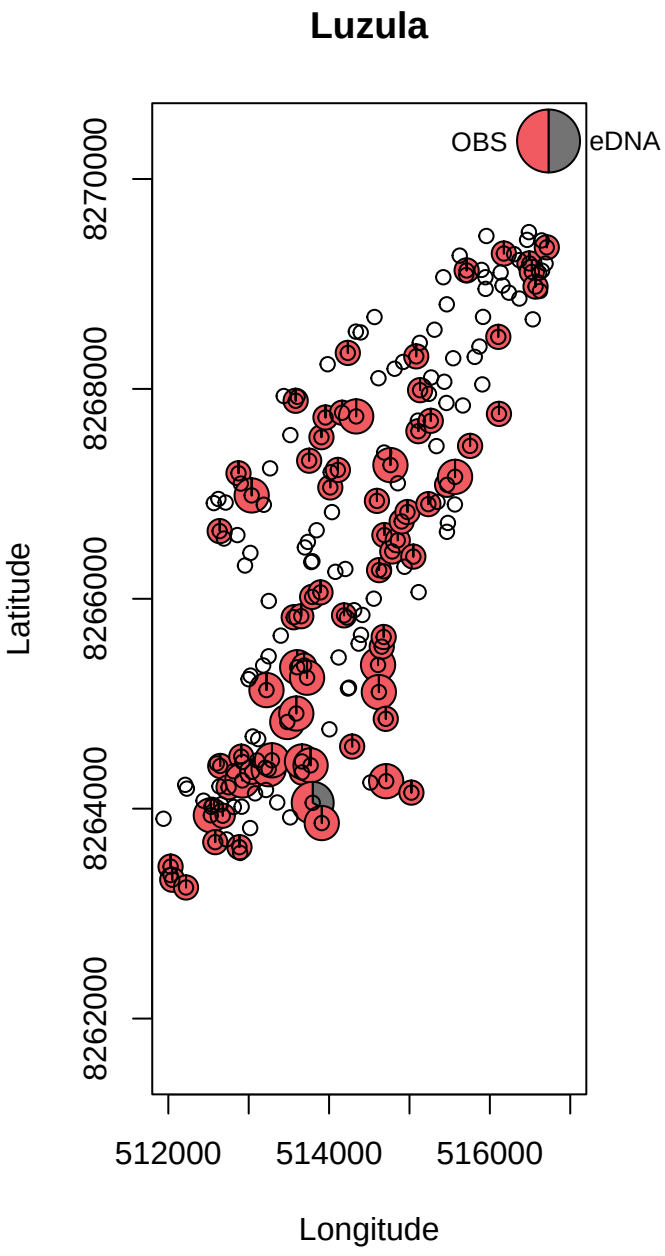
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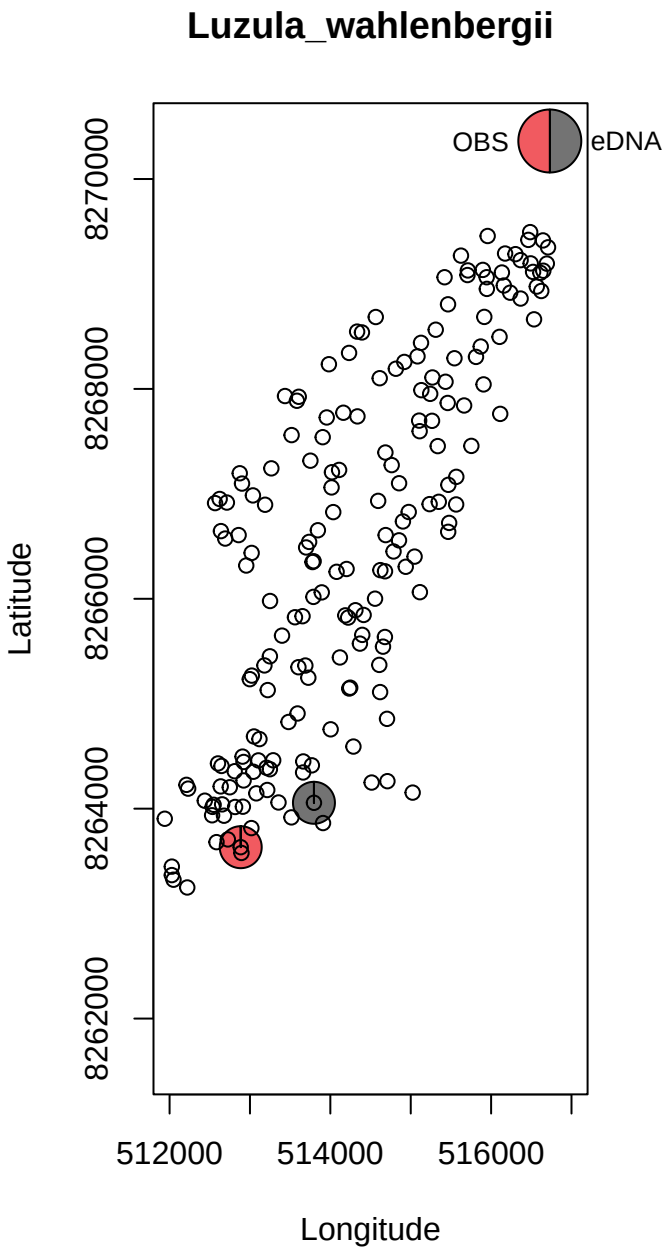
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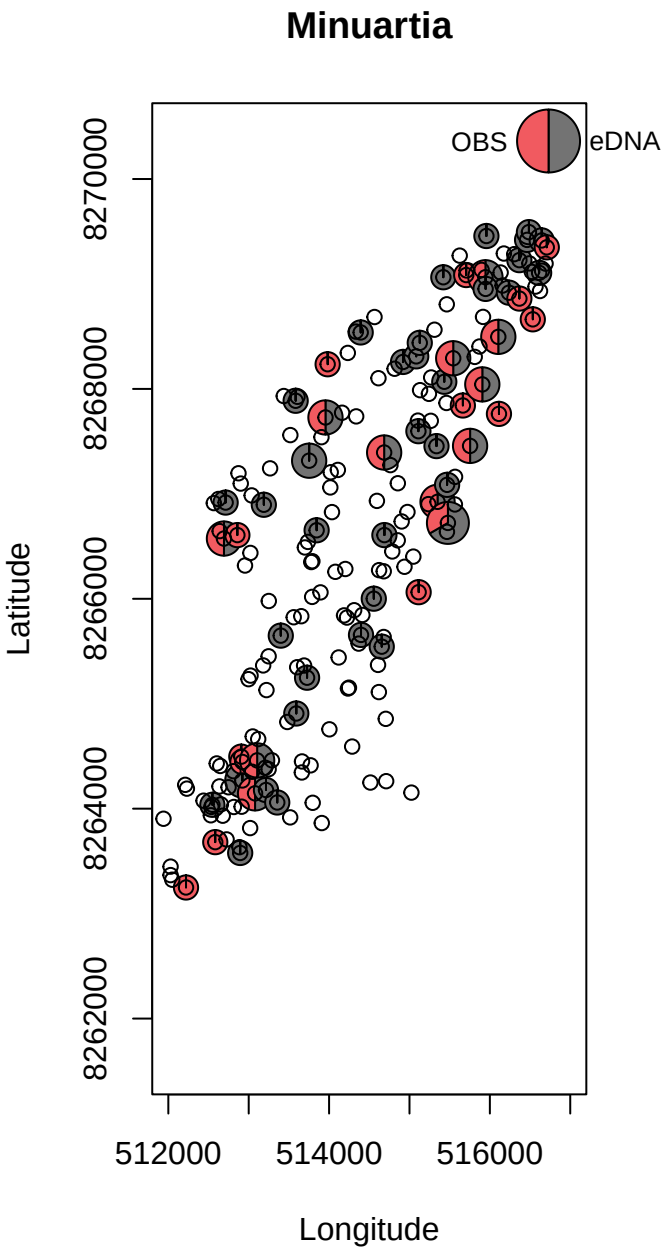
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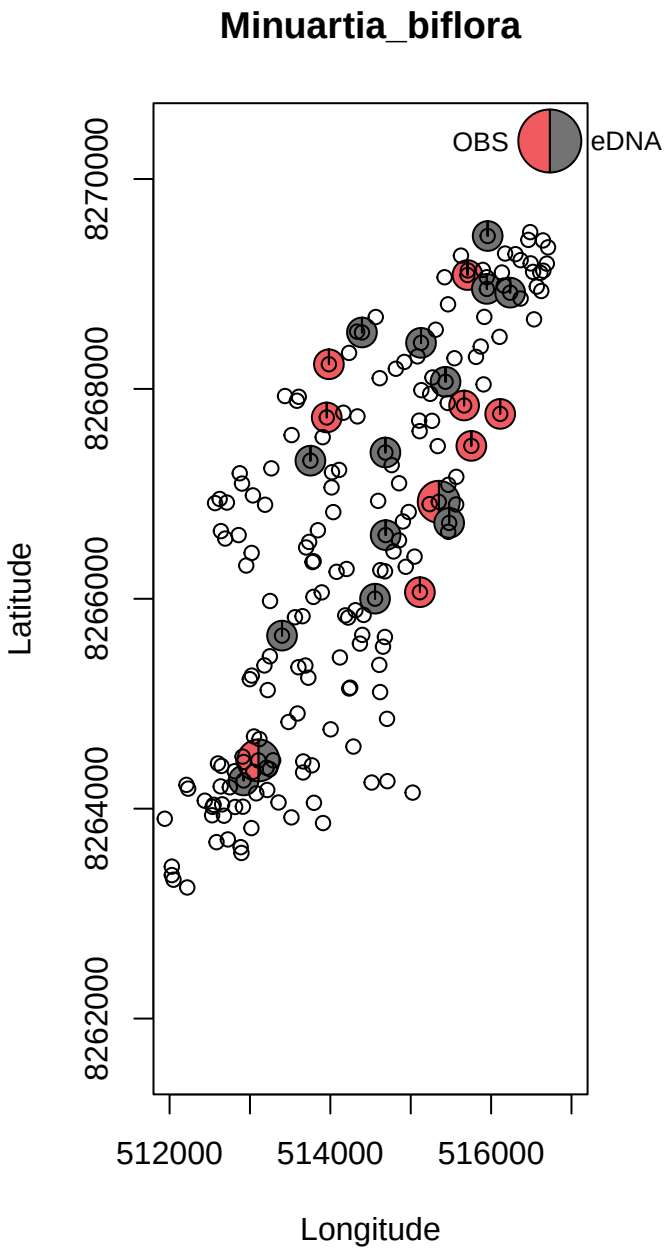
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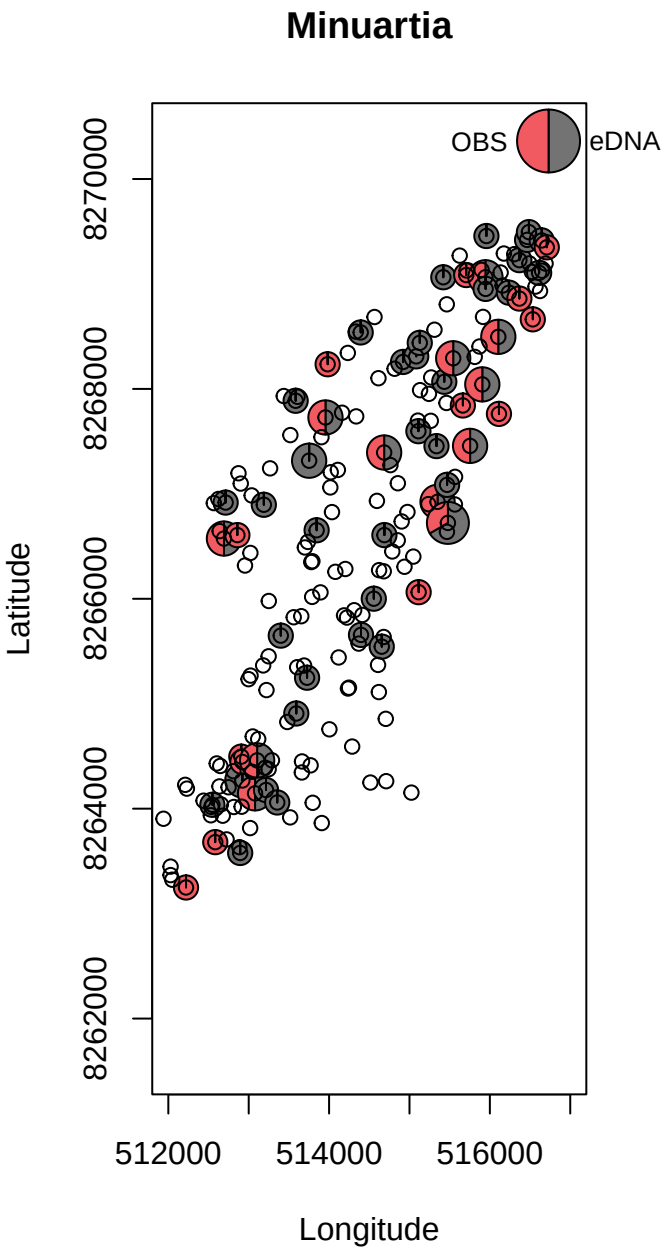
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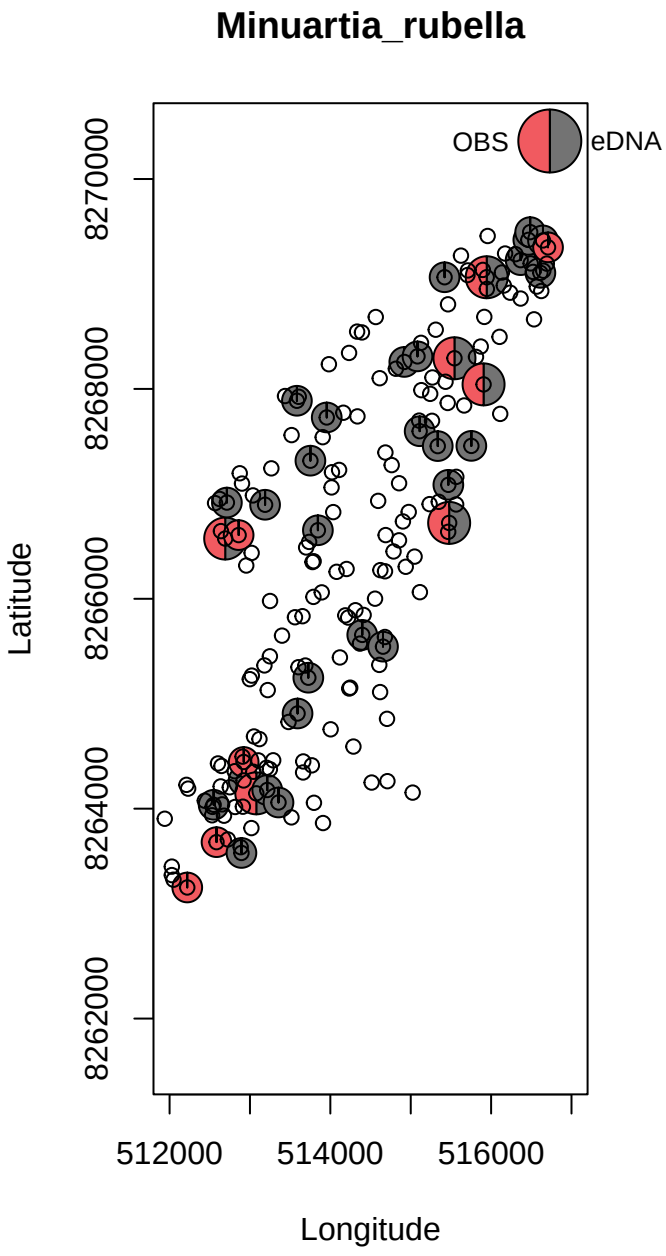
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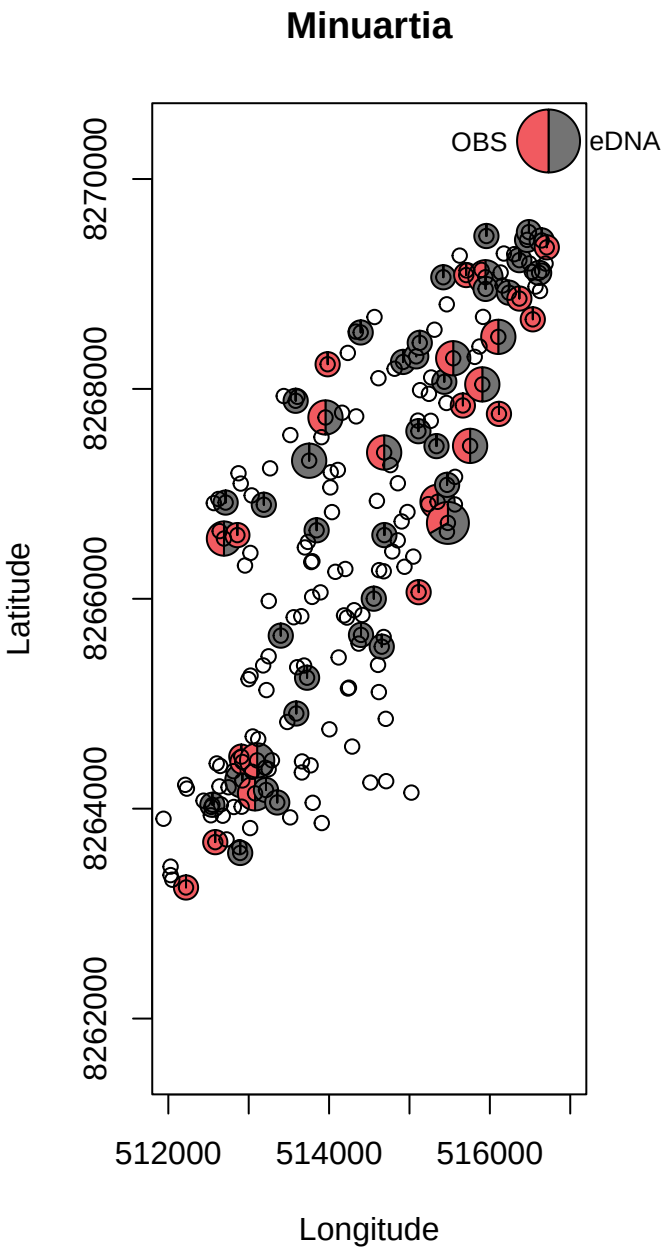
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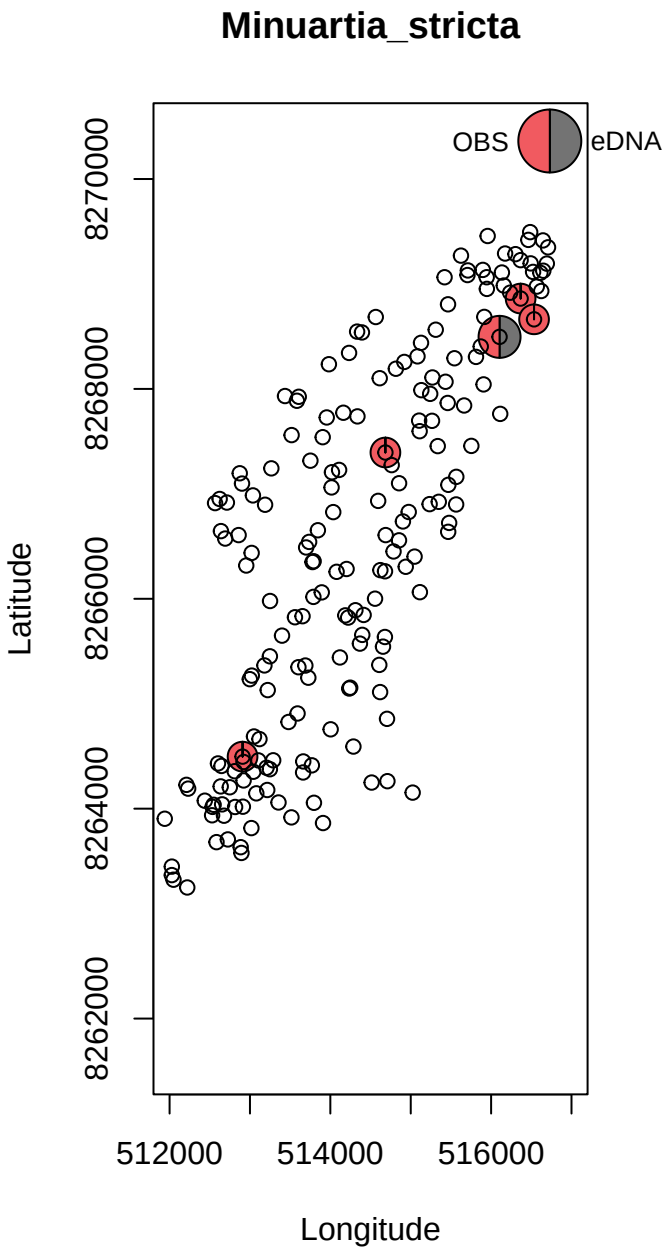
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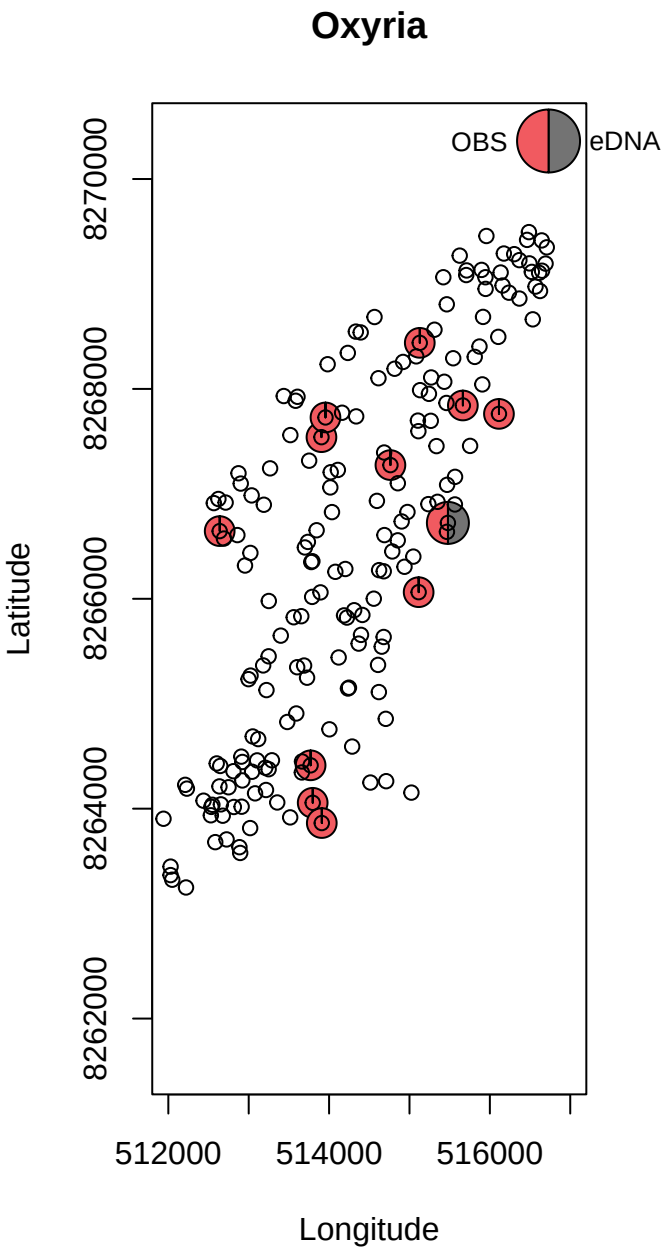
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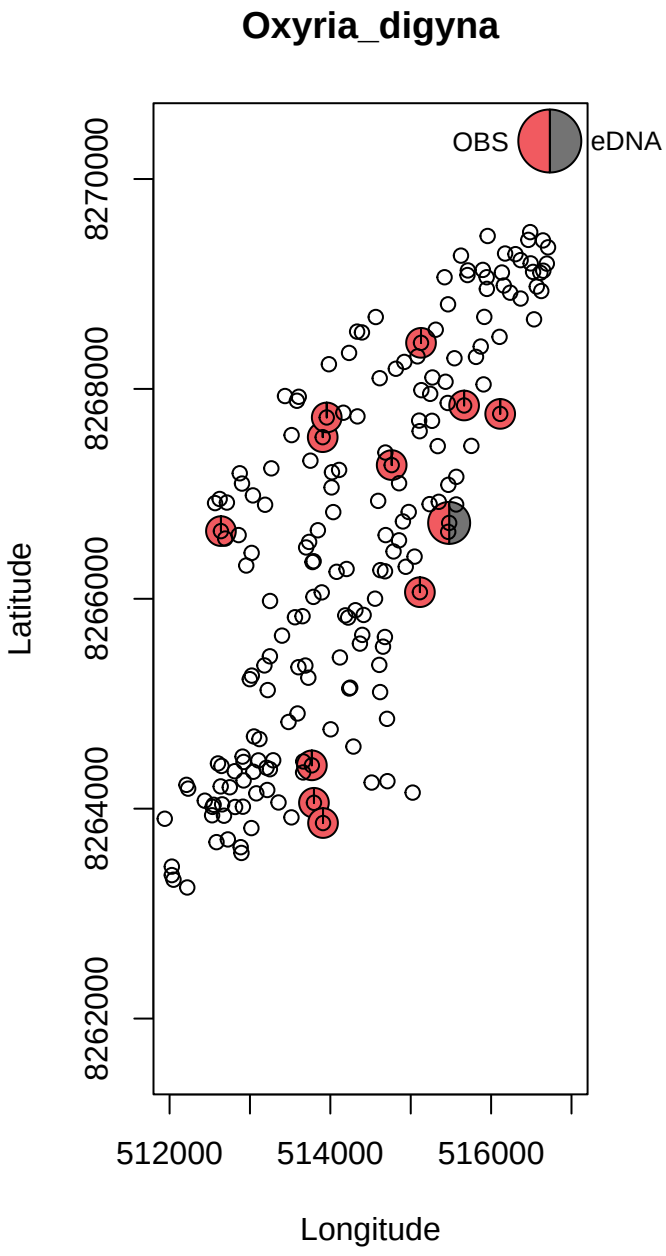
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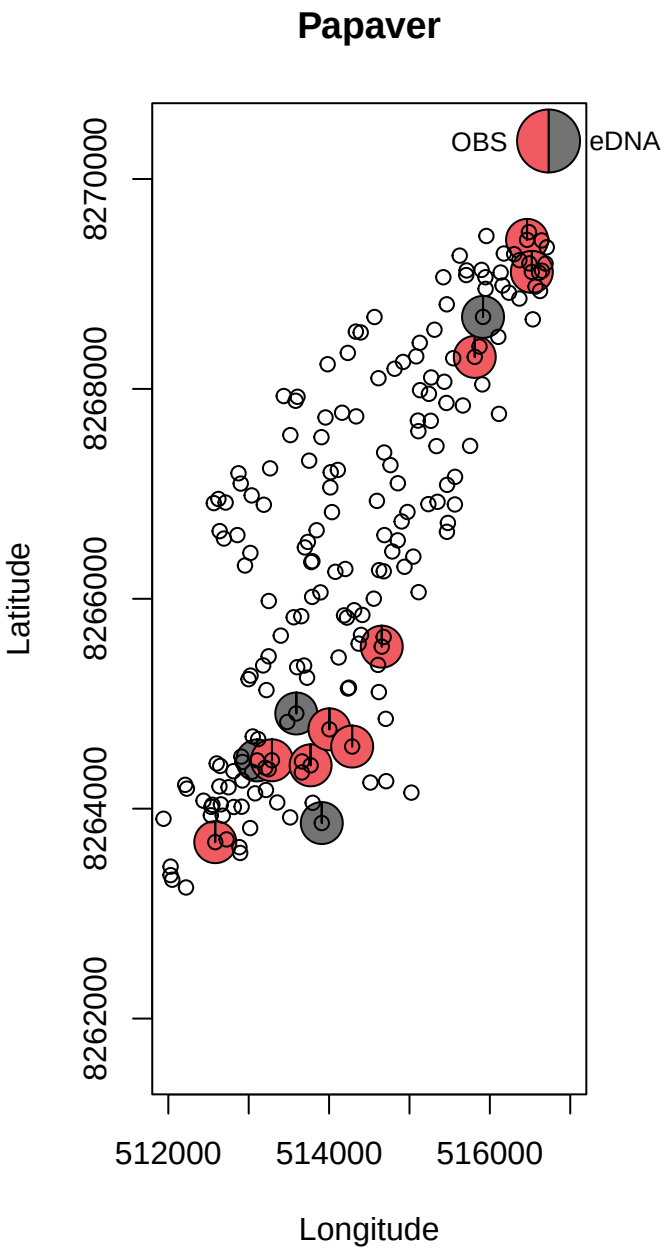
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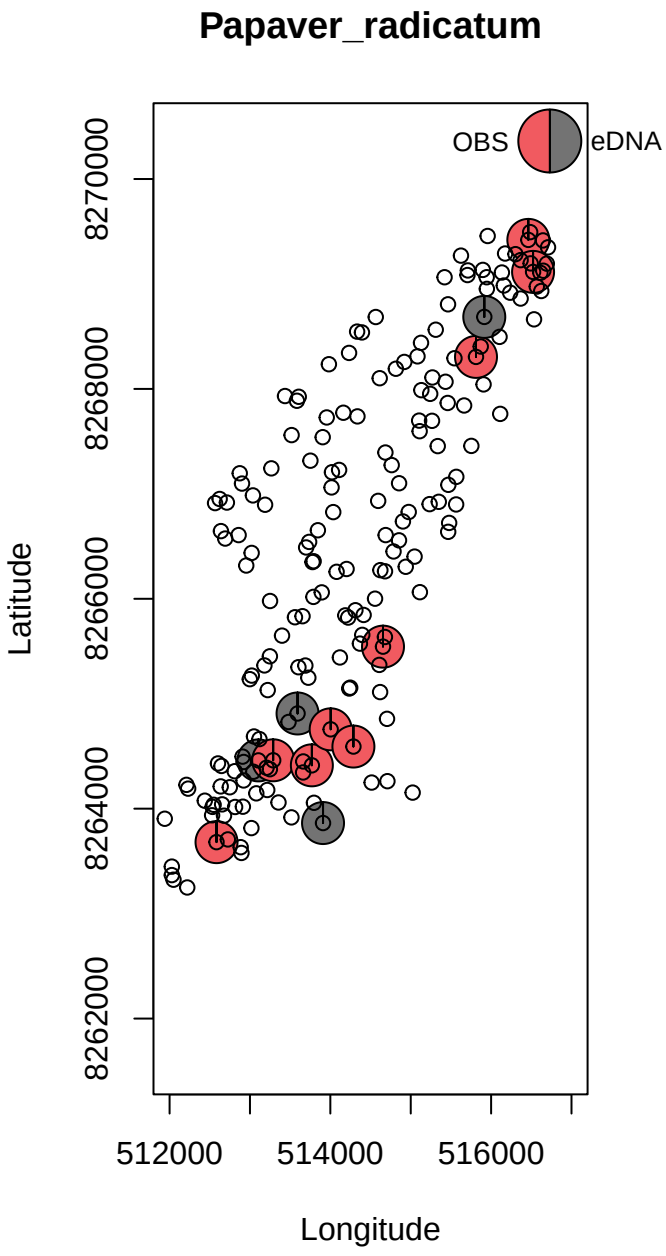
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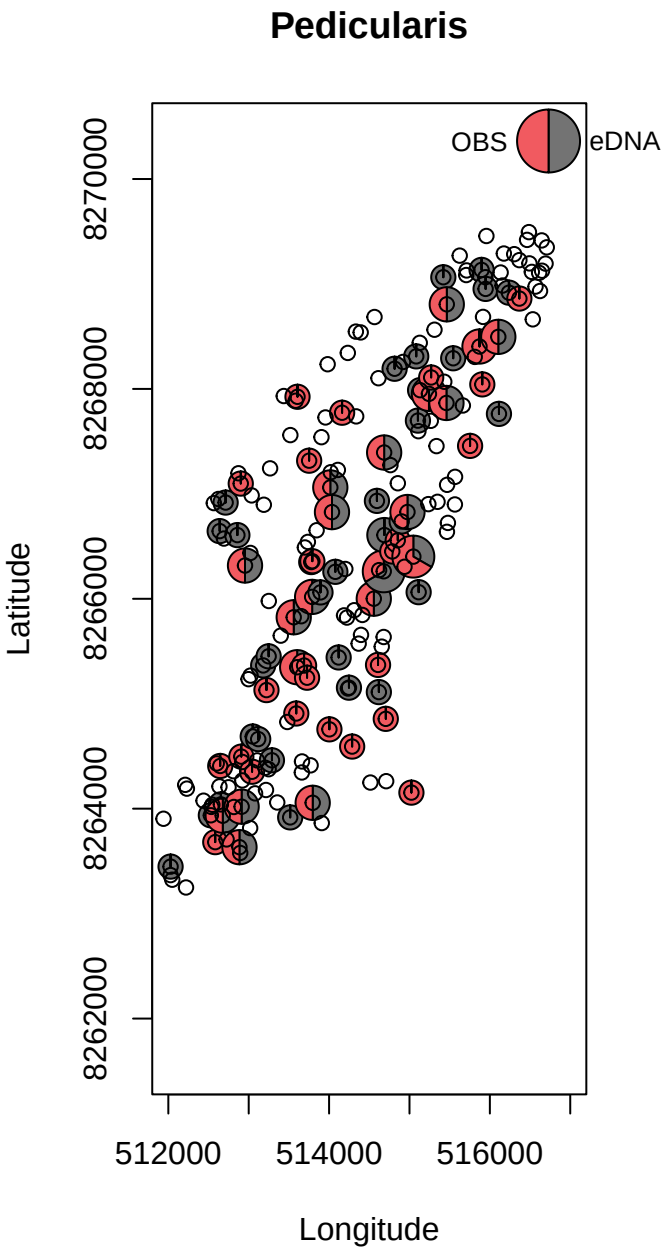
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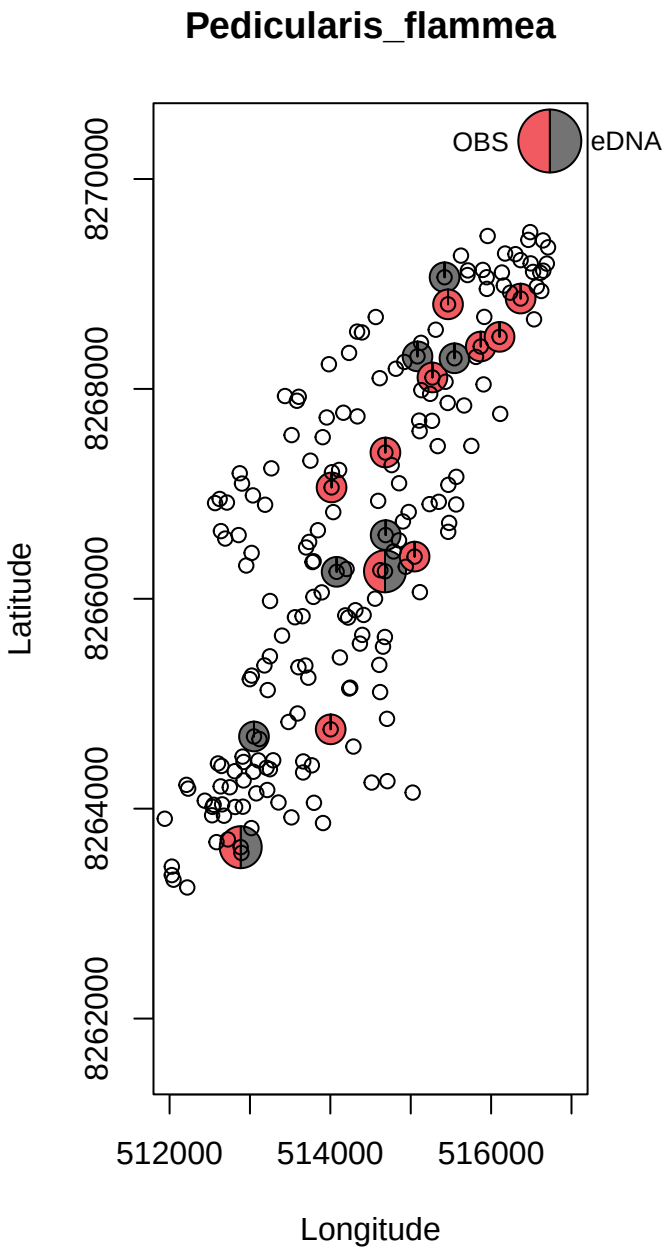
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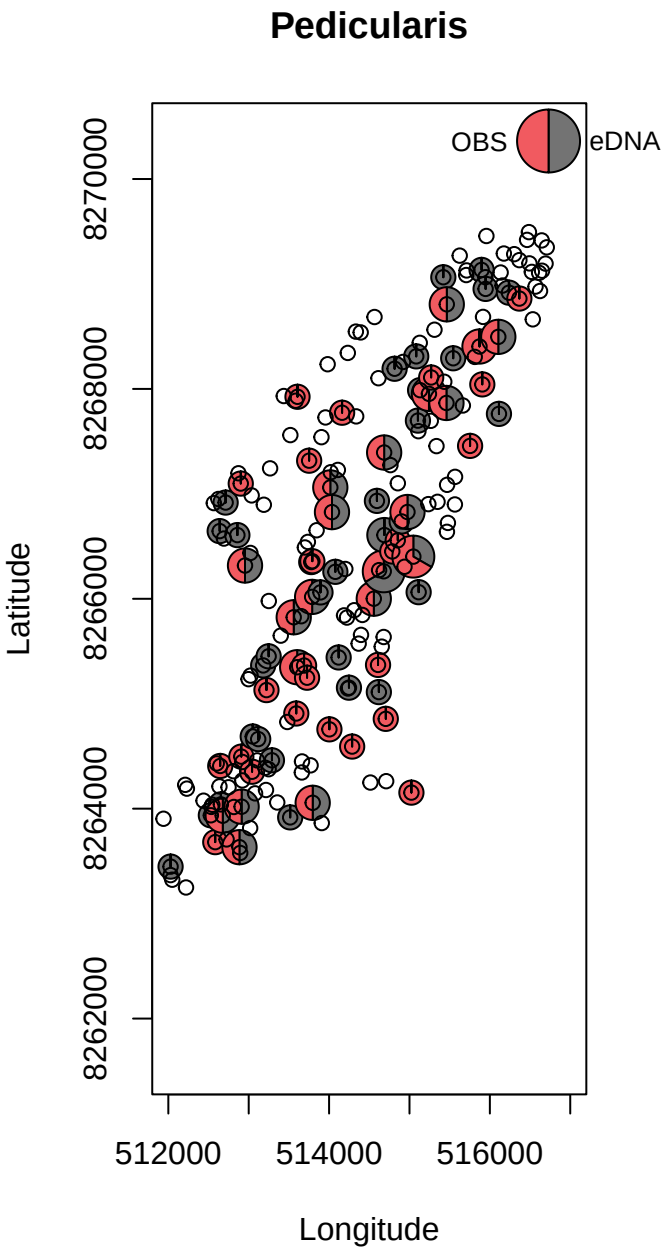
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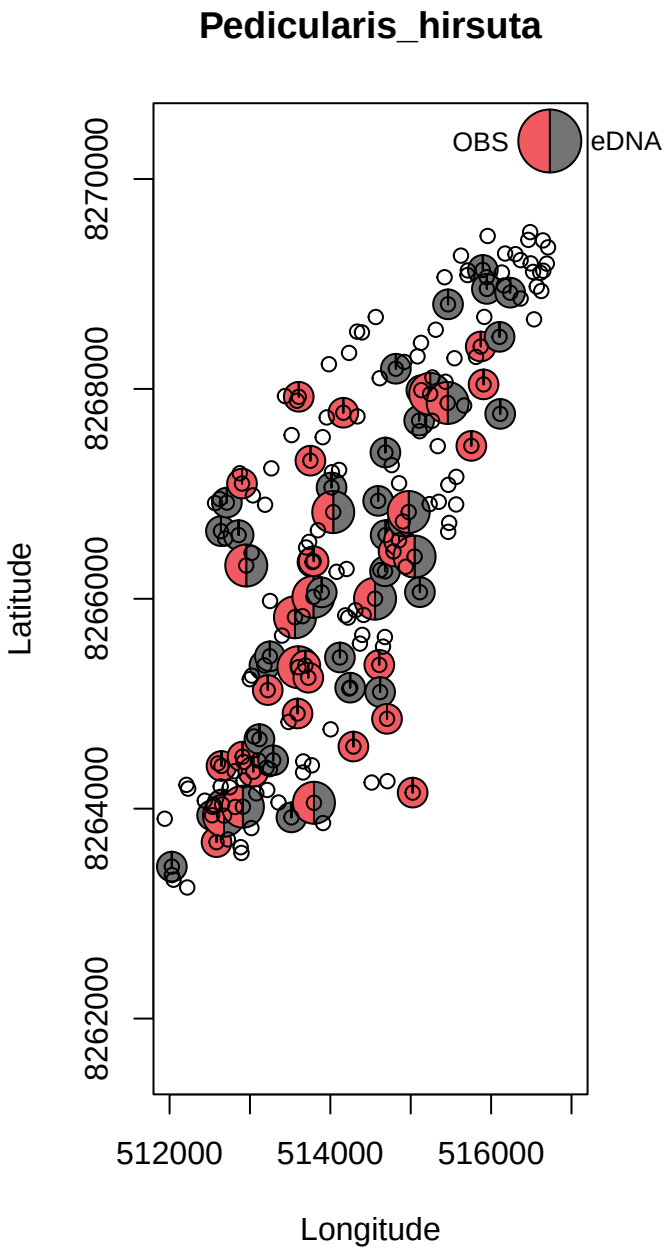
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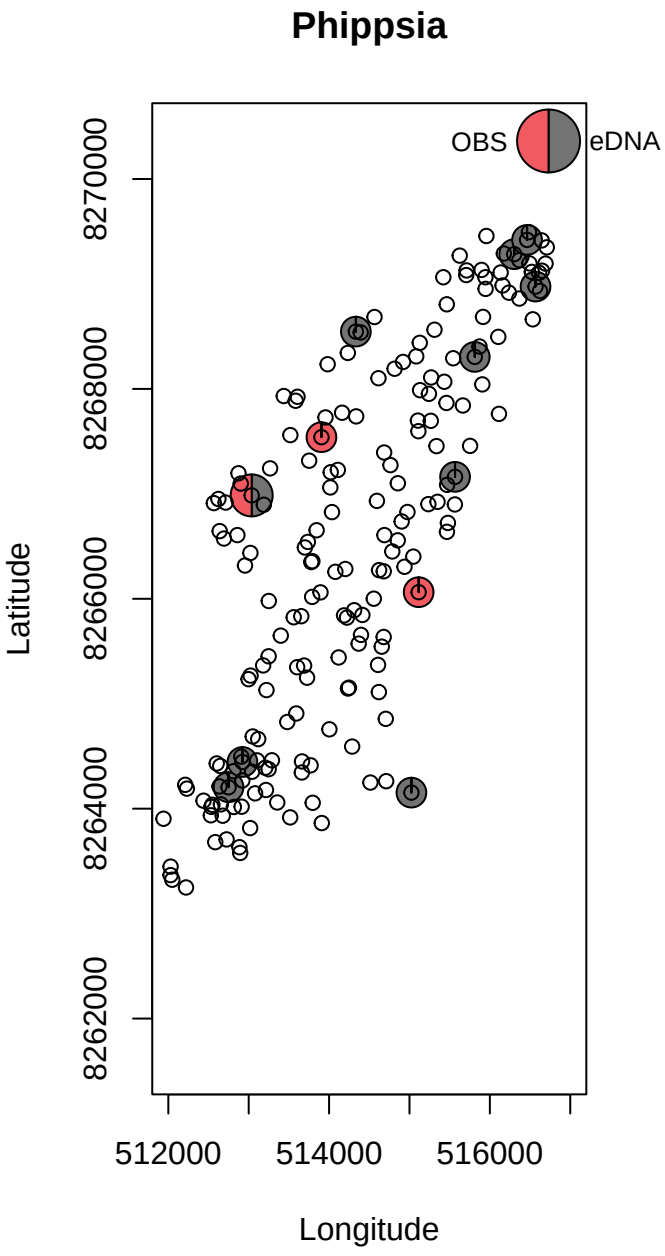
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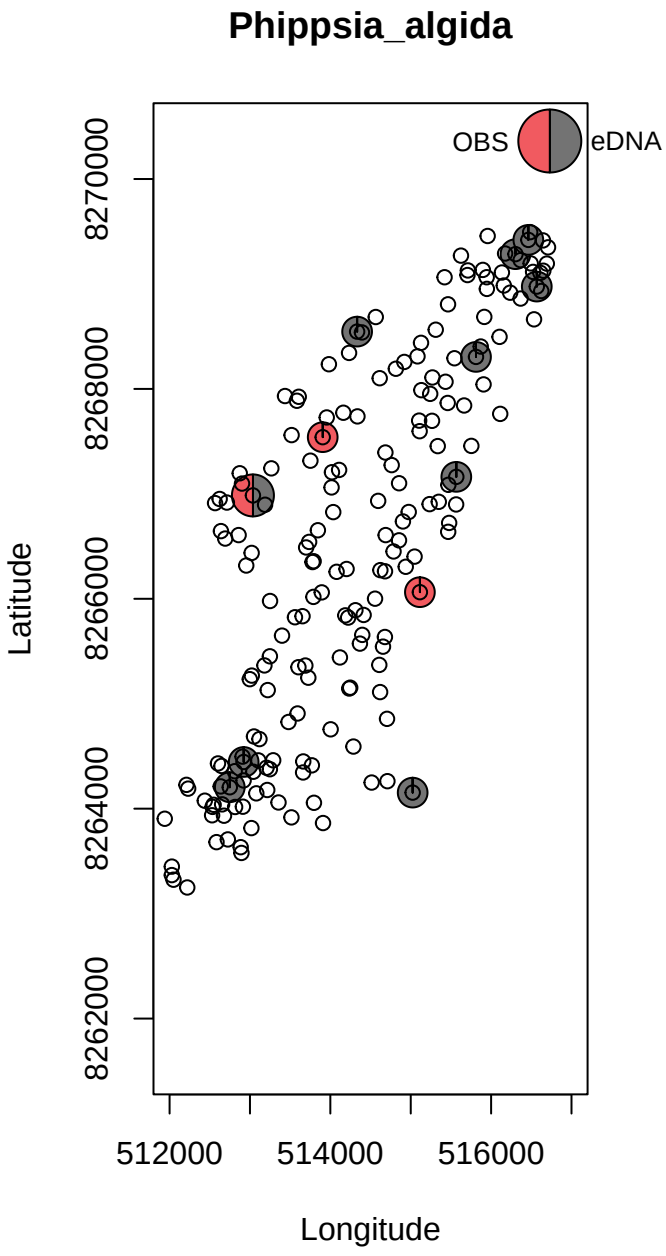
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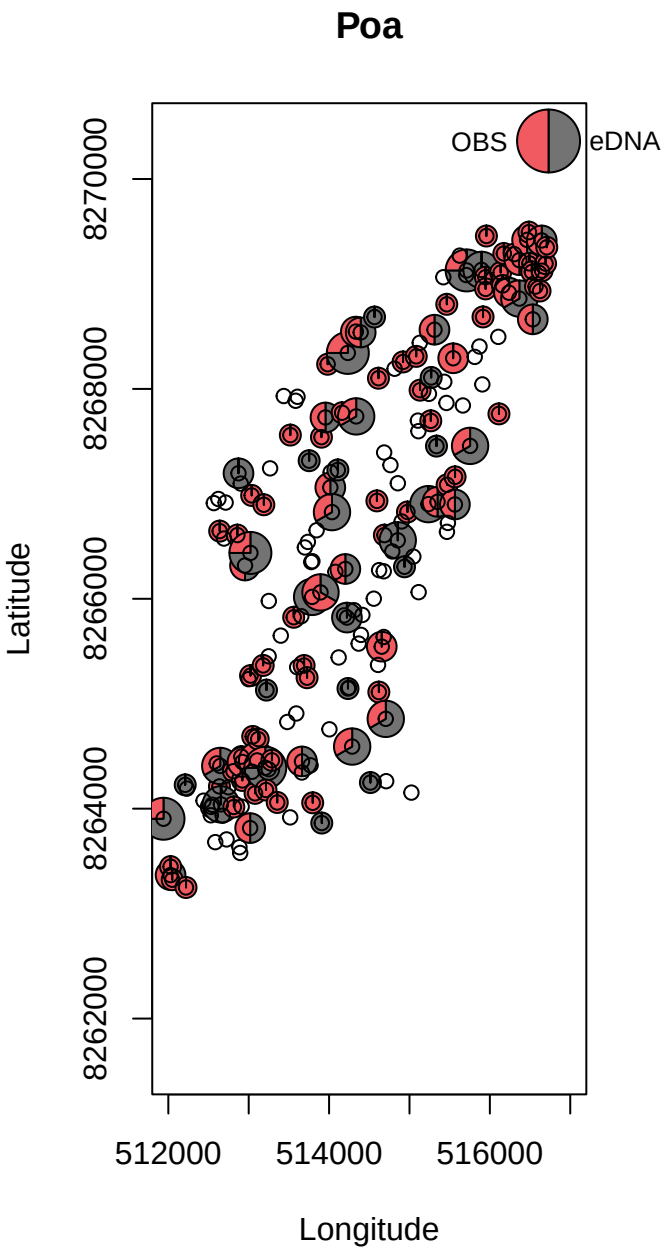
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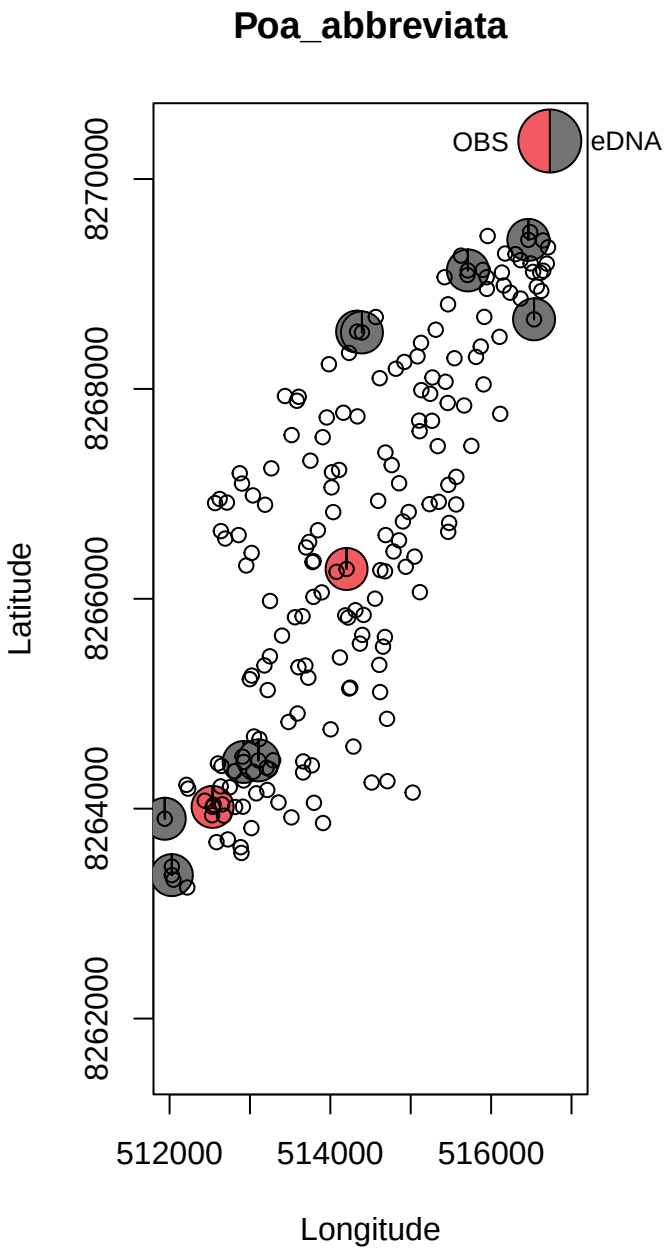
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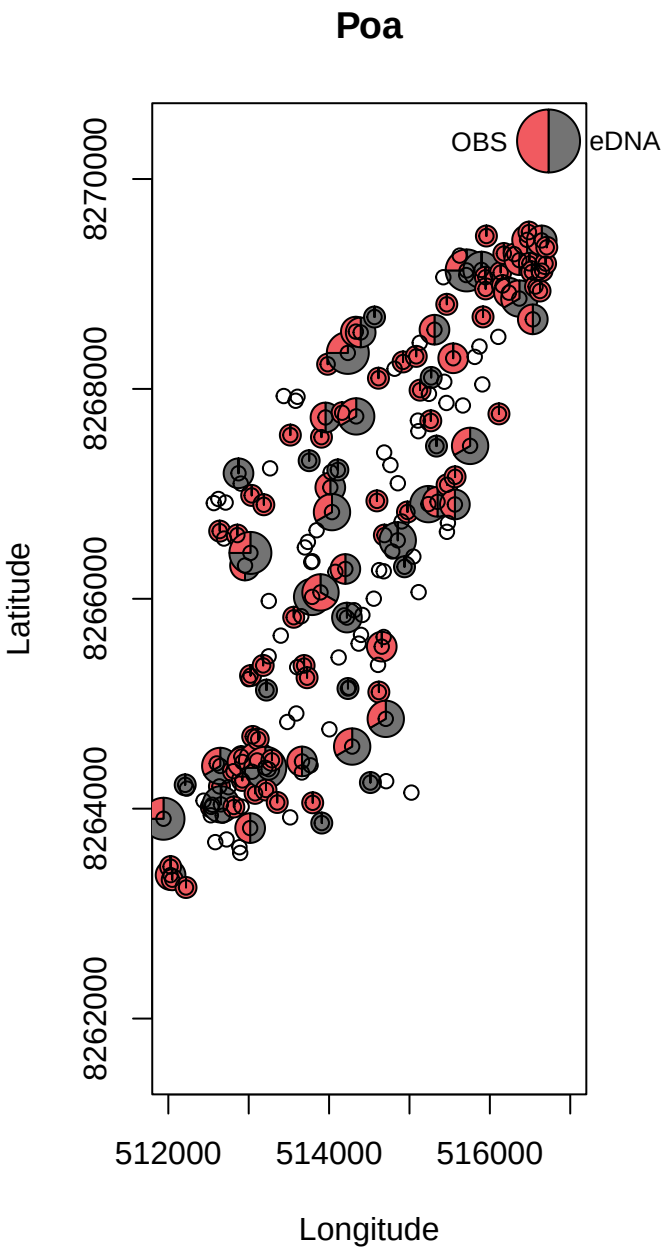
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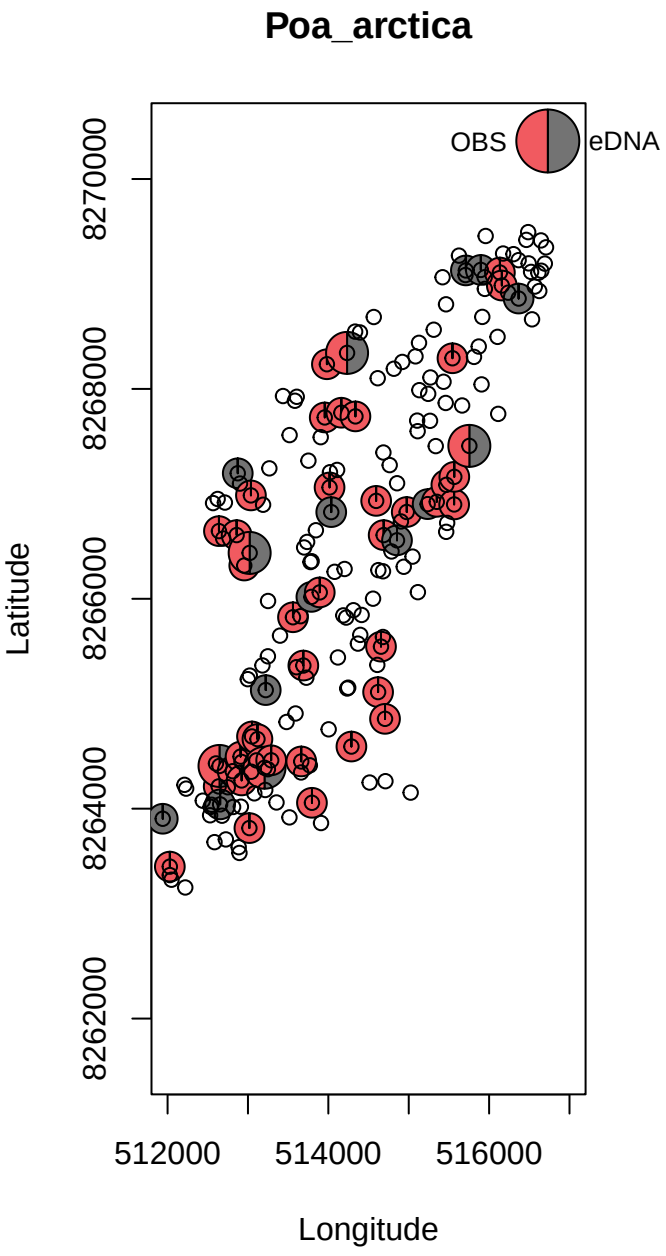
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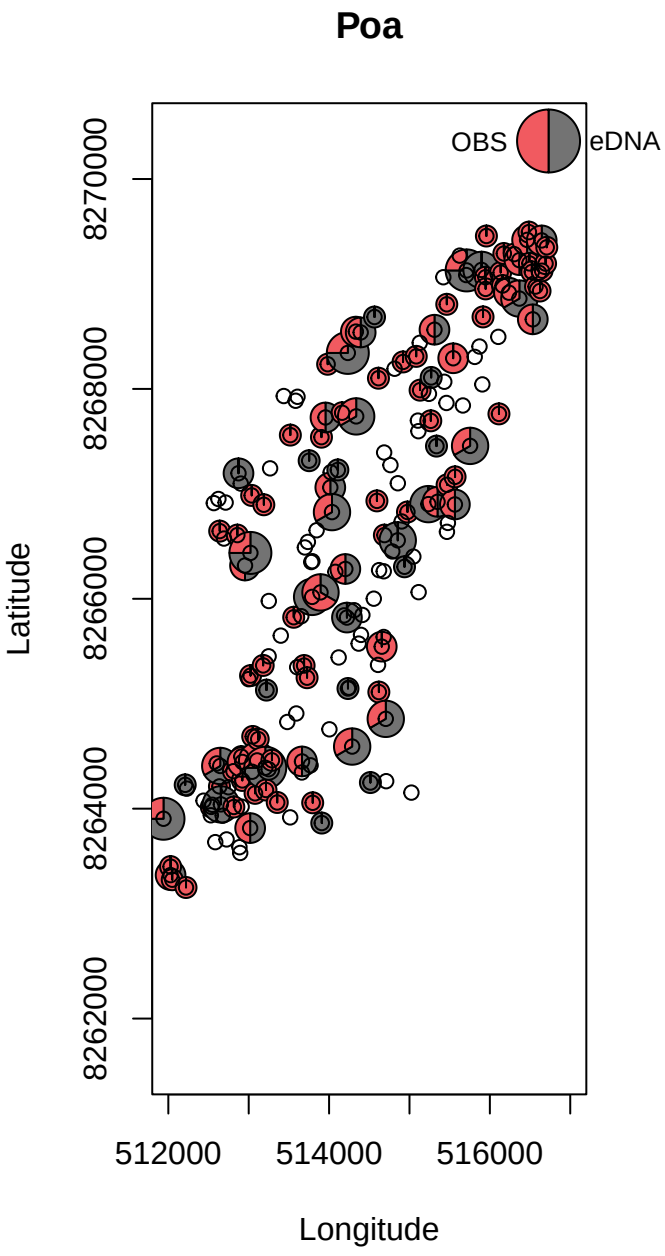
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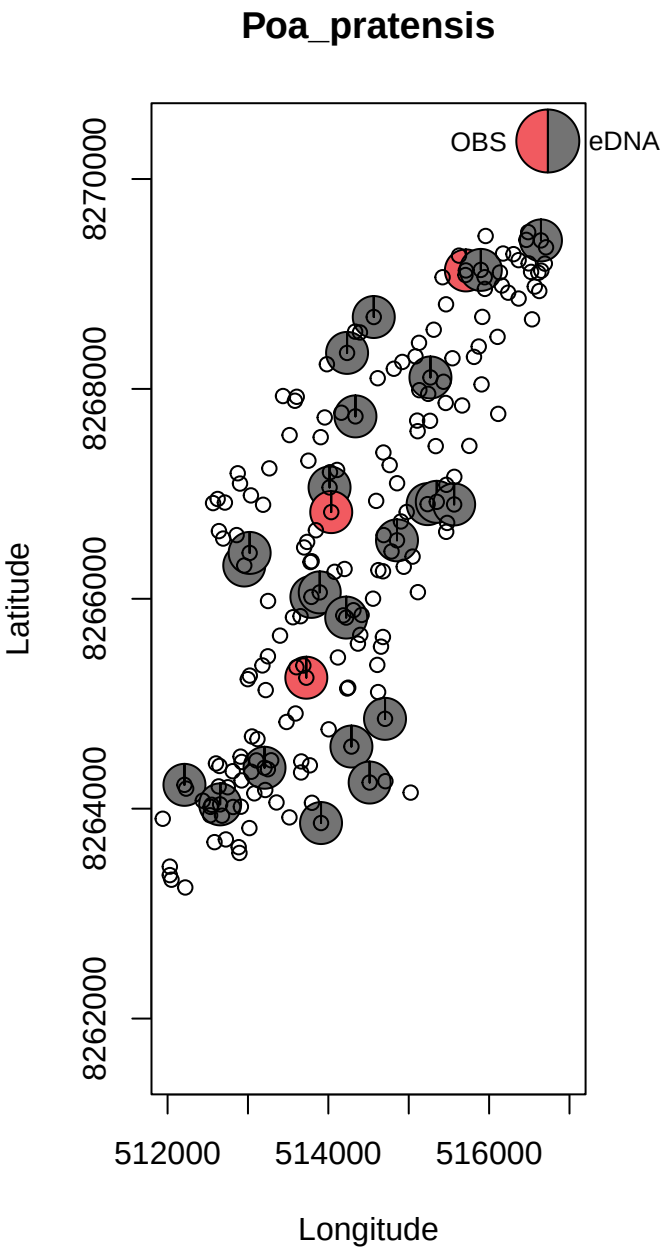
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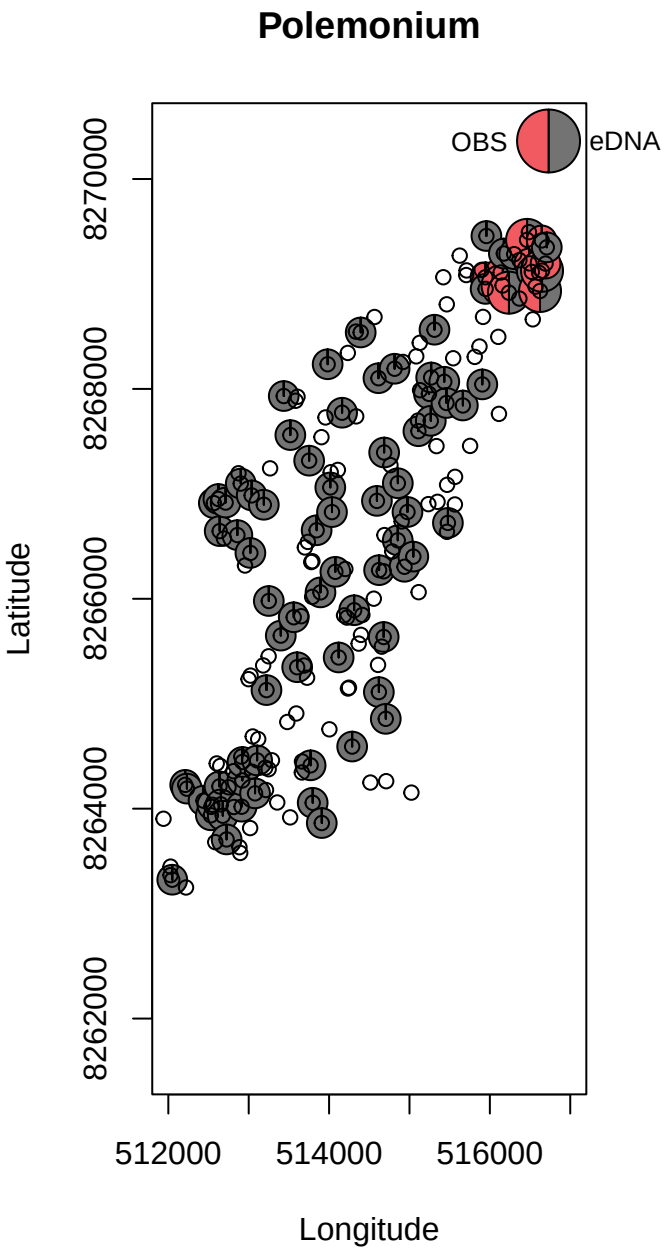
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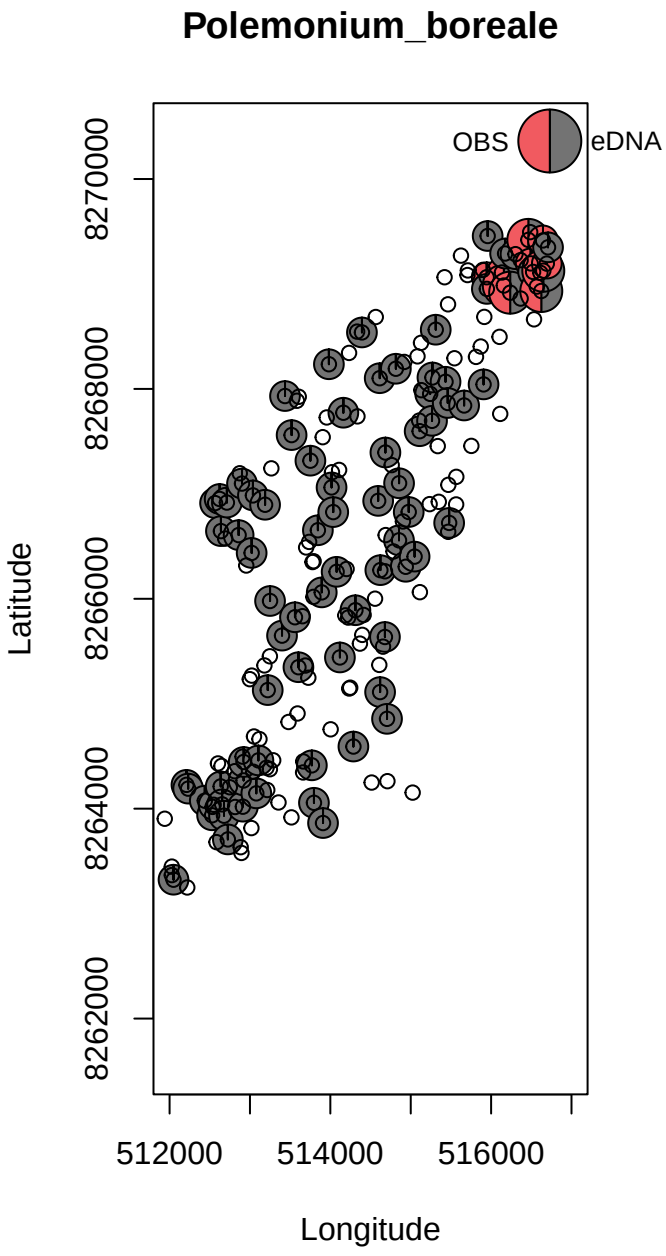
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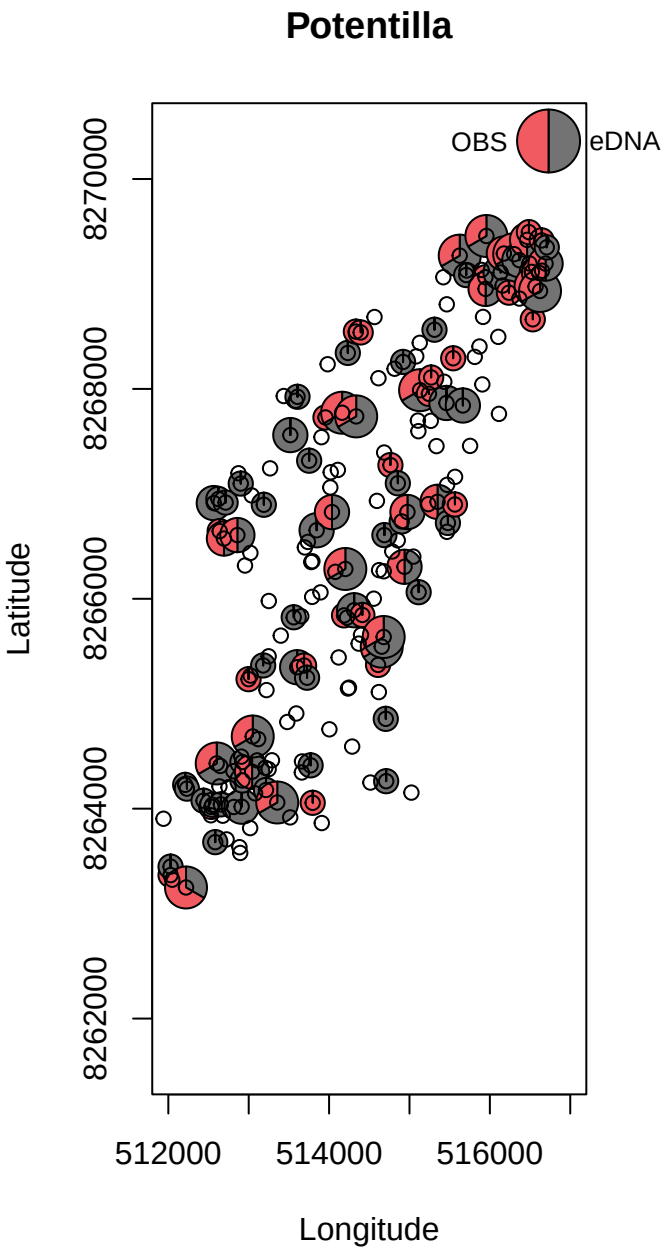
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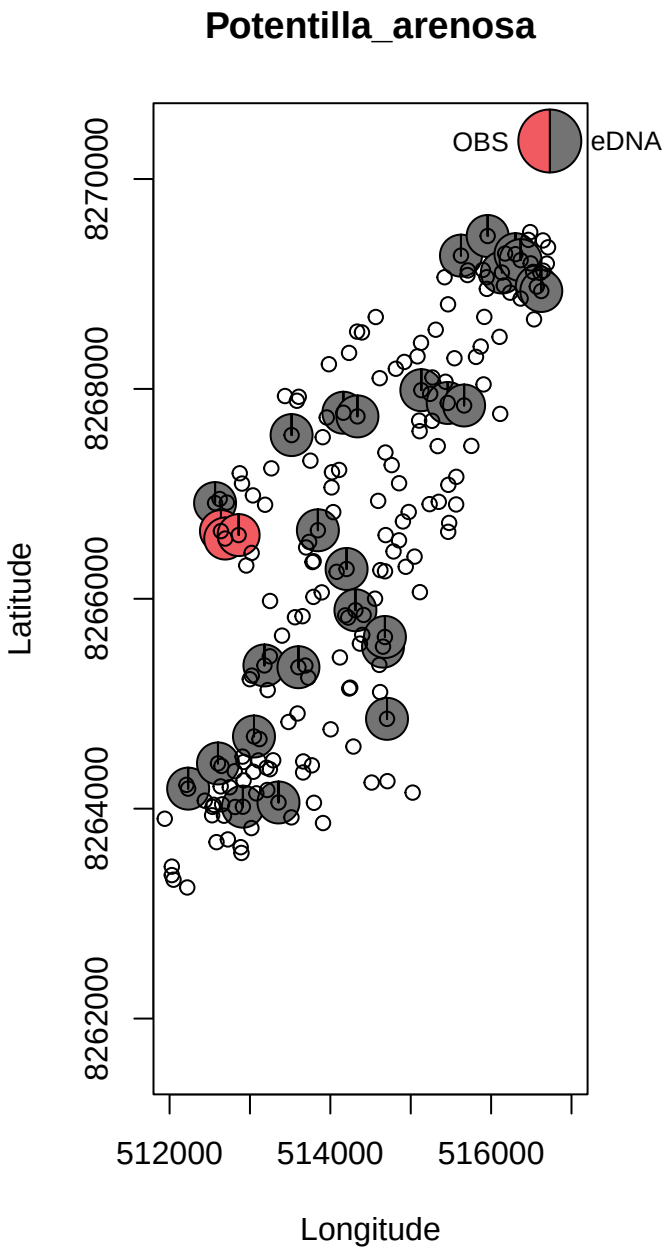
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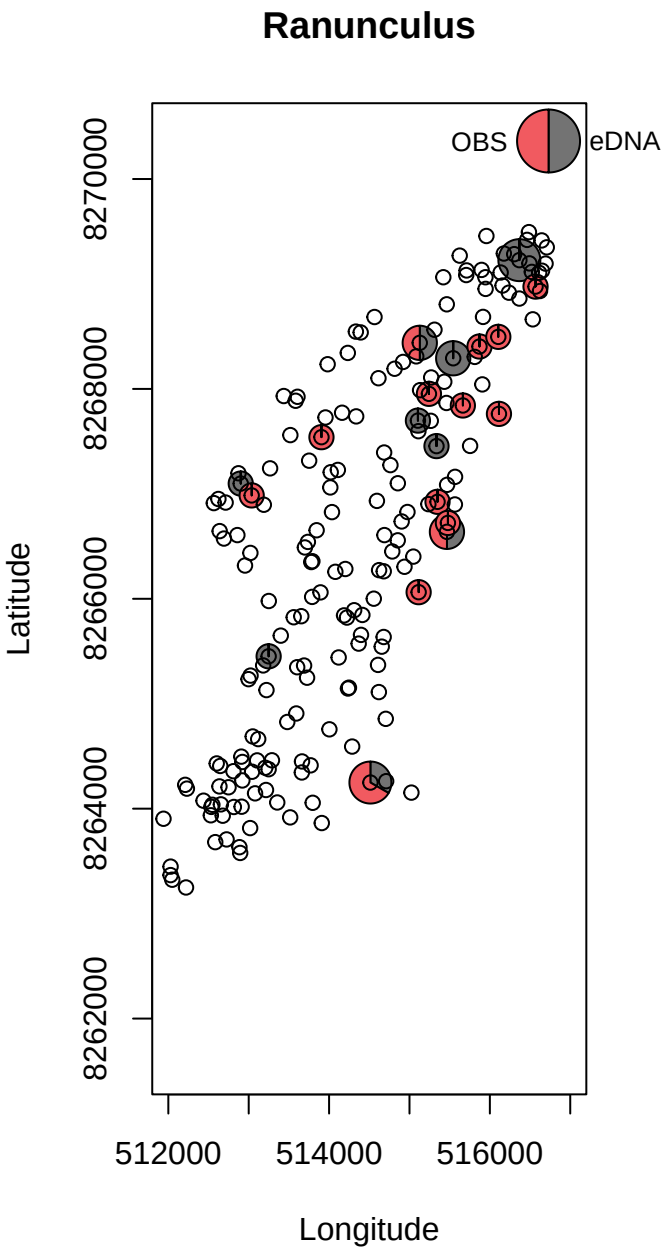
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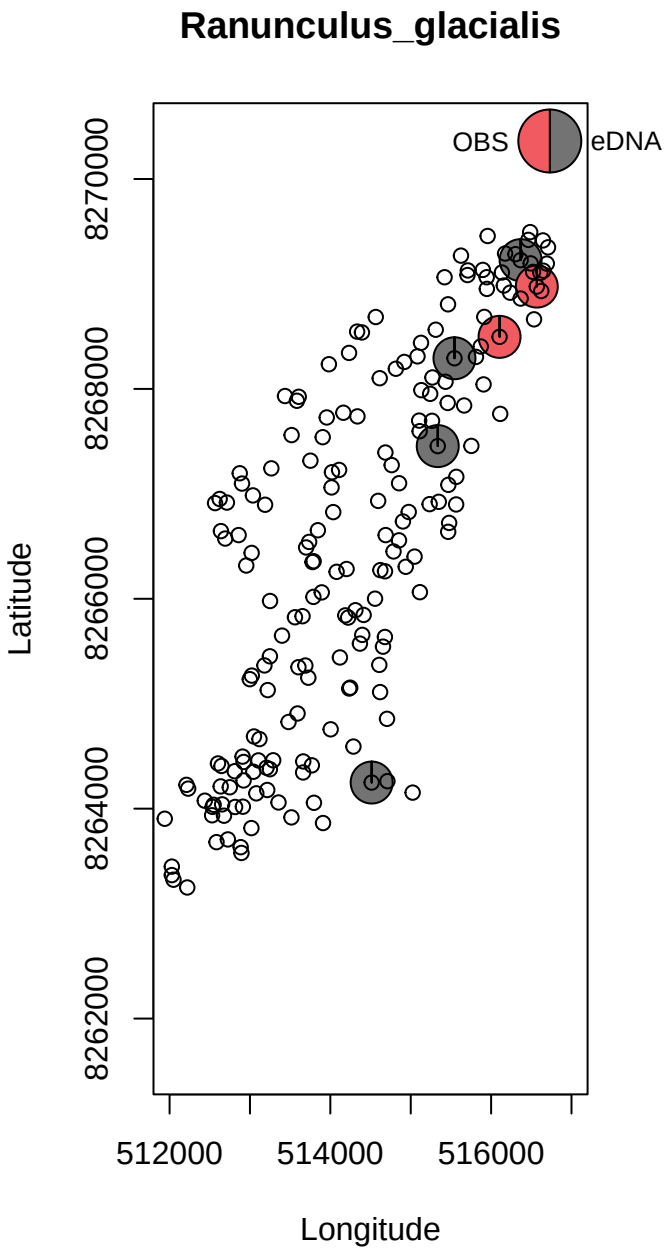
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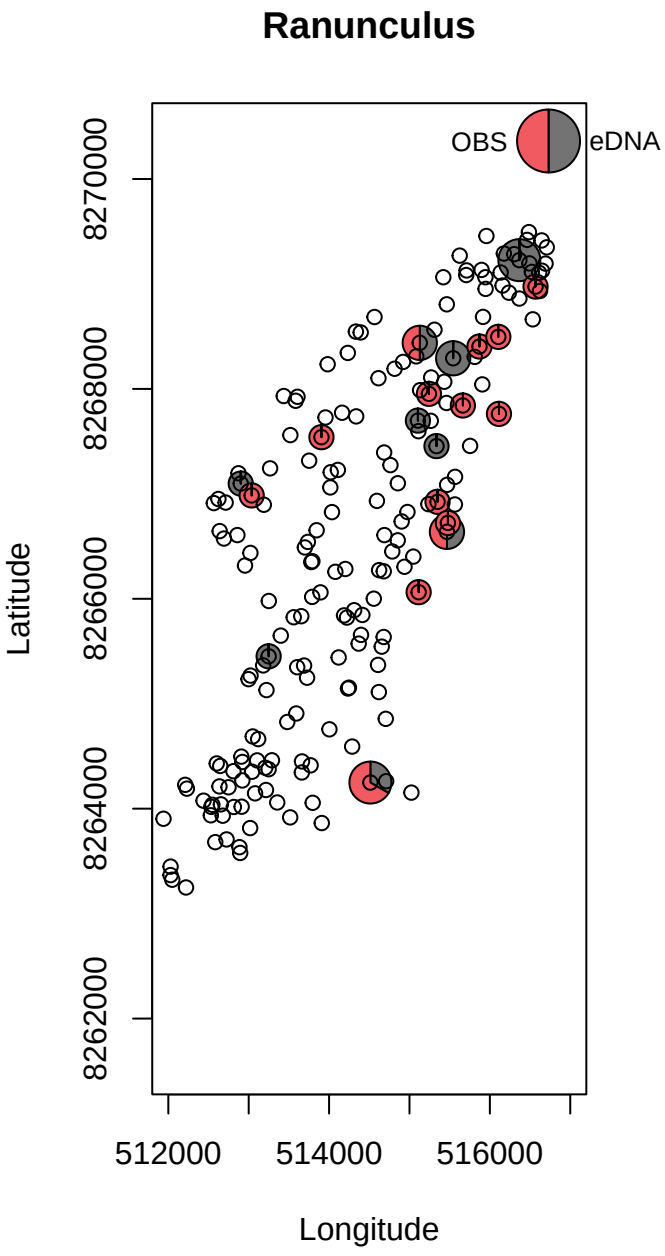
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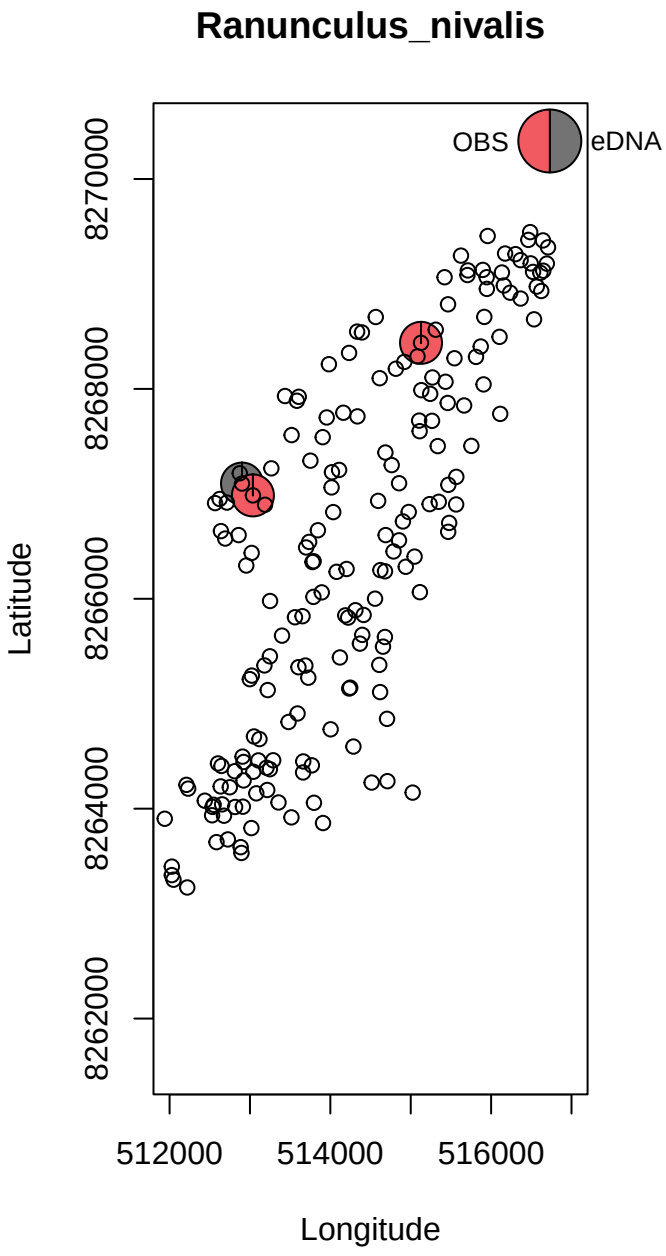
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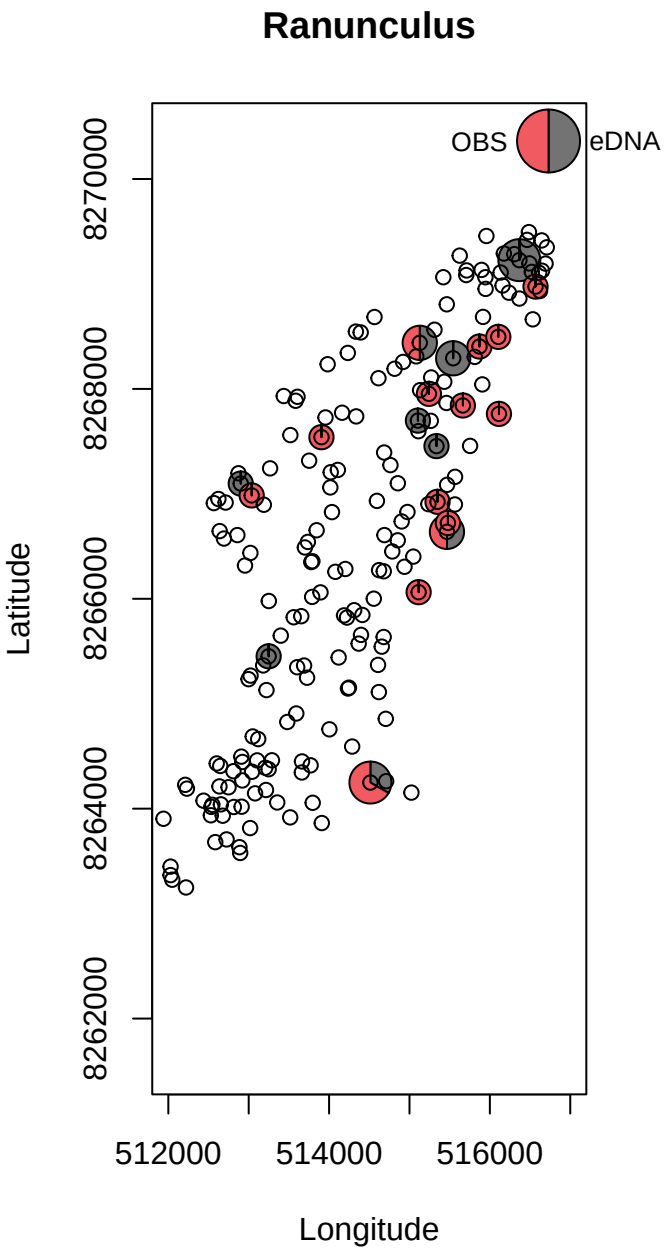
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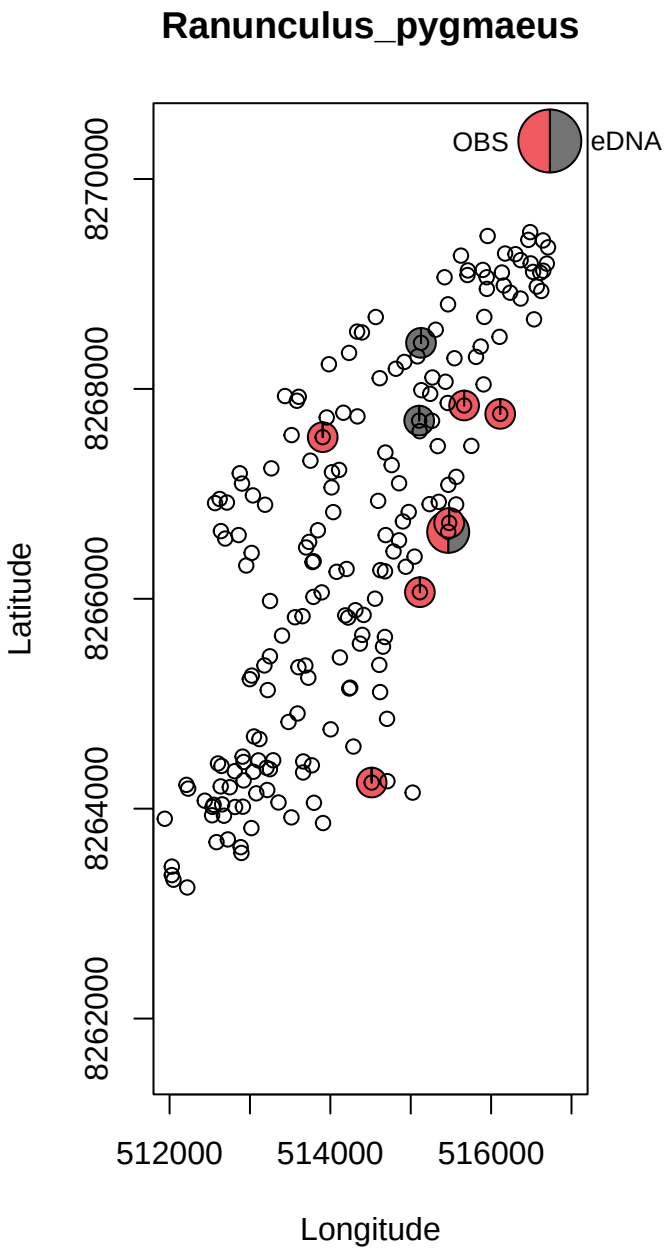
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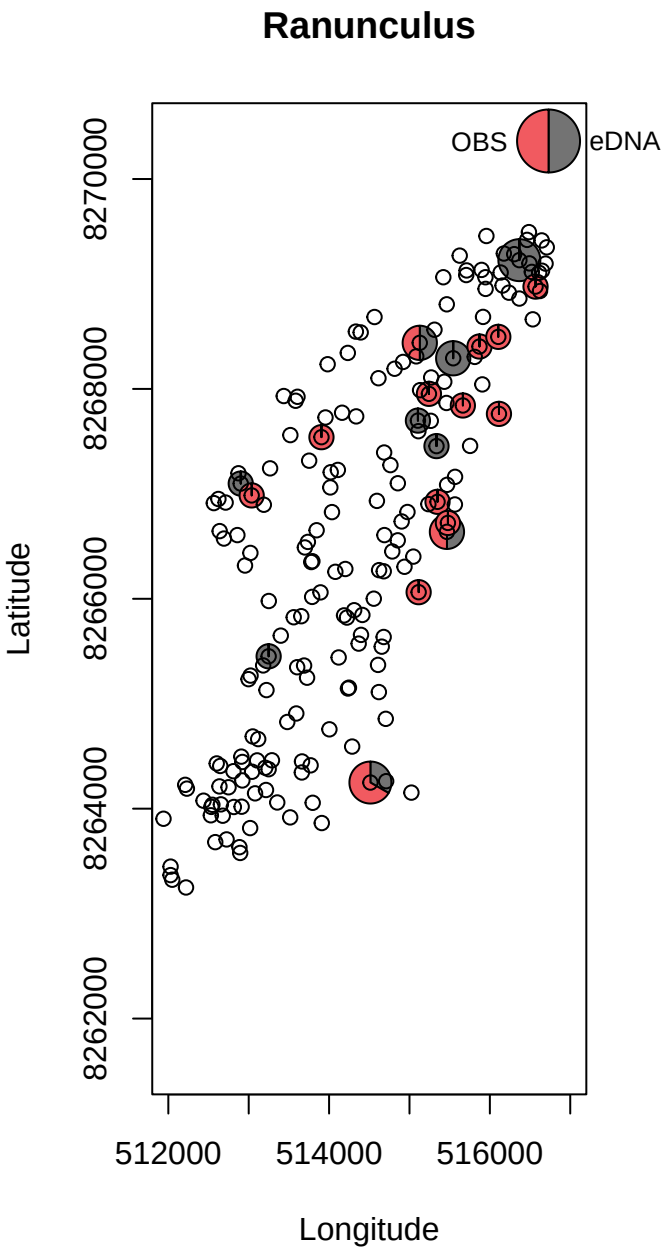
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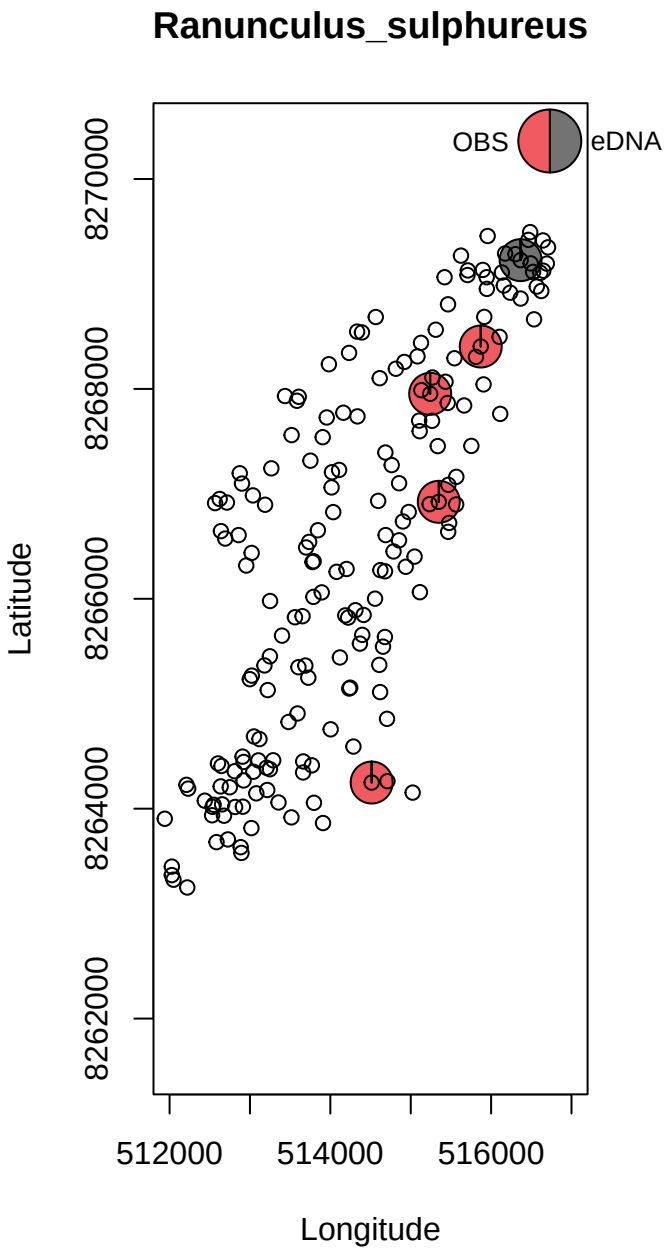
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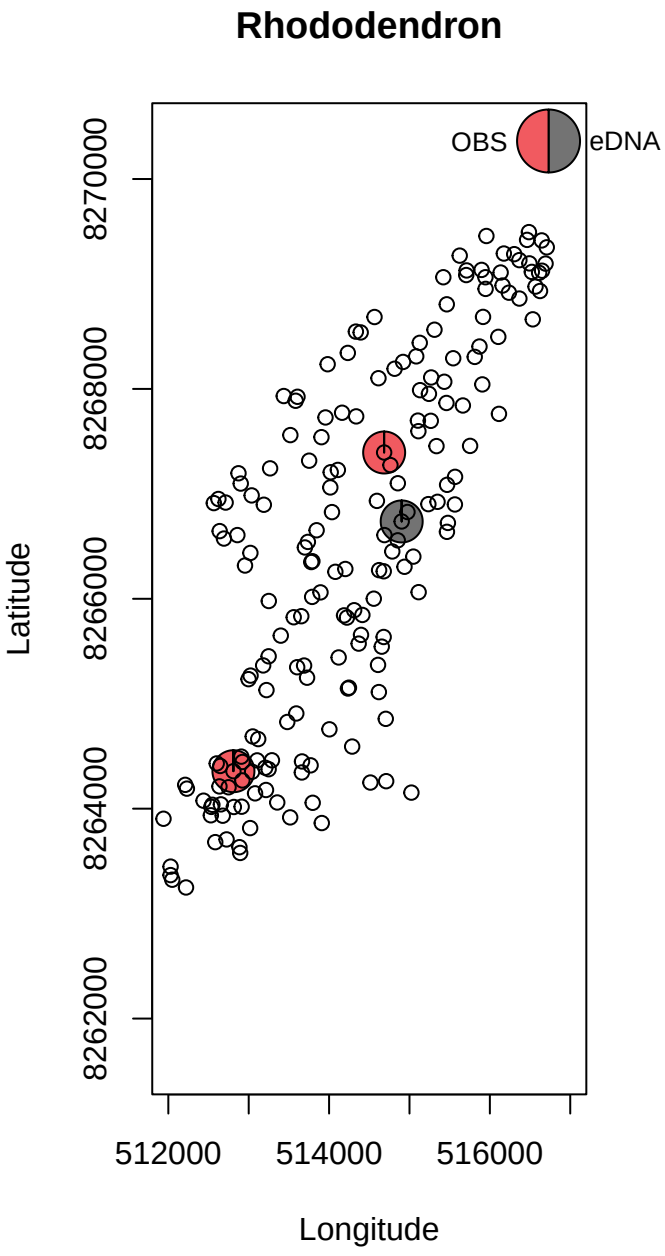
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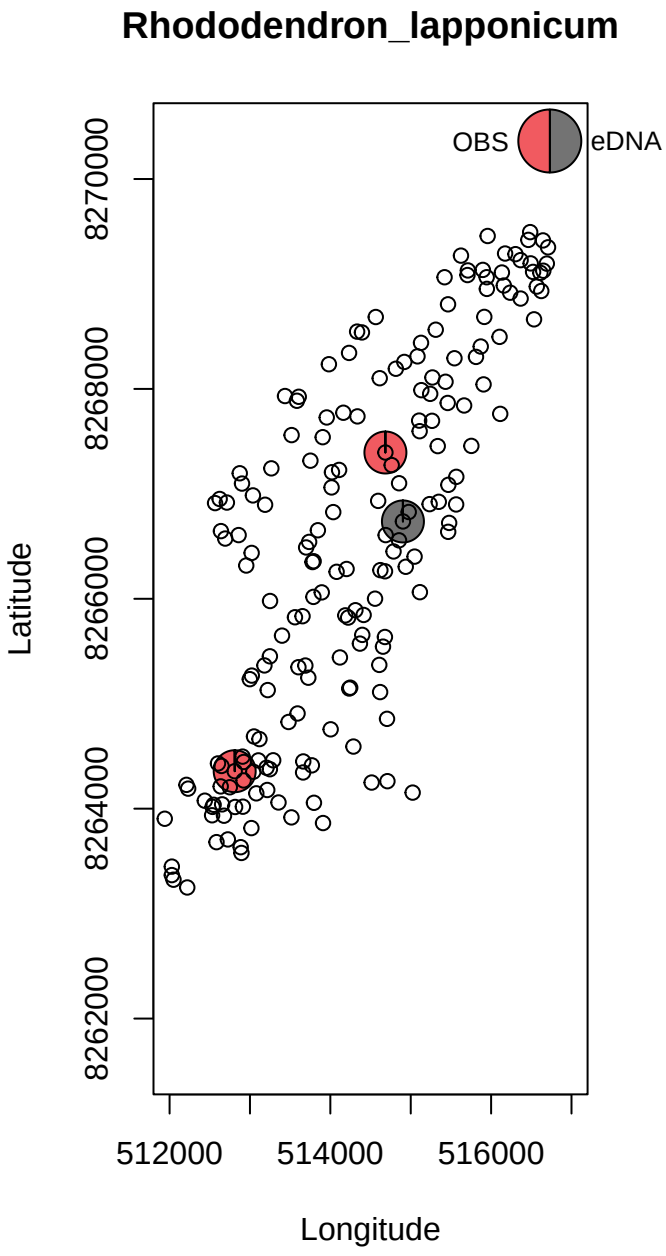
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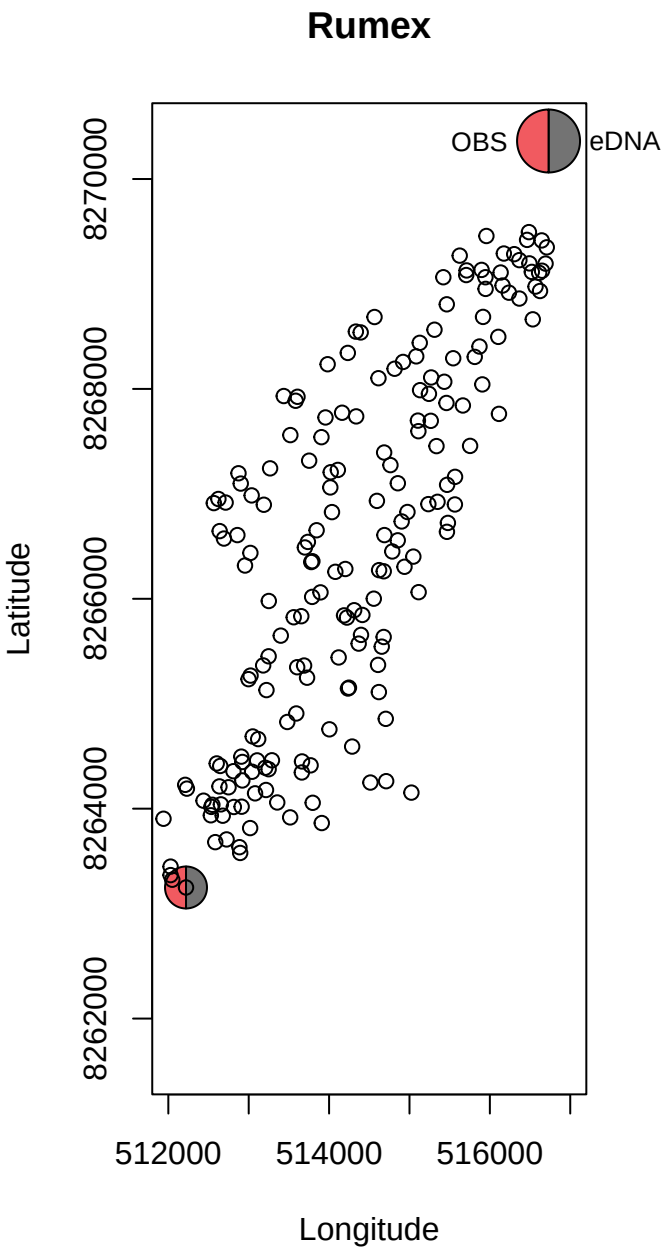
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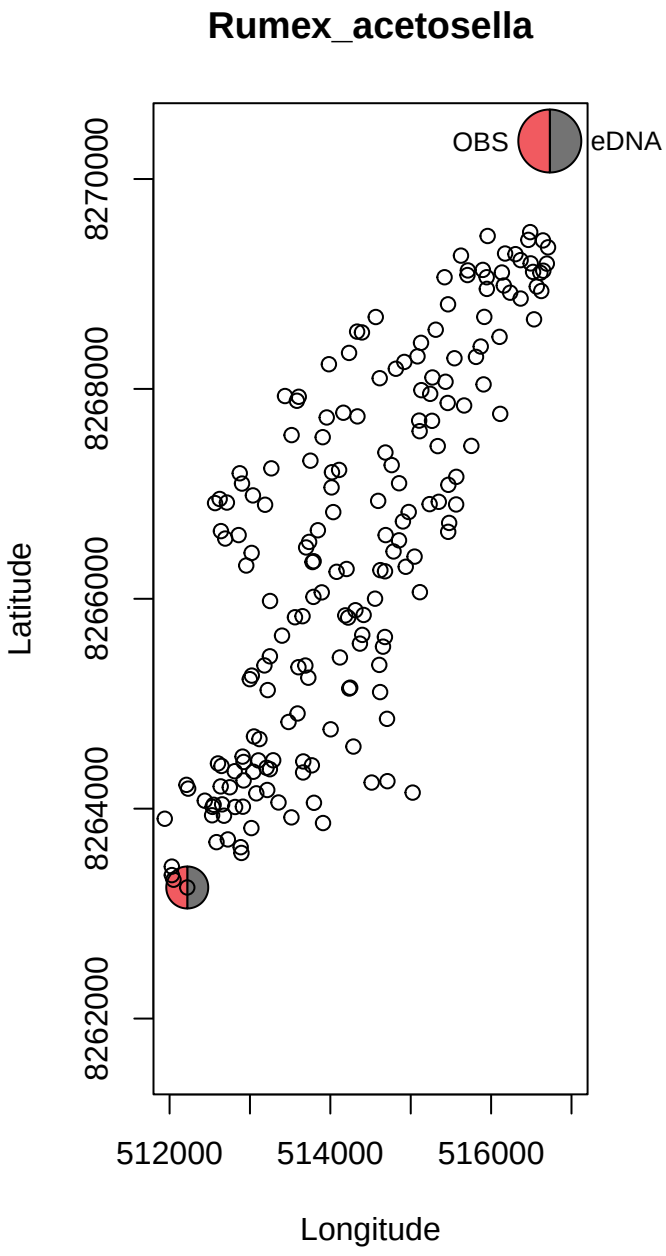
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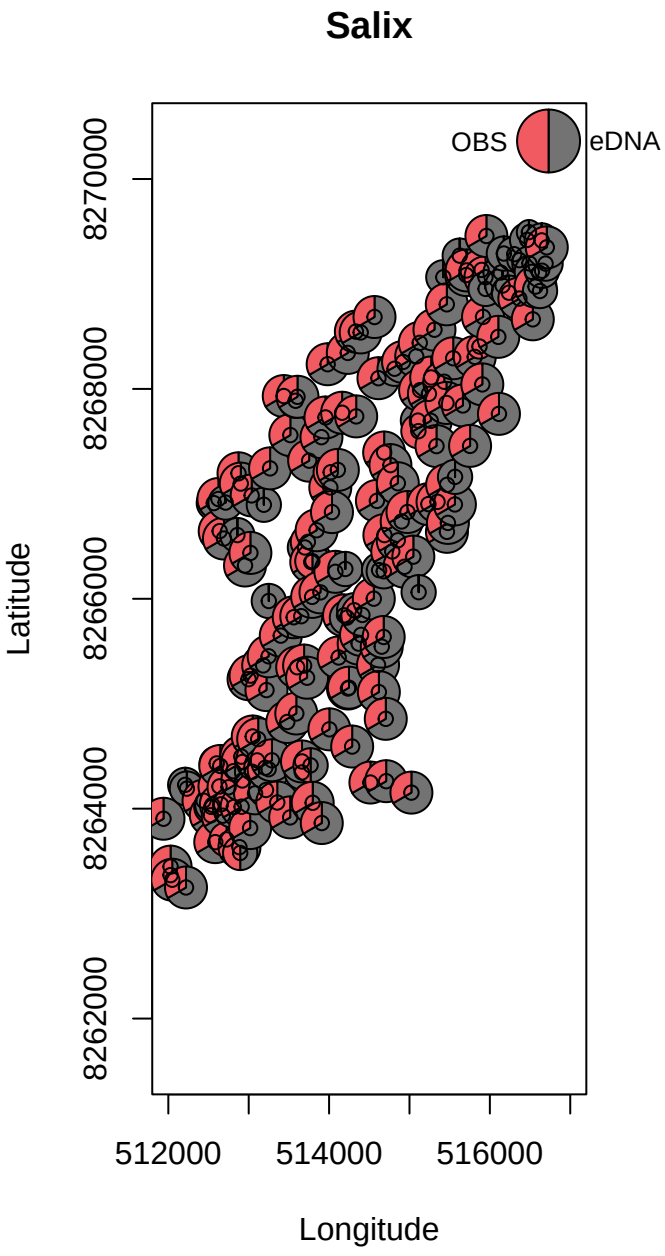
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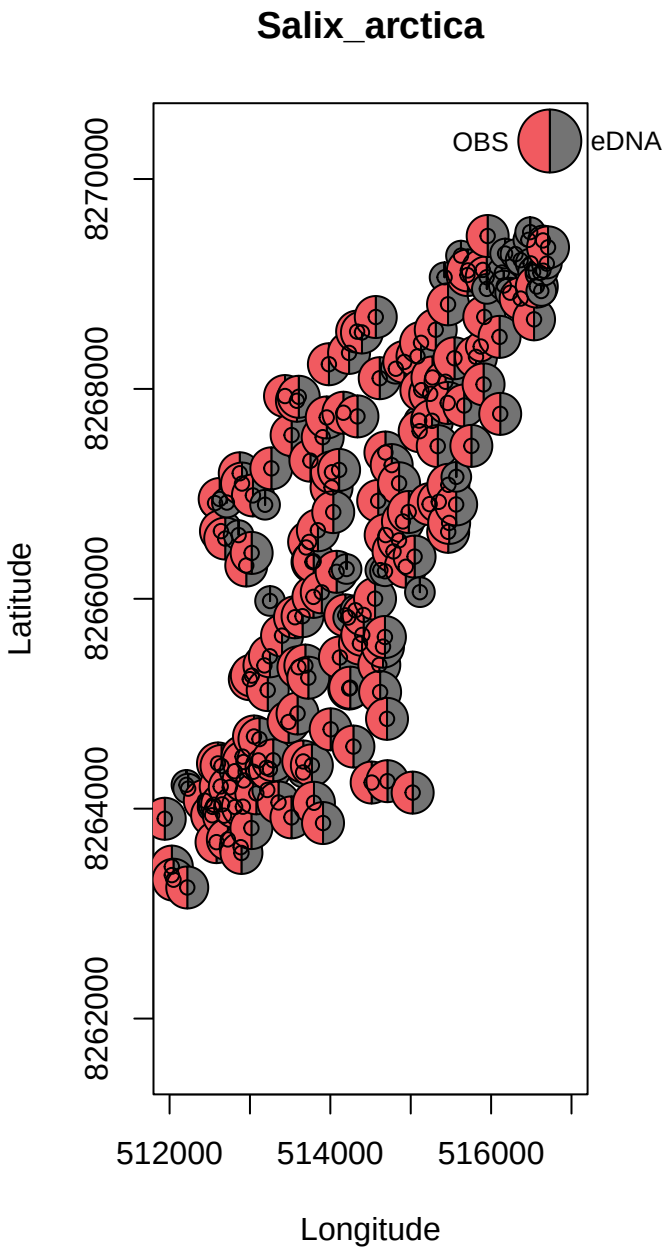
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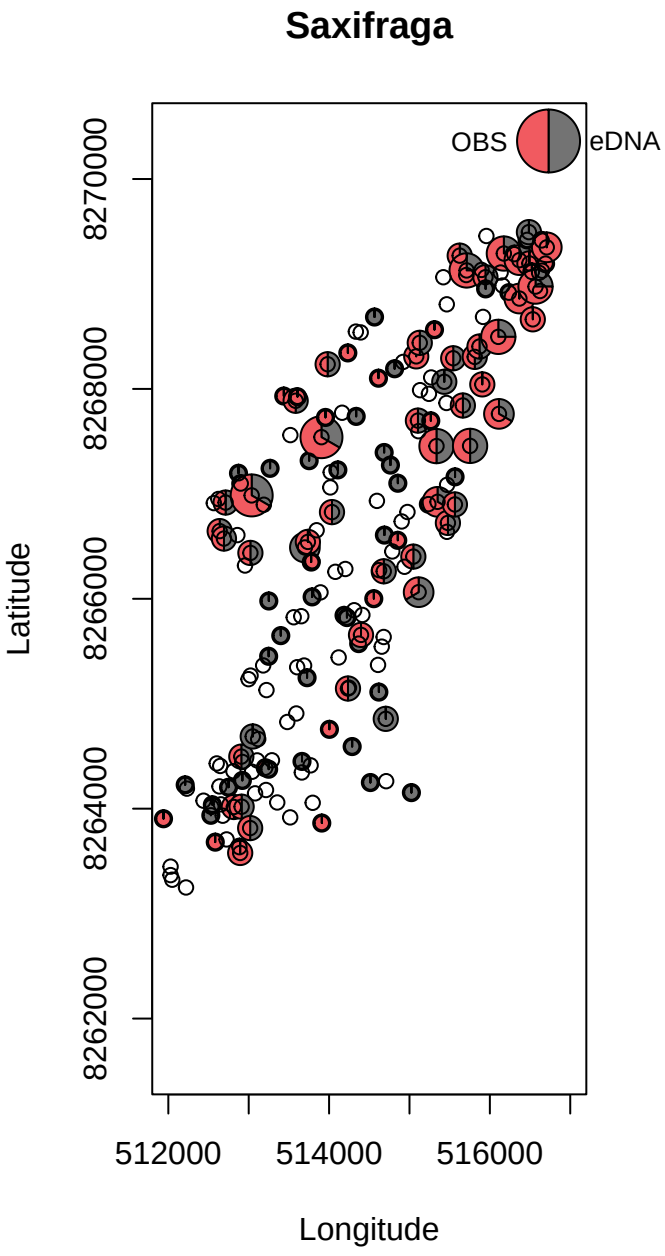
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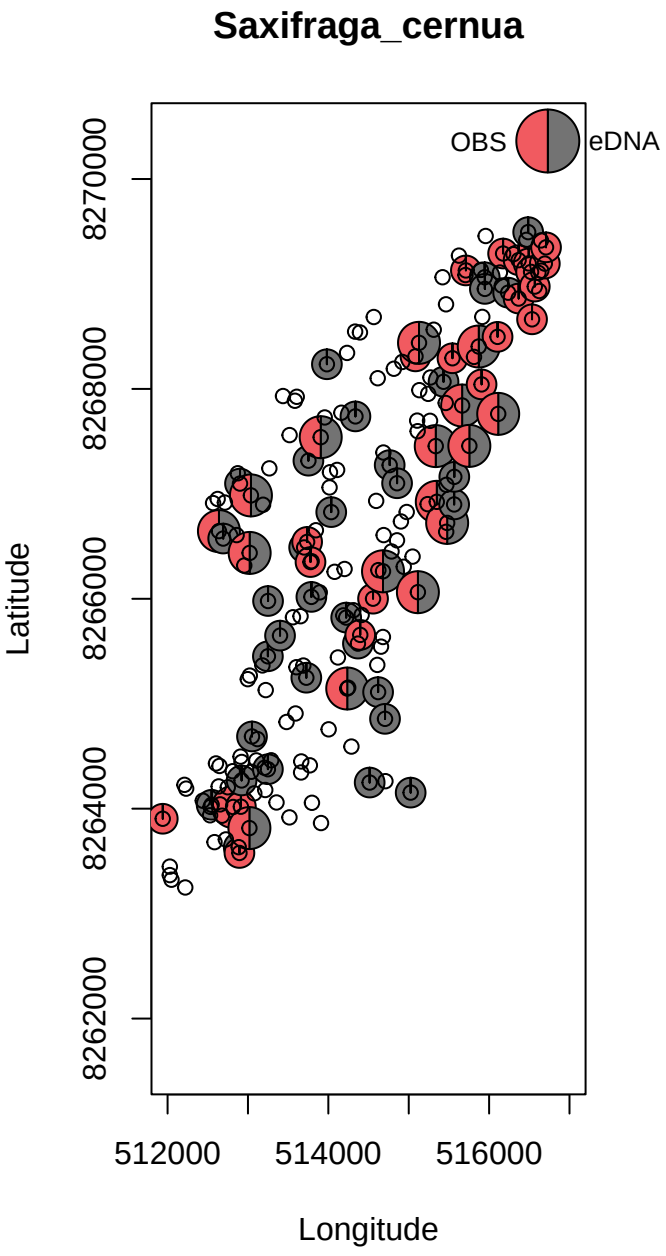
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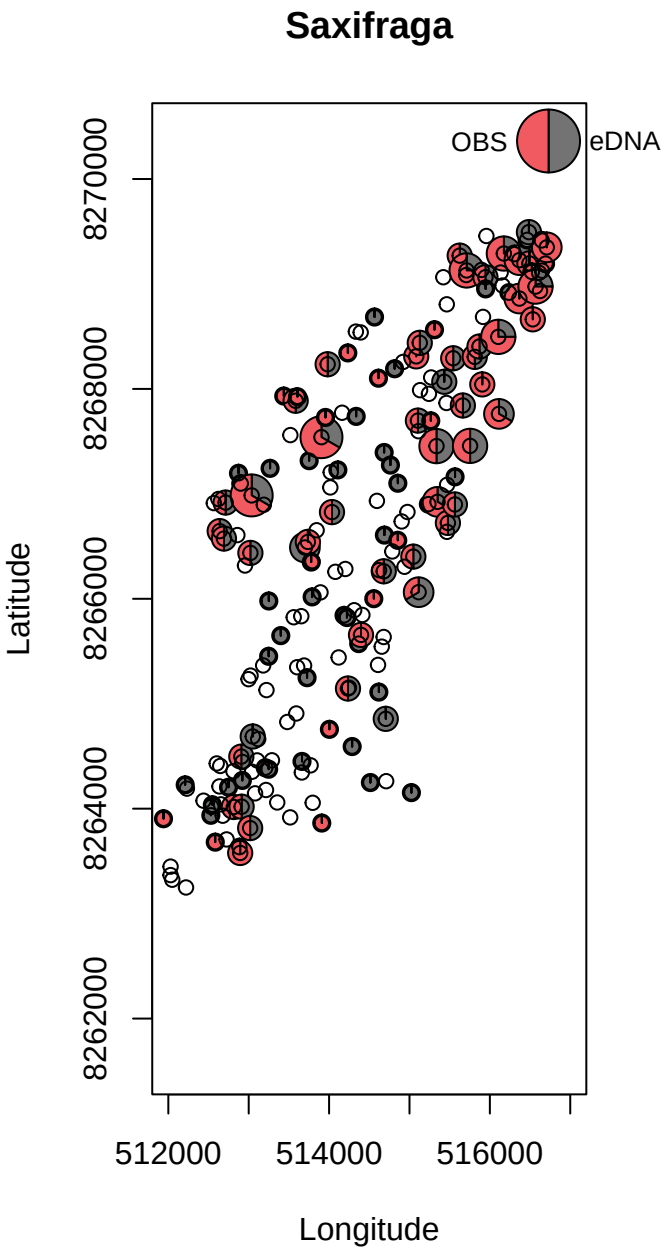
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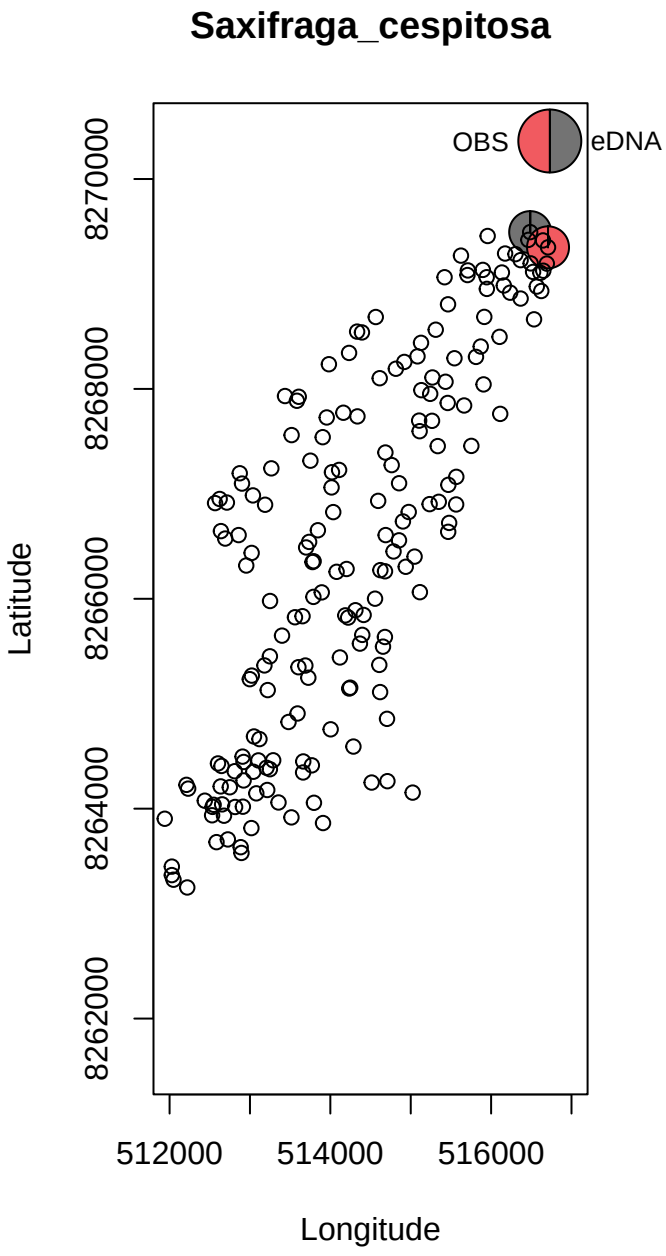
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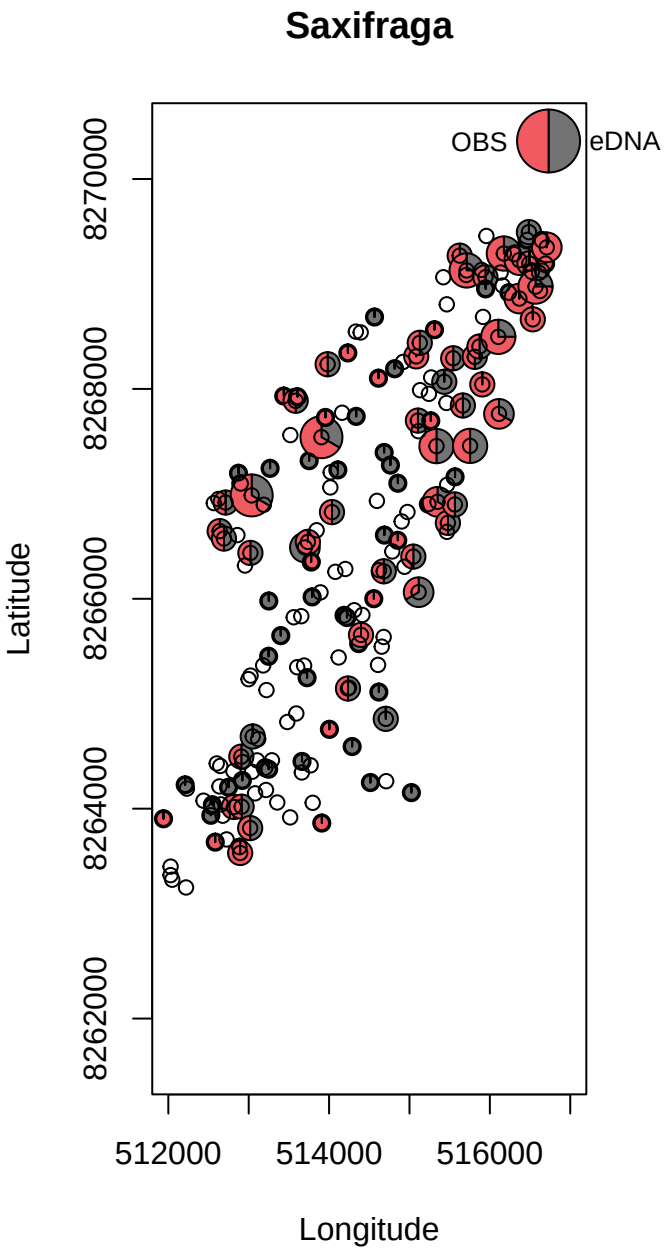
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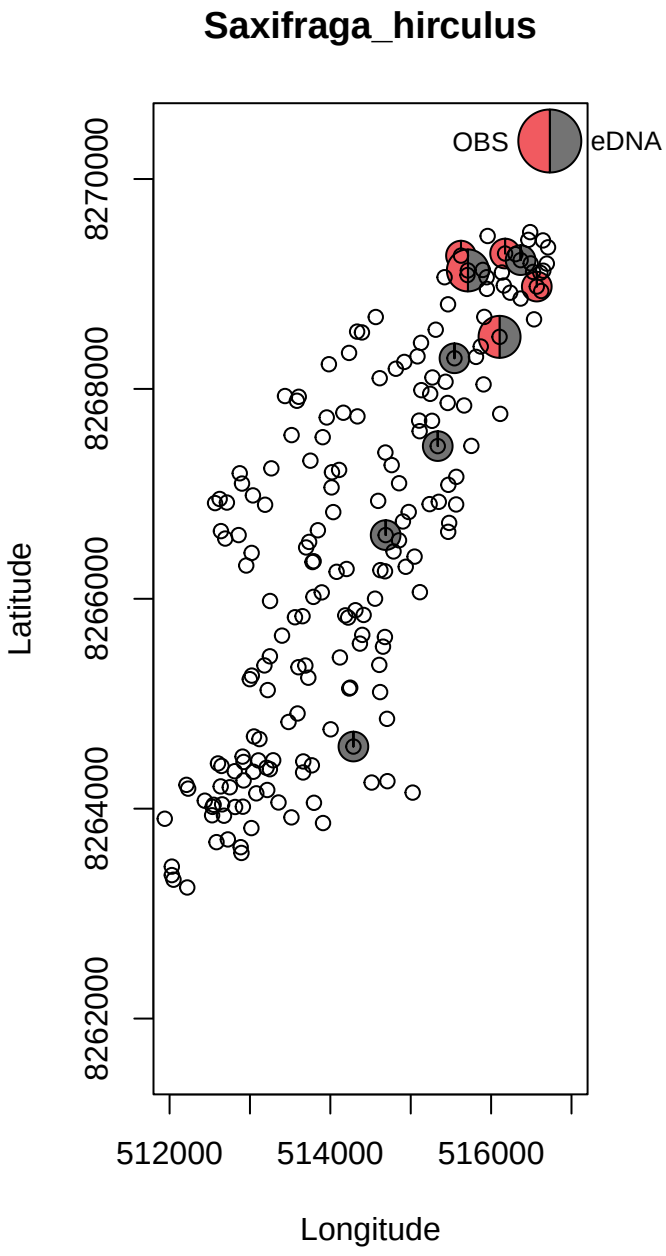
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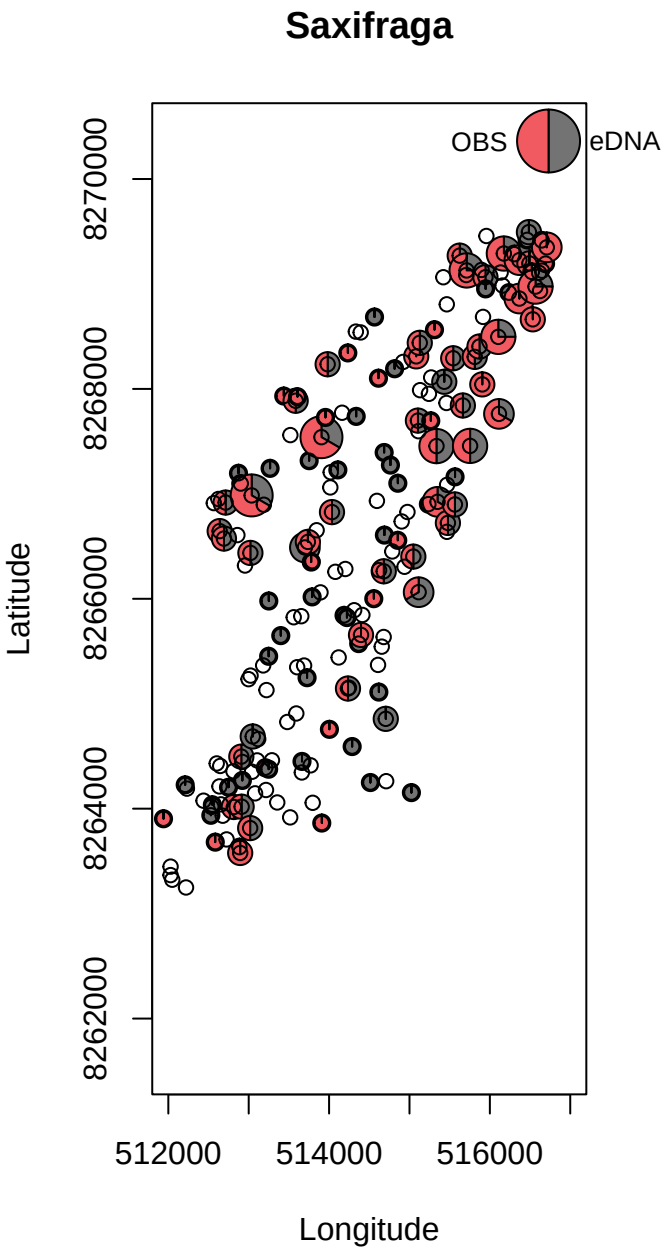
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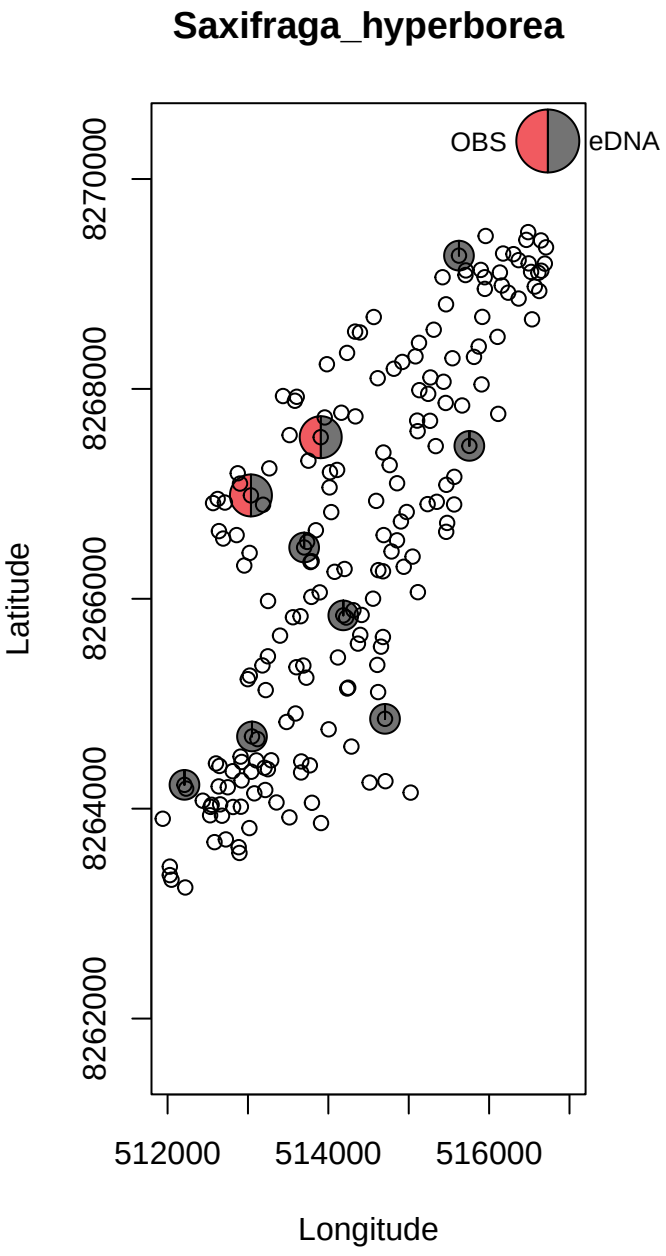
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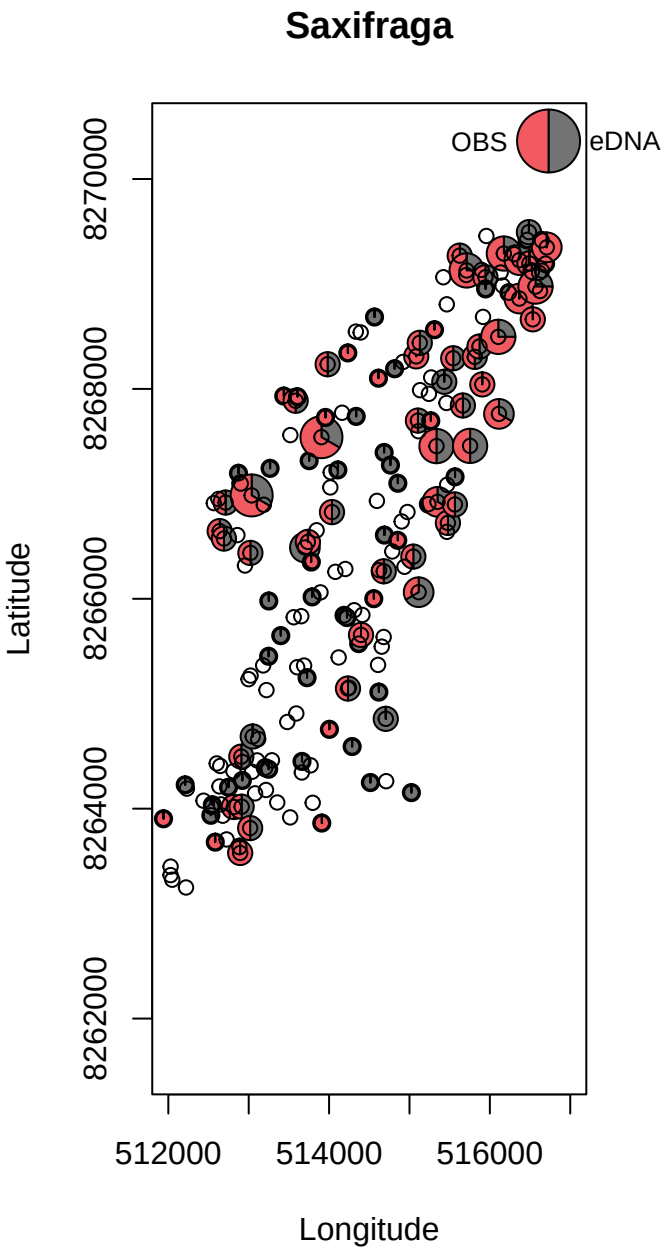
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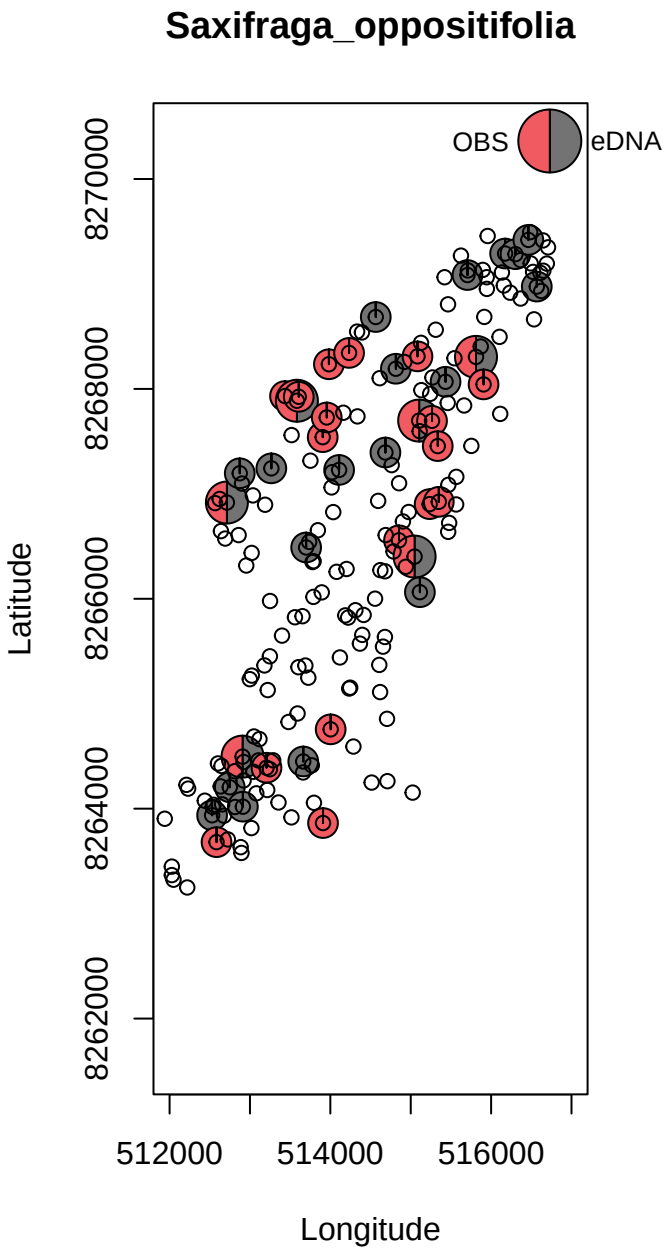
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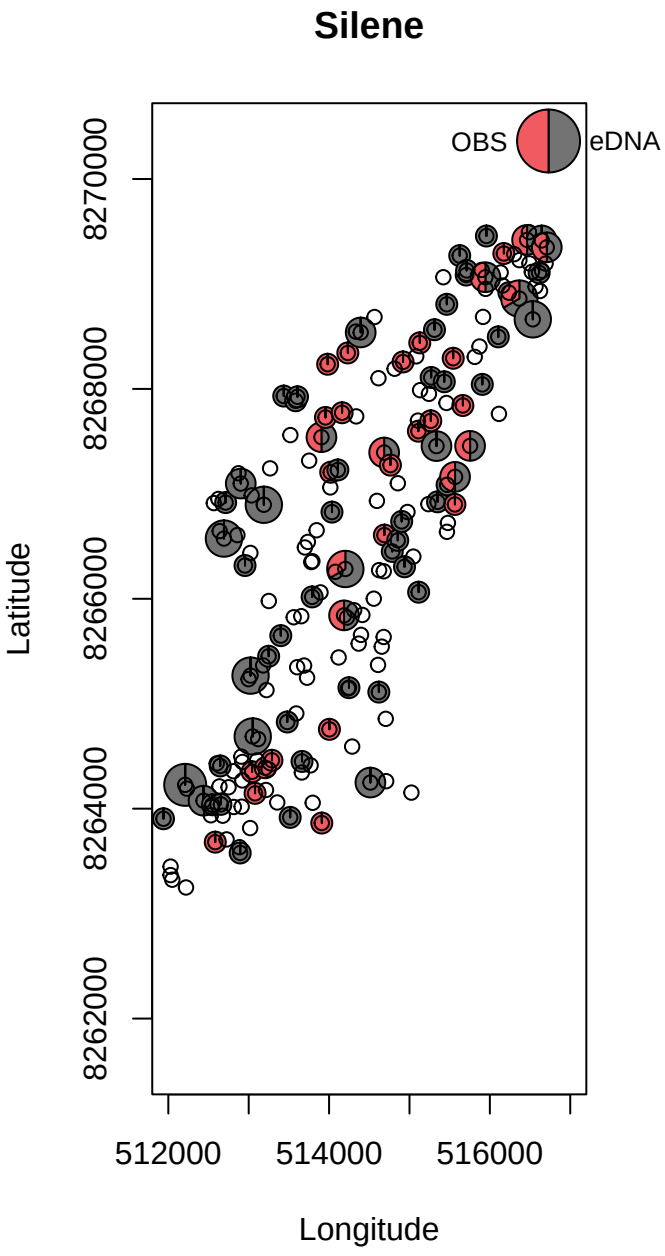
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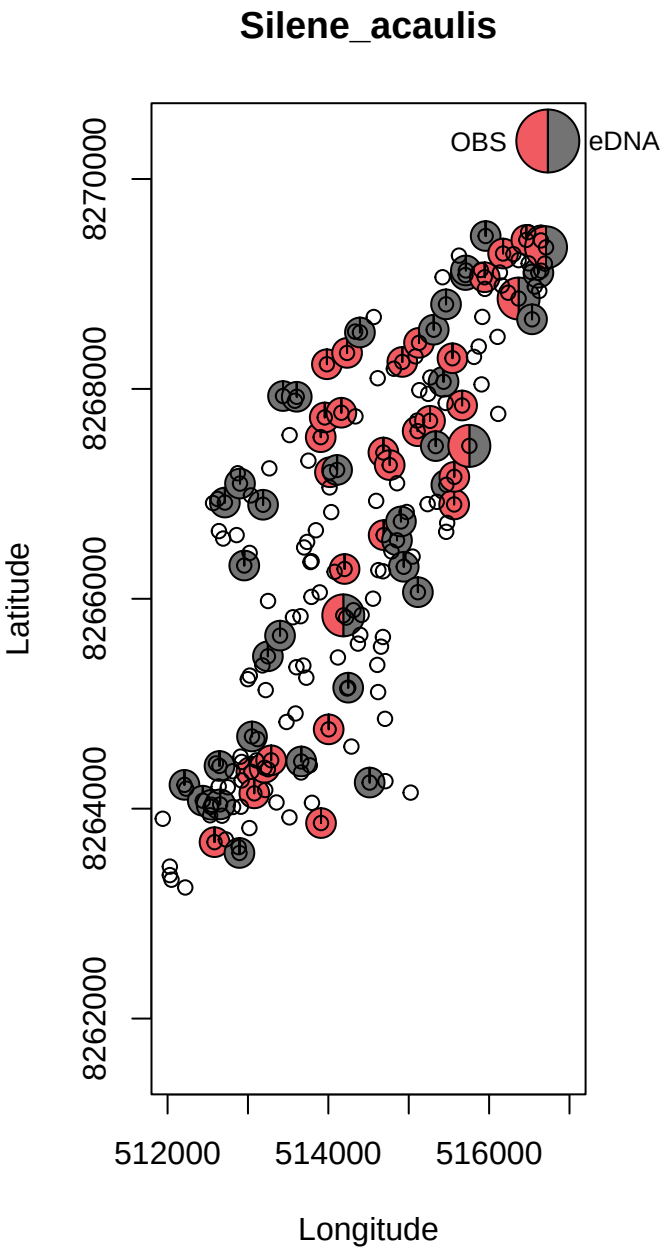
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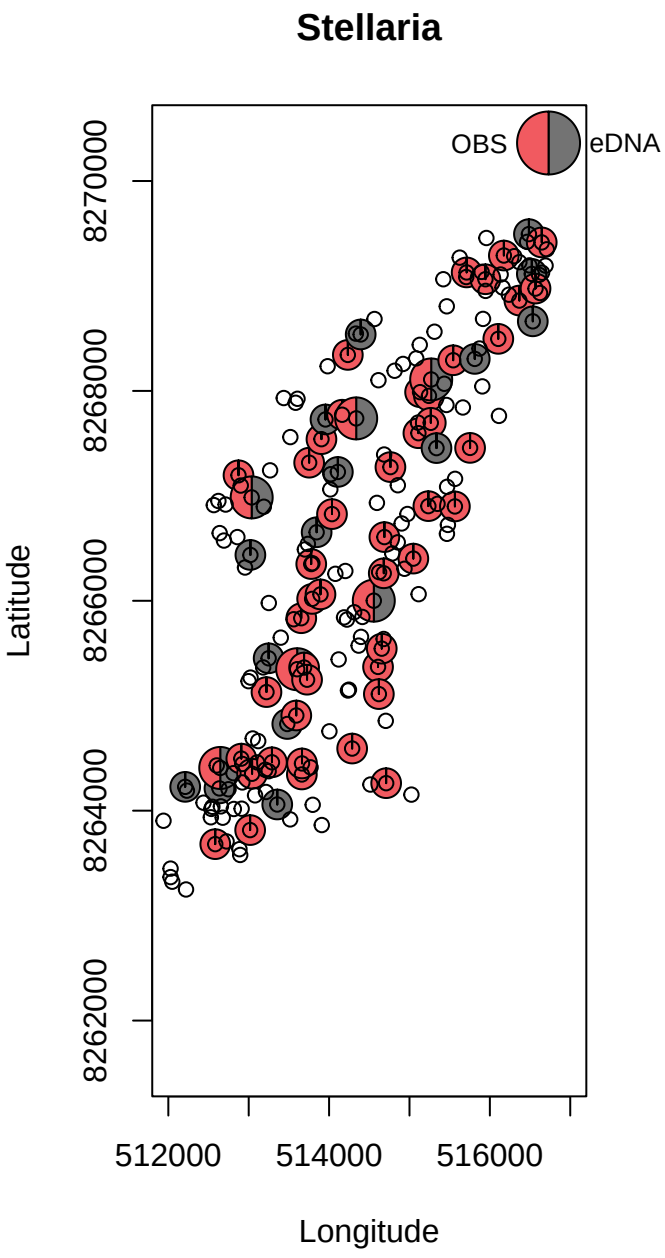
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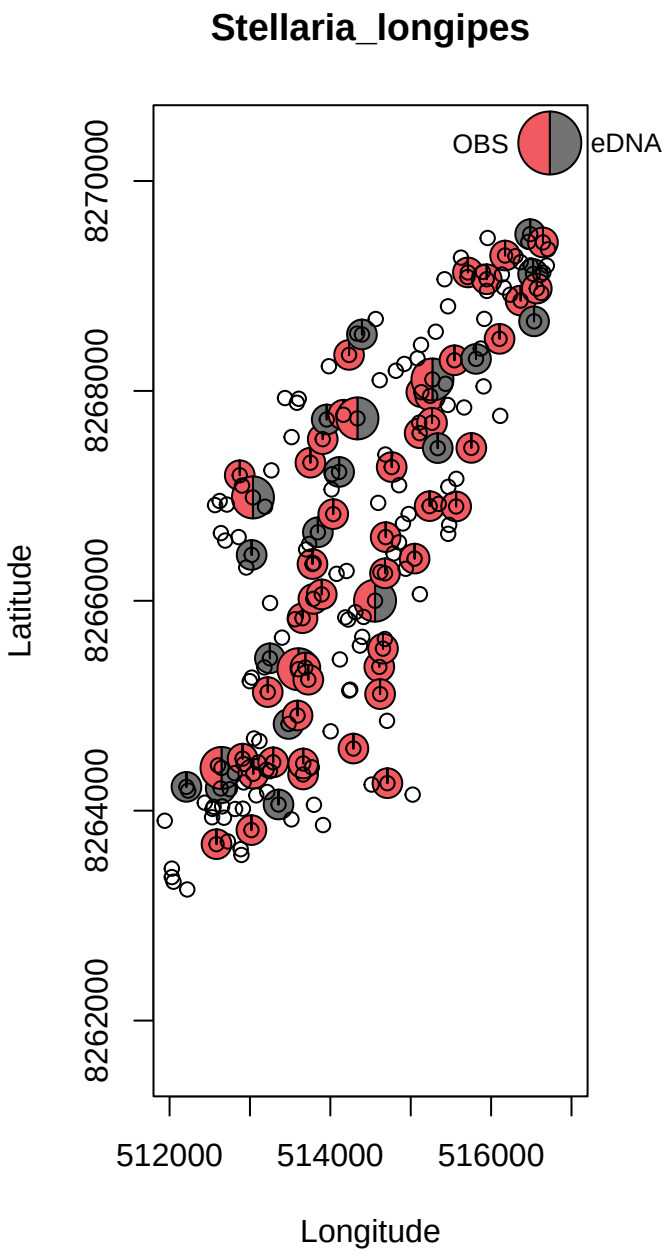
Longitude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8262000
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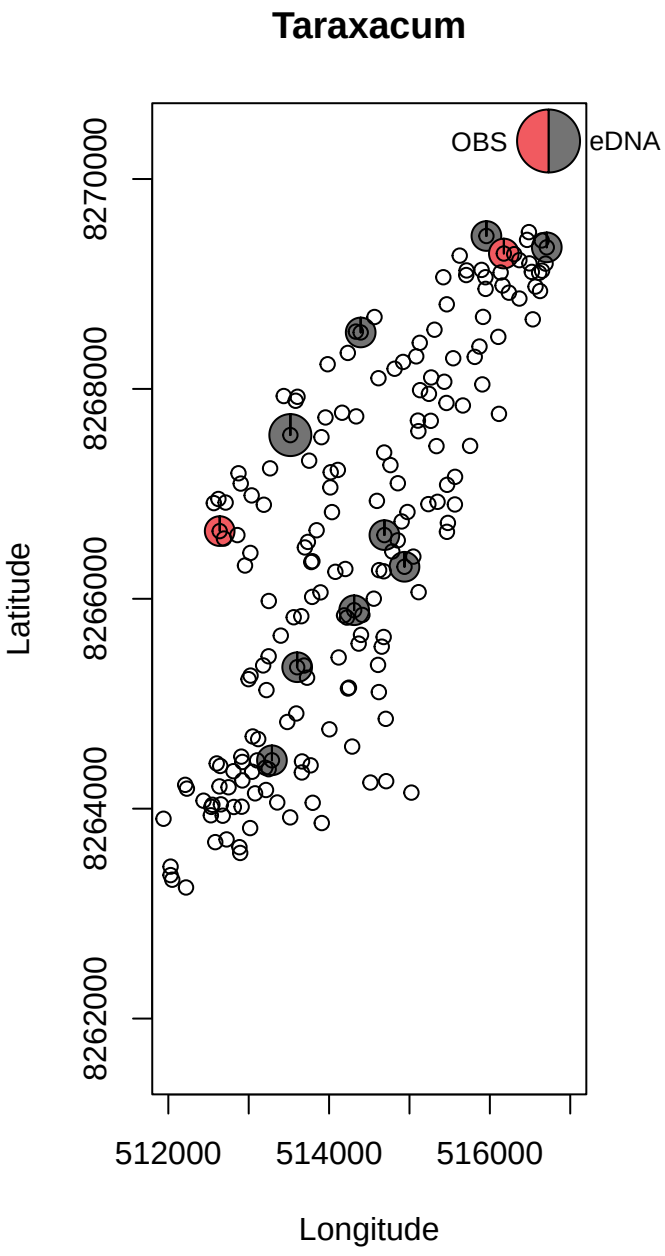
Longitude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OBS
eDNA
Latitude
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512000
514000
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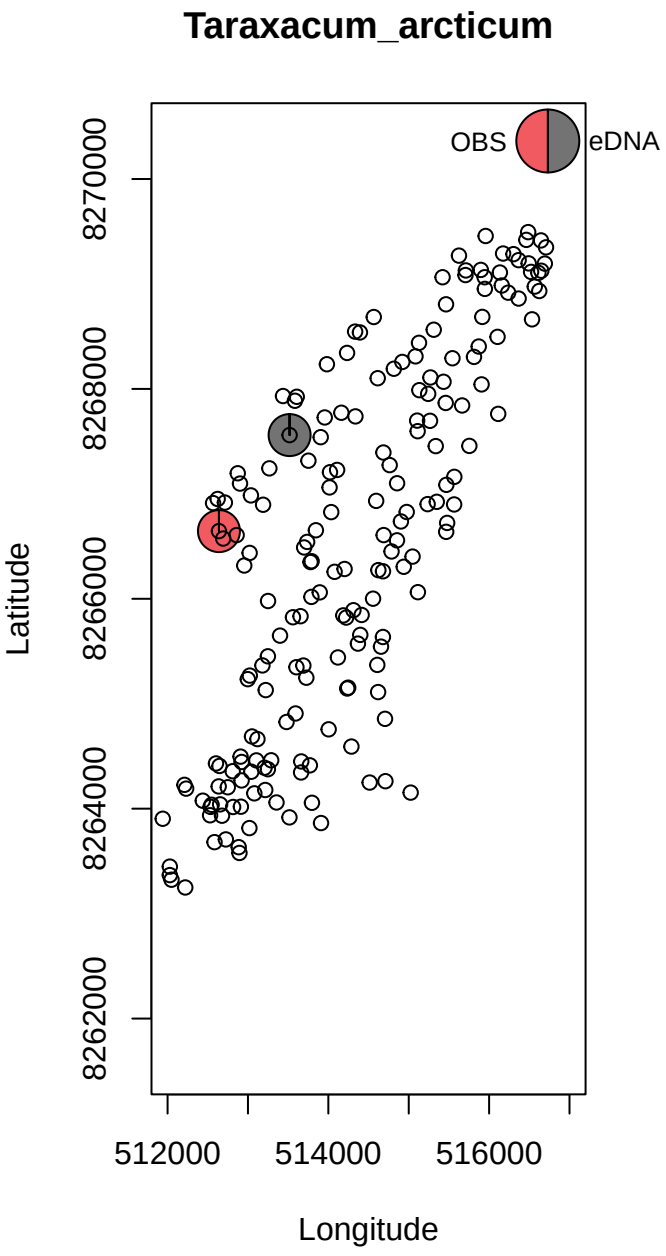
Longitude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eDNA
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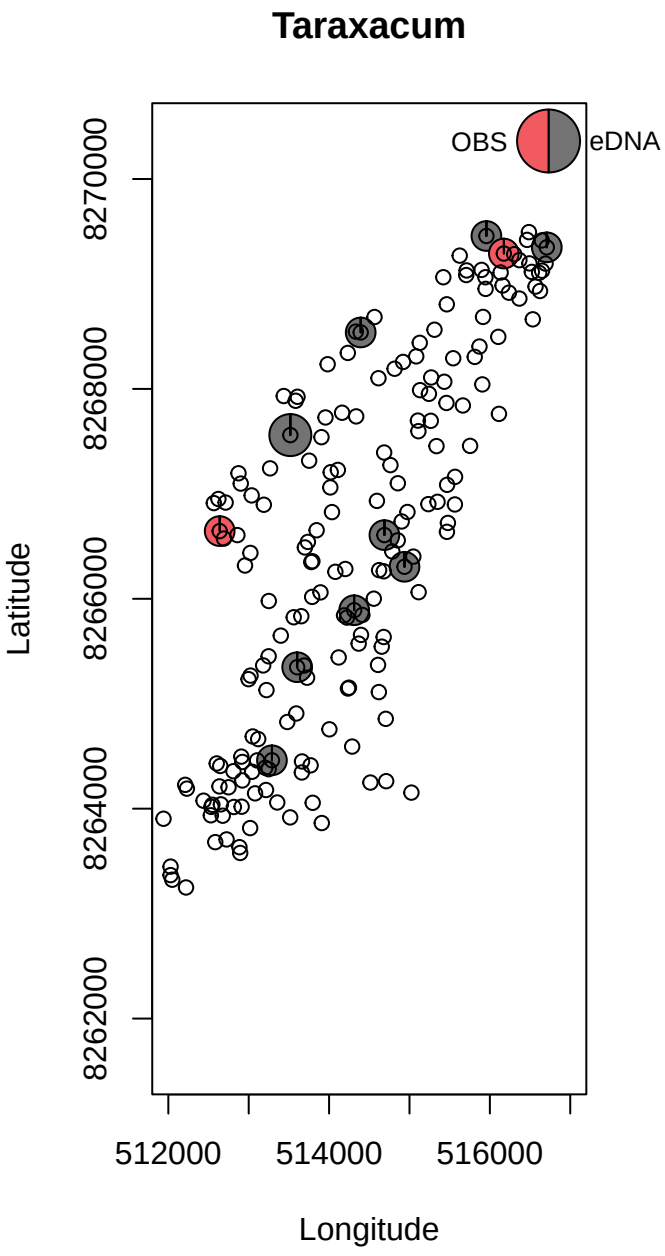
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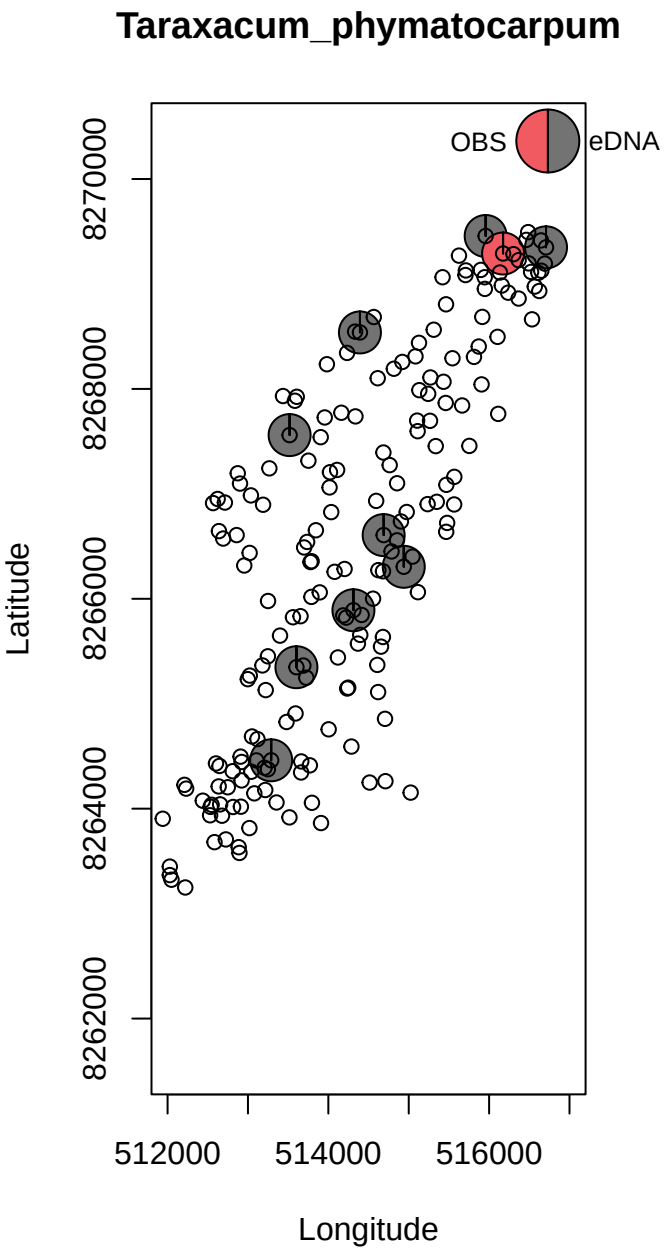
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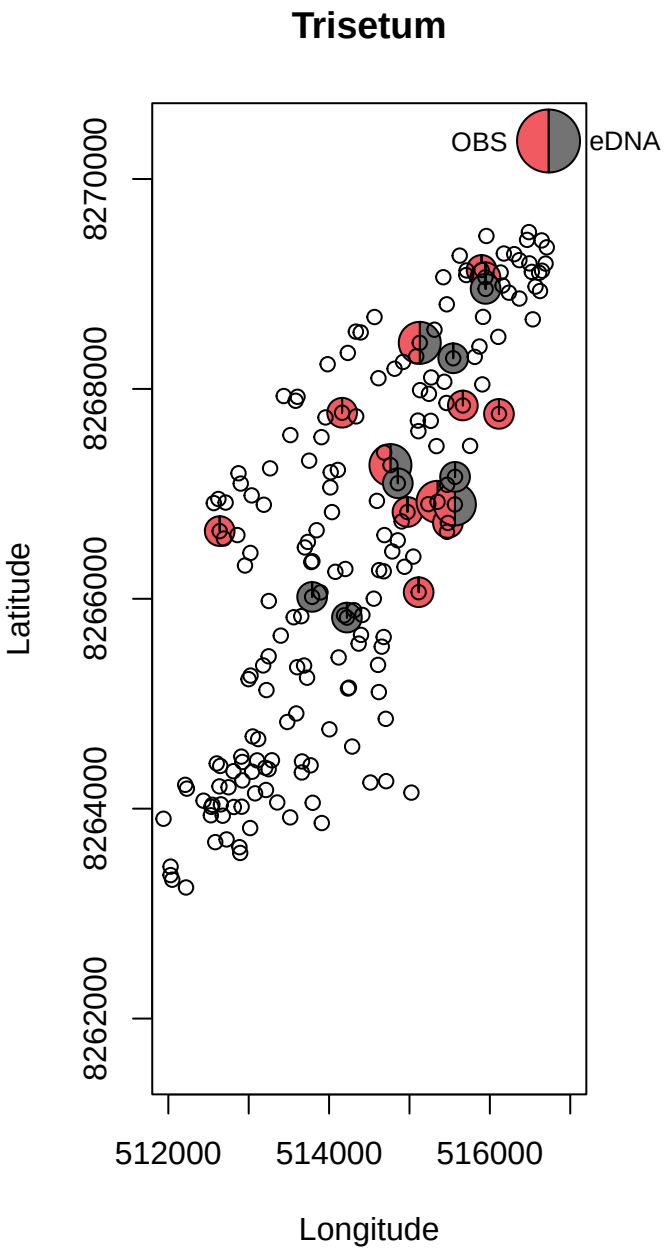
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Latitude
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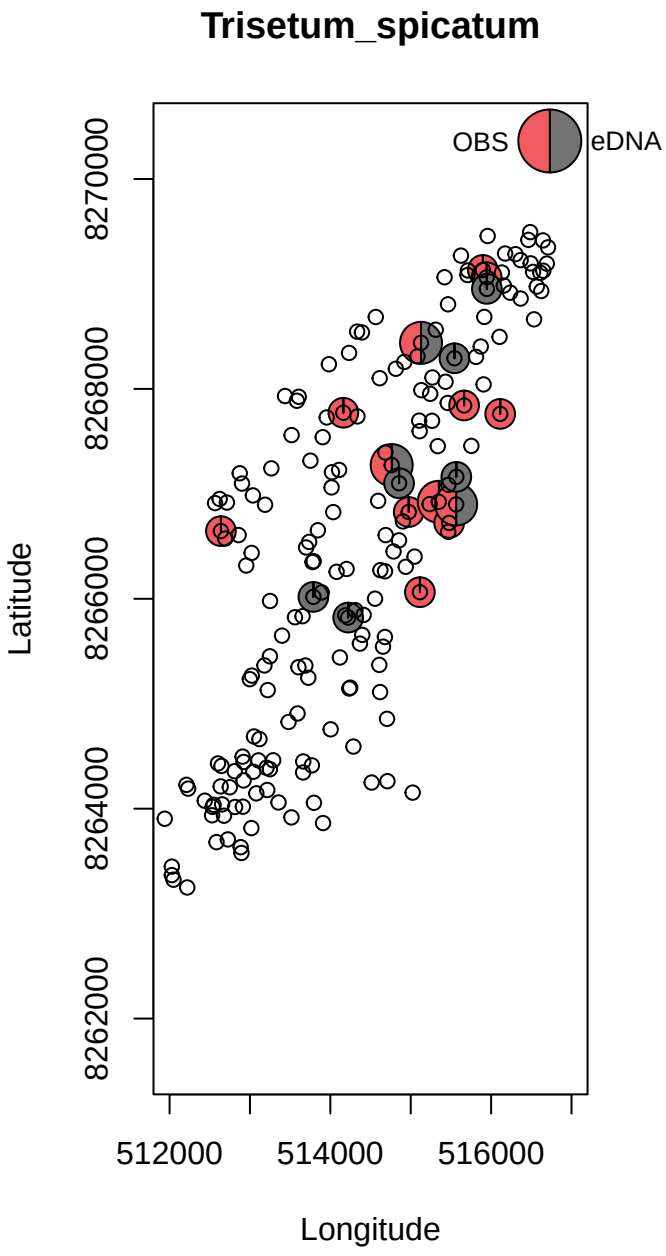
Longitude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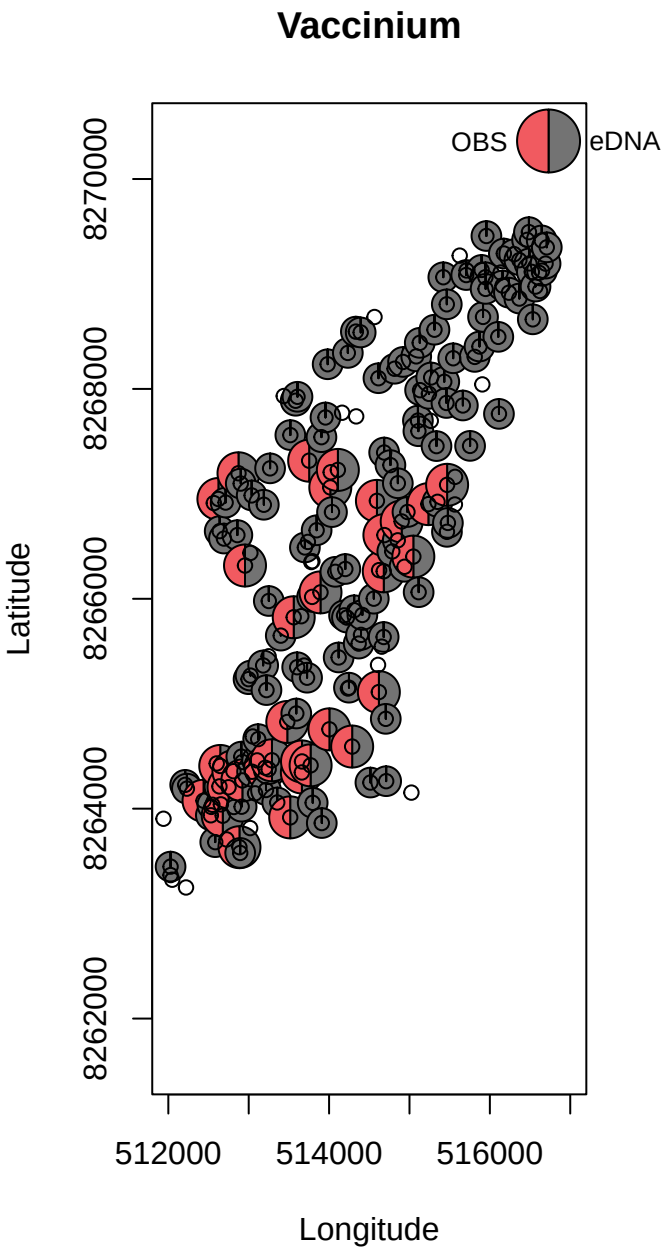
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eDNA
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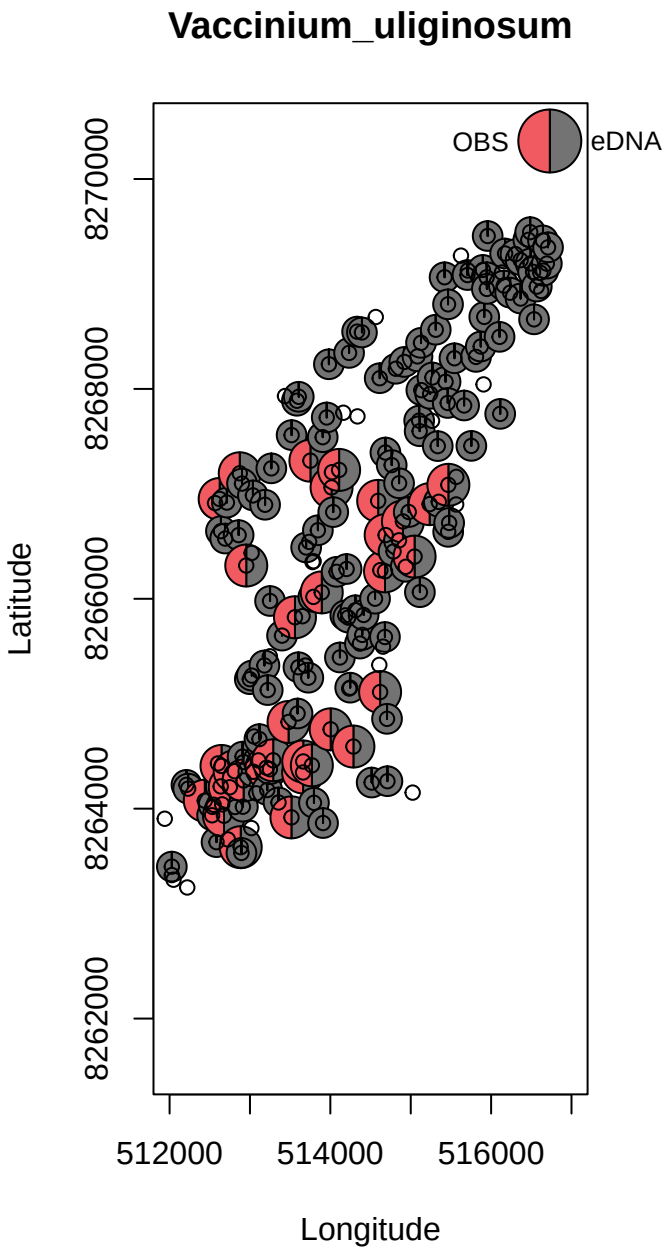
Vaccinium_uliginosum
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eDNA
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Longitude

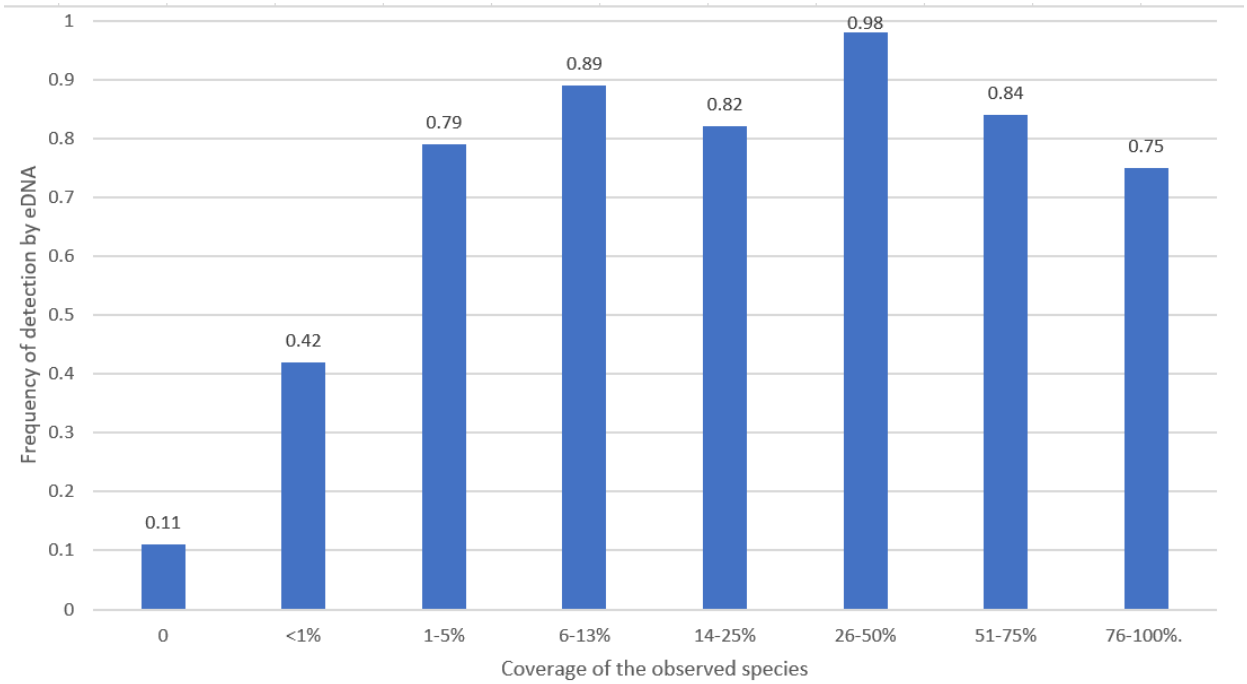


Fig. S4. Summary of the frequency of detection of a species by eDNA (y-axis) as a function of the semiquantitative scoring of the relative coverage of the same species (x-axis) as scored by direct observation.

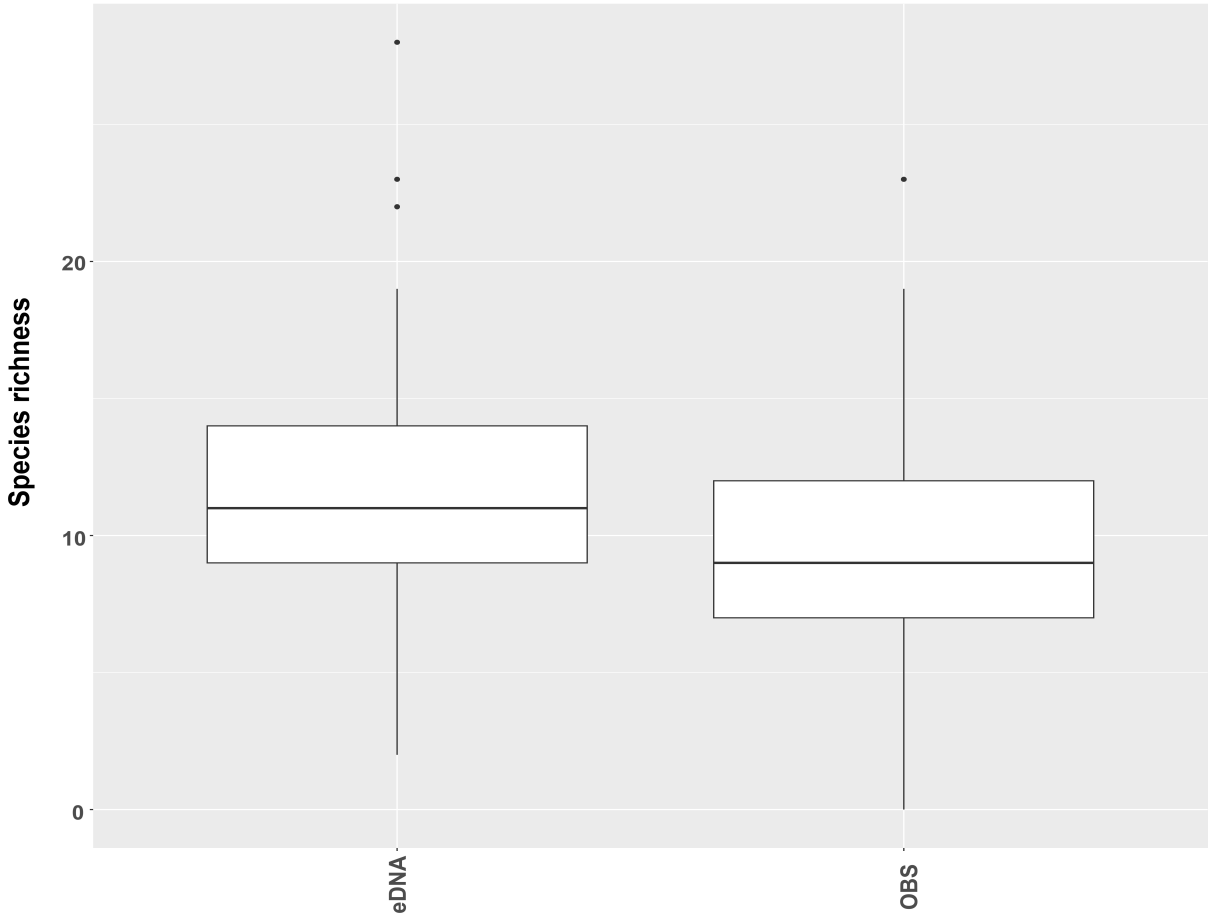
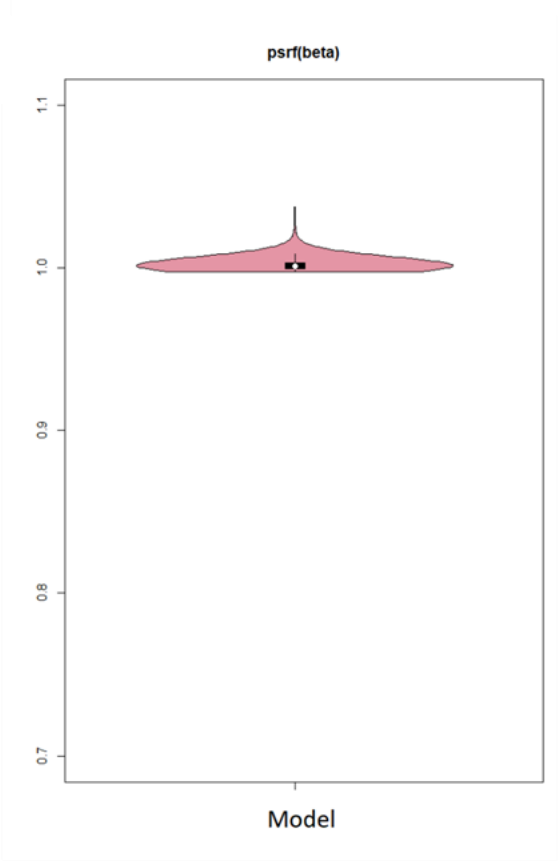


Fig. S5. Boxplot of plant species richness per plot for the two methods of identification. OBS stands for the species richness of plants scored by observation and eDNA for the richness plants by combining ITS2 and rbcLa.

A)



B)

		Model performance indices				Predictors and raw variance explained					
		Tjur R^2	AUC	Cross-validation TjuR²	Cross-validation AUC	Soil temperature	Soil pH	Soil moisture	Readcount	Random: site	Random: Soil type
Model	Plant-observation	0.20	0.84	0.1	0.72	1.4	1.9	4.6	0.0	8.4	3.8
	Plant-eDNA	0.08	0.75	0.03	0.56	0.6	0.7	1.2	2.3	3.0	0.6
	Bacteria	0.38	0.92	0.09	0.71	0.7	1.0	3.9	6.0	25.5	1.0
	Fungi	0.17	0.85	0.04	0.64	1.6	0.7	3.1	1.8	11.7	1.1
	Total mean model	0.30	0.89	0.08	0.69	0.8	1.1	3.6	4.3	19.3	1.3

Fig. S6. Model convergence and discrimination success achieved for the HMSC model. In (A), the violin plot describes *the MCMC convergence of the model. The potential scale reduction factor was close to the theo-rical optimum of one. The left-hand part of Table (B) summarizes the discriminatory power of the model, as based on two indices: Tjur R^2 and AUC (see main text for definitions). Two aspects are evaluated: explanatory power (as reflected by Tjur R^2 and AUC) and predictive power (as reflected by cross-validation Tjur R^2 and cross-validation AUC). The right-hand part of the Table shows the average proportion of variation explained by each variable included in the model.*

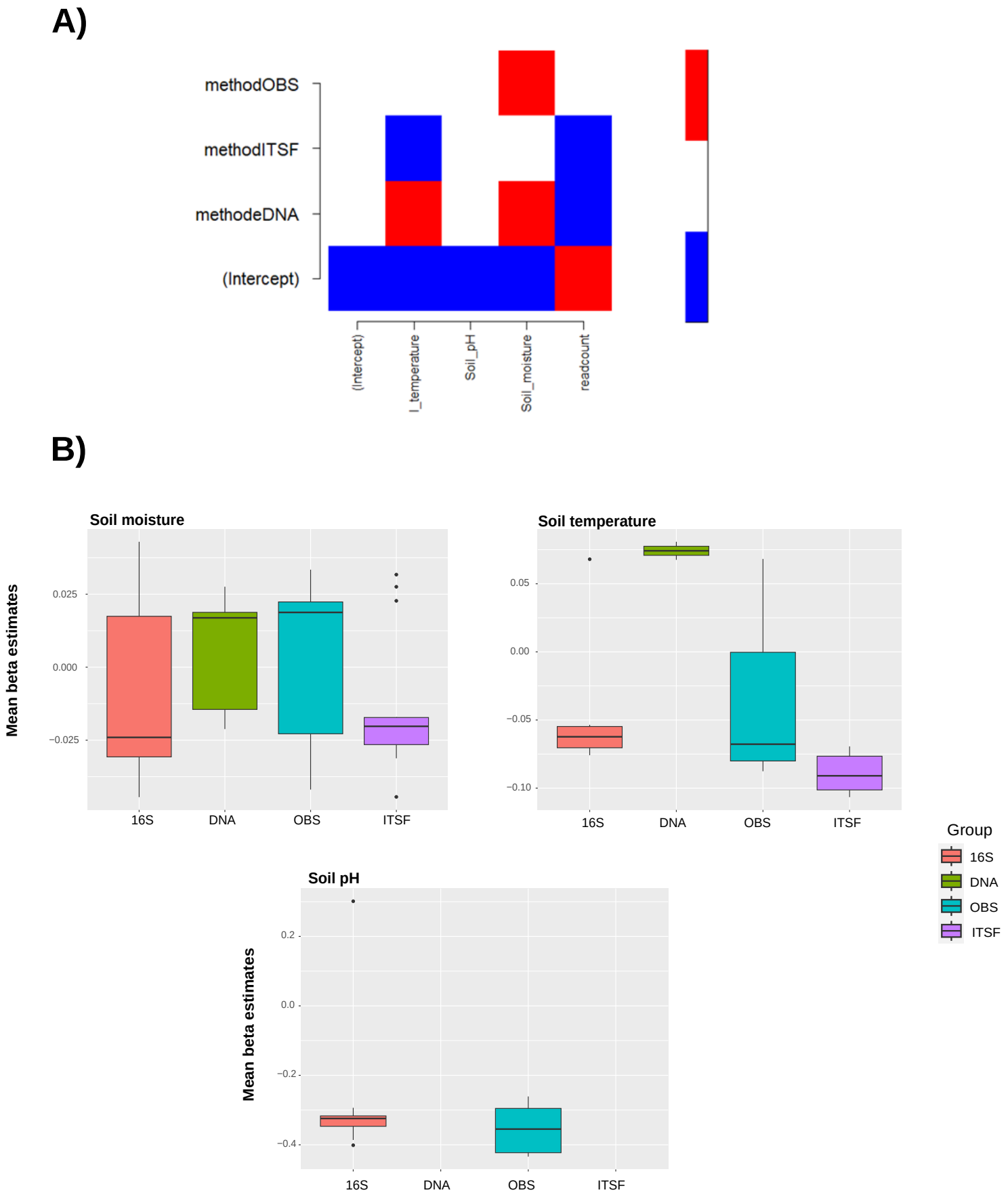
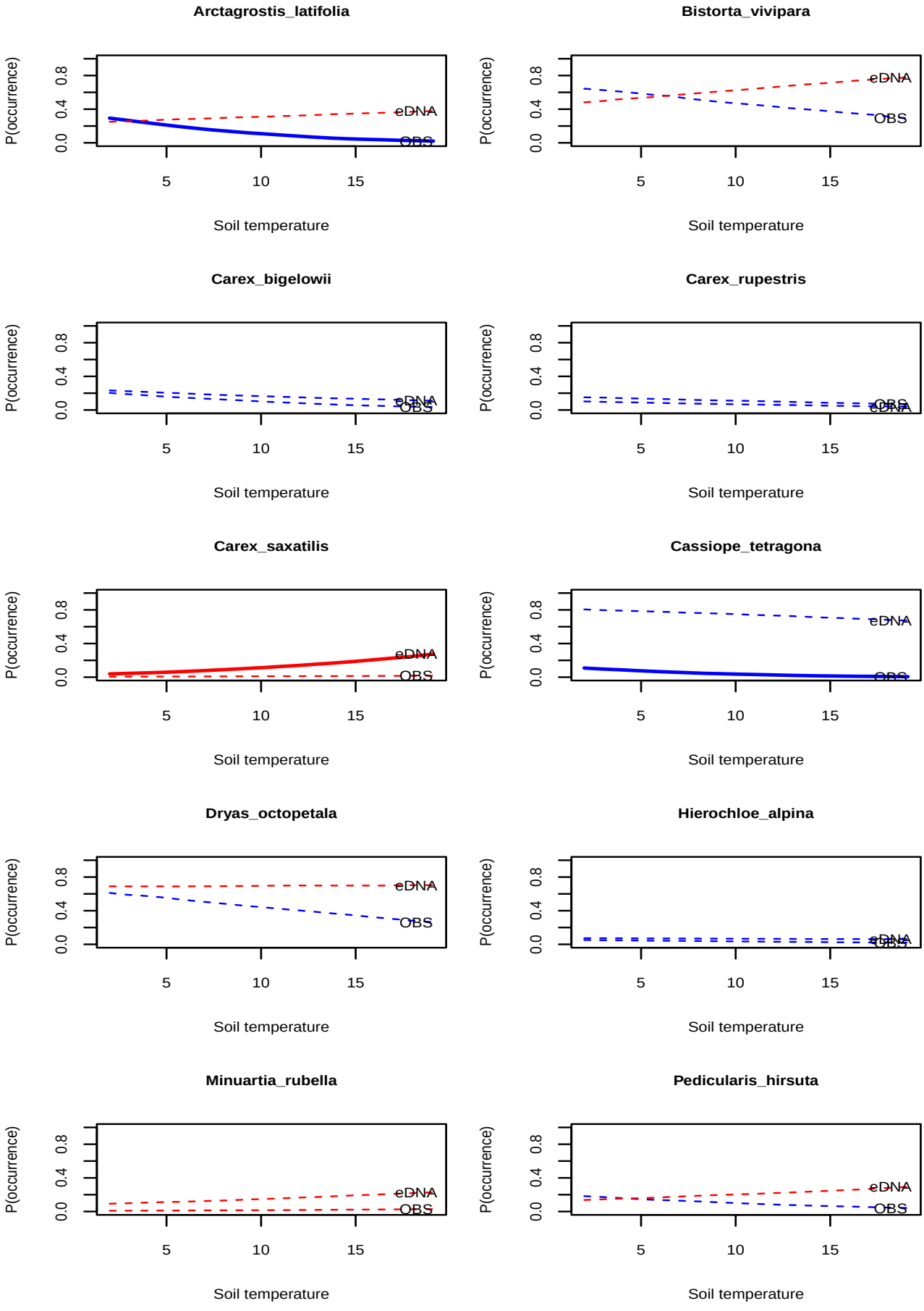


Fig. S7. The top panel (A) shows estimates of the gamma parameter, as reflecting the impact of the trait (i.e. organism group or scoring method) on the estimated response. The intercept corresponds to bacteria detected using locus 16S. Blue or red tiles indicate, when compared to bacteria, that a group of organisms is responding stronger or weaker to a specific covariate (posterior support >0.95).To illustrate the corresponding differences in species-specific responses within the respective groups, we show the distribution of beta parameter (i.e., taxa specific estimates of environmental responses, equivalent to regression coefficients) values as a box plot in panel (B).

Fig. S8. Summary of taxon-specific responses to environmental covariates. Cell entries correspond to the number of taxa for which a statistically supported response was detected. The scoring of taxa is based on a statistically supported beta-parameter (i.e) in the HMSC model, akin to a regression coefficient detectably different from zero. Overall, the analysis includes 44 plant taxa scored by direct observation (Plant_OBS), 37 plant taxa observed by eDNA (Plant_eDNA), 222 bacterial OTUs (Bacteria) and 29 fungal taxa (Fungi).

		Environmental covariables			
Taxonomic group	Sign of response	**Soil temperature**	**Soil moisture**	**Soil pH**	**Readcount**
Plant_OBS	**+**	5	15	0	0
	0	36	37	33	0
	-	2	10	9	0
Plant_eDNA	**+**	2	4	0	13
	0	35	36	37	19
	-	0	3	0	5
Bacteria	**+**	1	29	1	211
	0	217	127	213	12
	-	5	67	9	0
Fungi	**+**	0	3	0	15
	0	20	16	29	14
	-	9	10	0	0

Fig. S9. Posterior predictions of the mean probabilities of occurrence of 19 plant species based on observational (OBS) vs eDNA data along gradients in soil temperature, pH and moisture. These are marginal predictions, meaning that the values of all fixed effects apart from the focal soil gradient were fixed at their mean value in the dataset.



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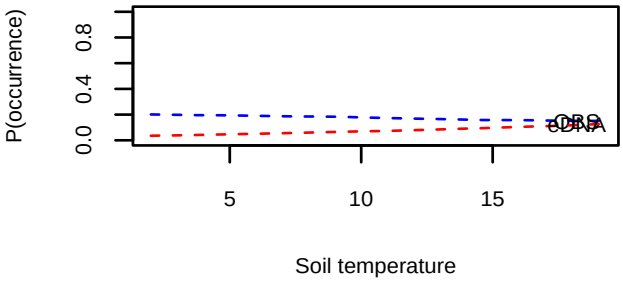
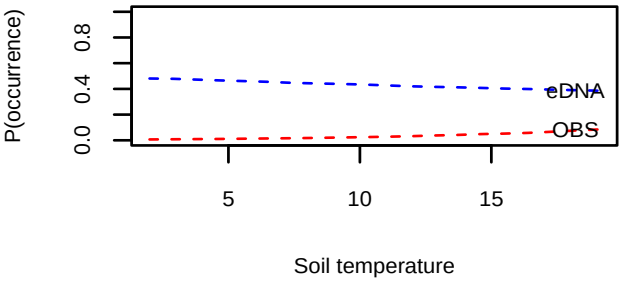
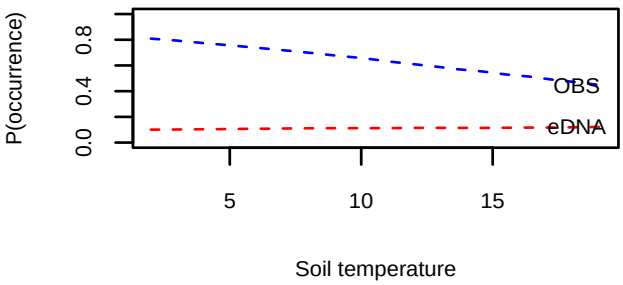


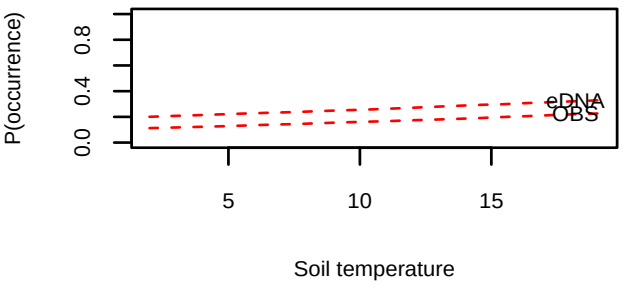
Polemonium_boreale



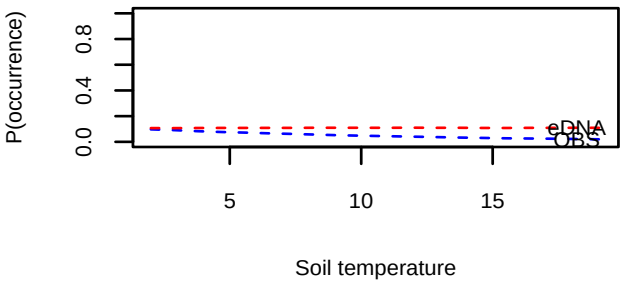
Salix_arctica



Saxifraga_cernua



Saxifraga_oppositifolia



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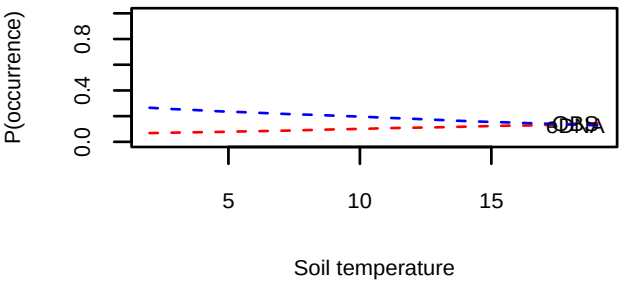

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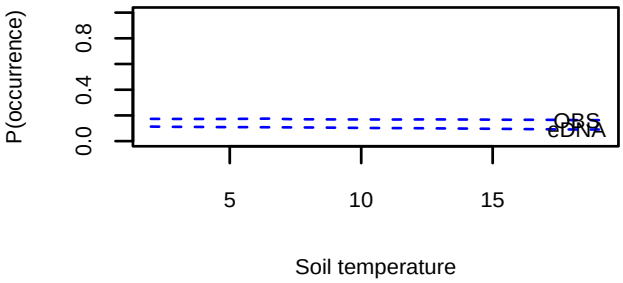

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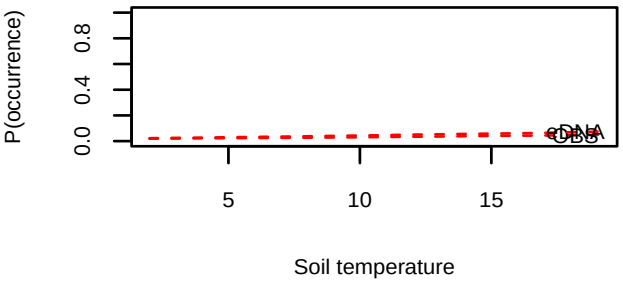

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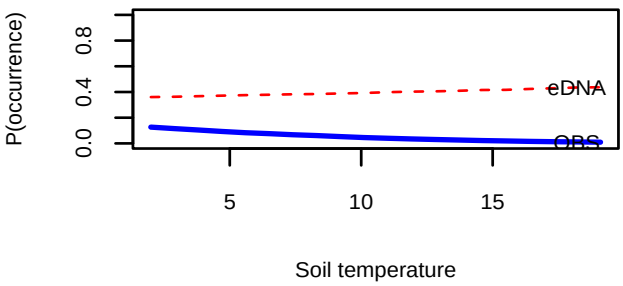

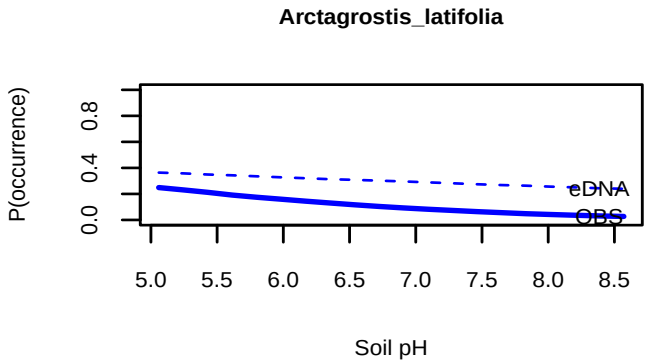
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P(occurrence)
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OBS
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7.0
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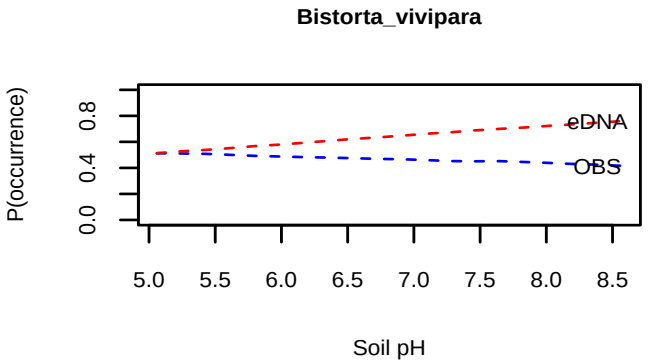
8.0
8.5
Soil pH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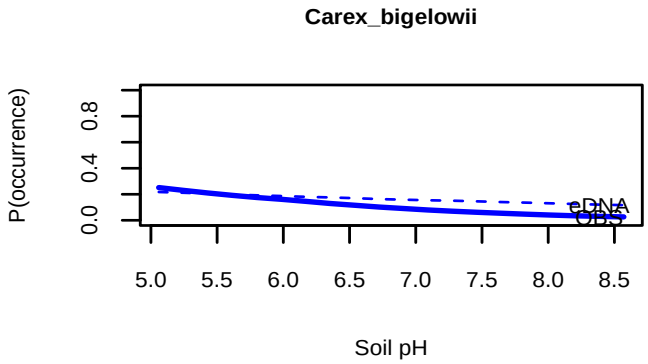
Soil pH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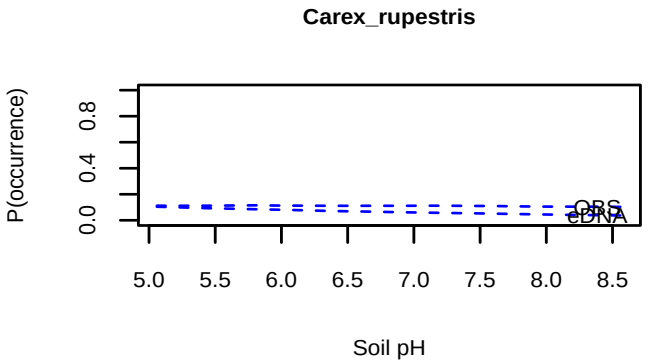
Soil pH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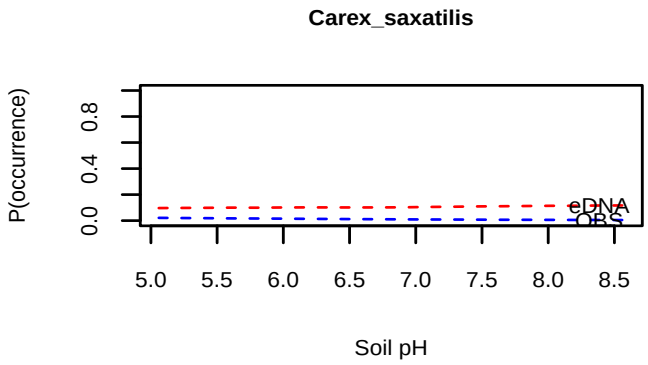
Soil pH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OBS
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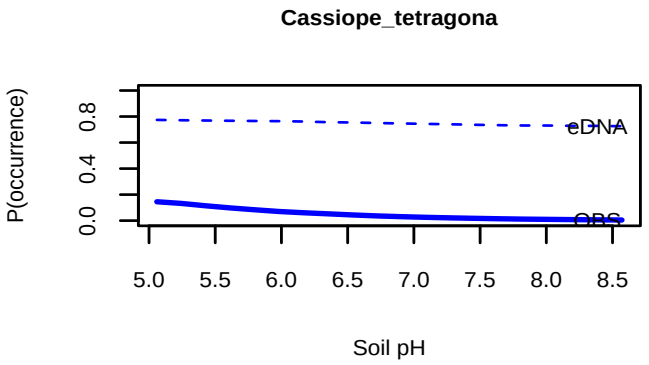
Soil pH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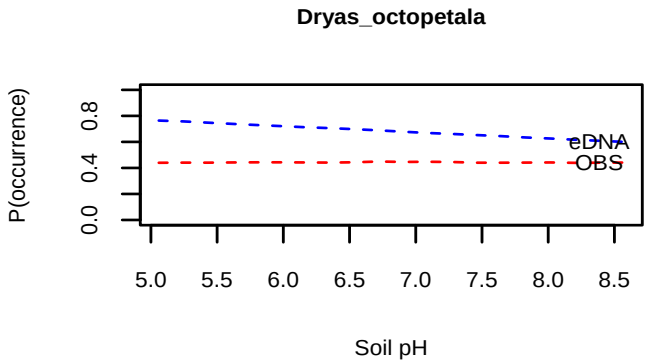
Soil pH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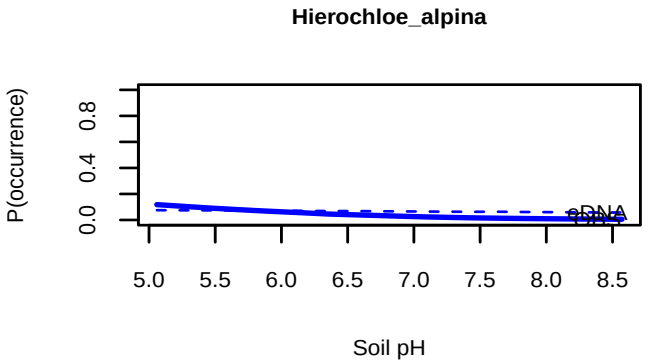
Soil pH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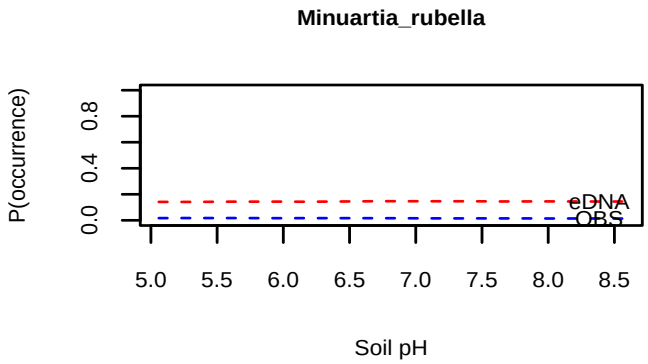
Soil pH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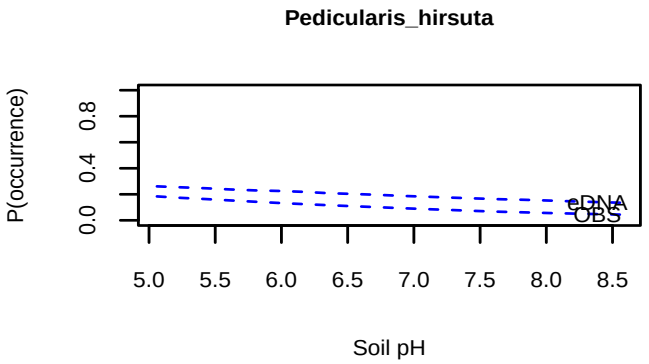
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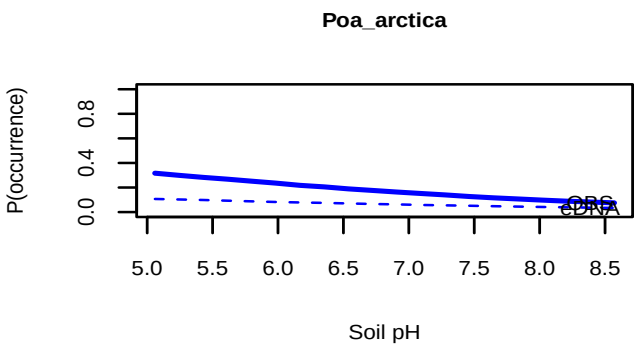
Soil pH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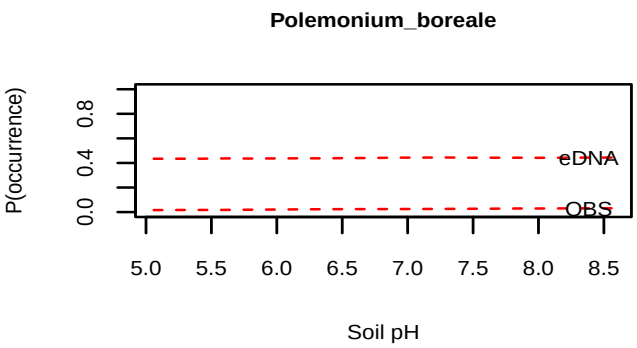
Soil pH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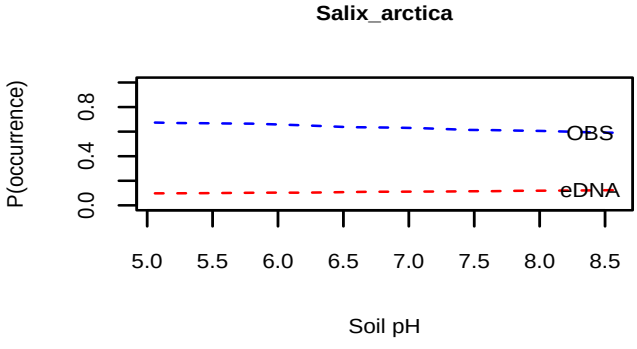
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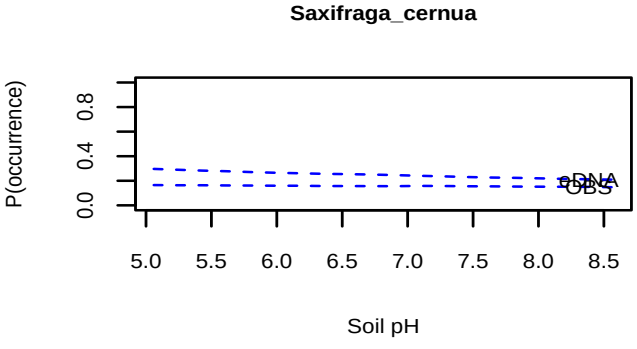
Soil pH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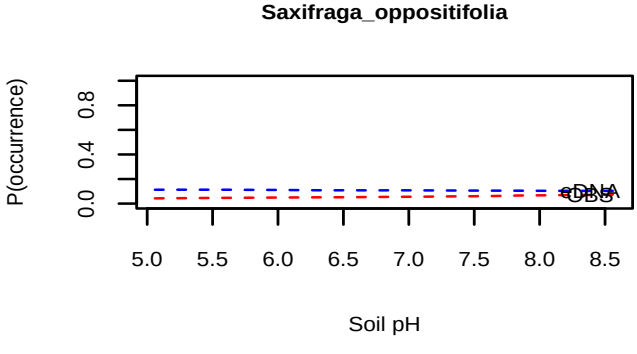
Soil pH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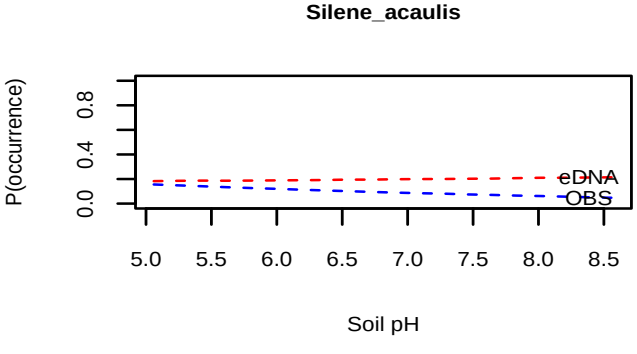
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OBS
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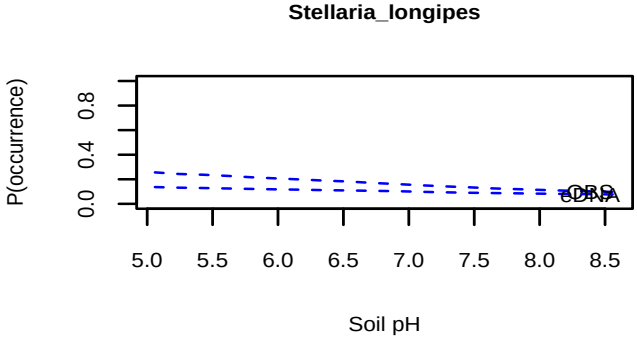
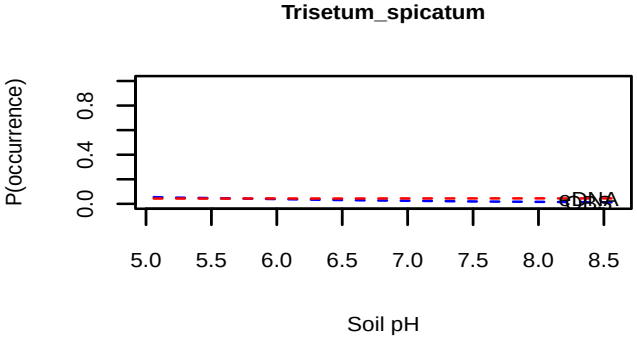
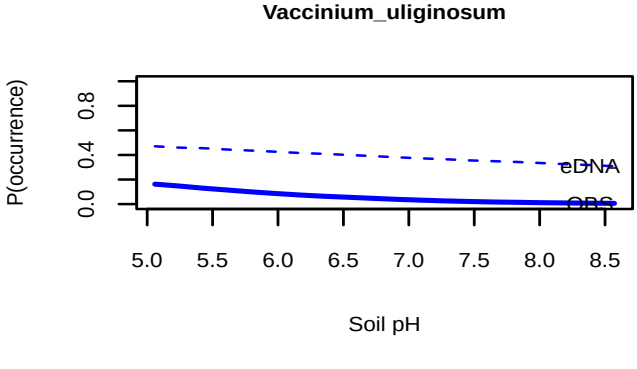
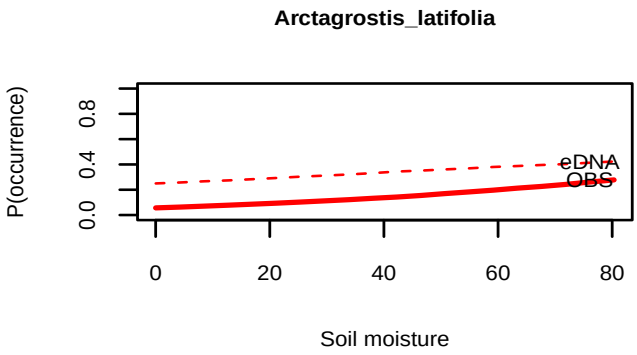
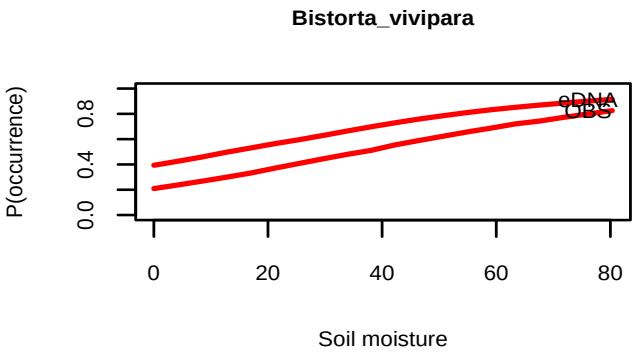
5.5
6.0
6.5
7.0
7.5
8.0
8.5
Soil pH

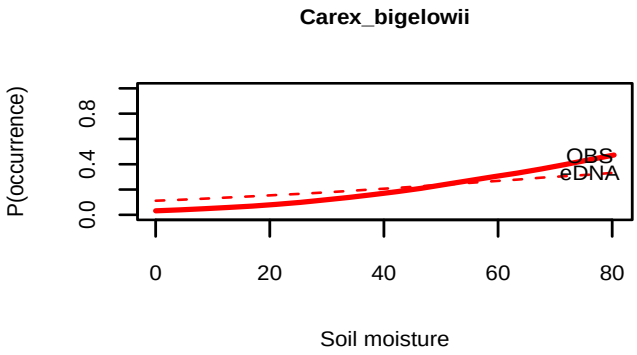

Stellaria_longipes
P(occurrence)
0.0
0.4
0.8
OBS
eDNA
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
Soil pH

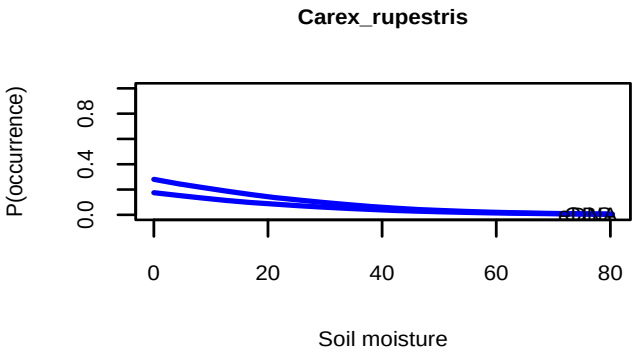

Trisetum_spicatum
P(occurrence)
0.0
0.4
0.8
eDNA
OBS
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
Soil pH

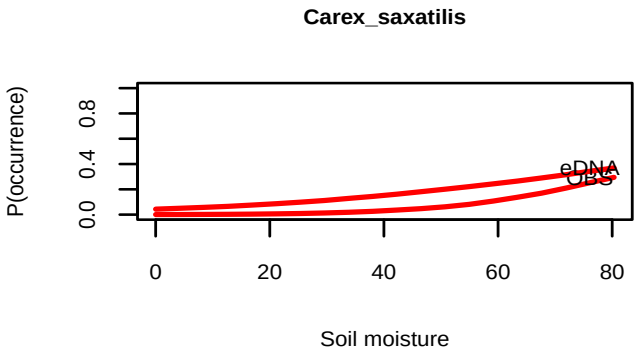

Vaccinium_uliginosum
P(occurrence)
0.0
0.4
0.8
eDNA
OBS
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
Soil pH

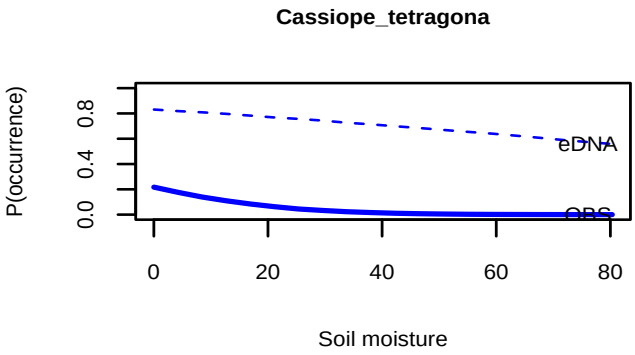

Arctagrostis_latifolia
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
eDNA
OBS

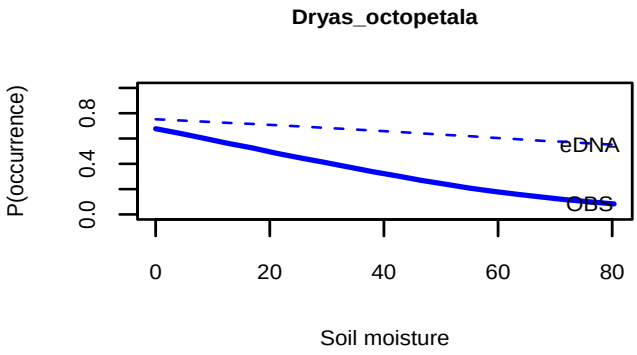

Bistorta_vivipara
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
eDNA
OBS

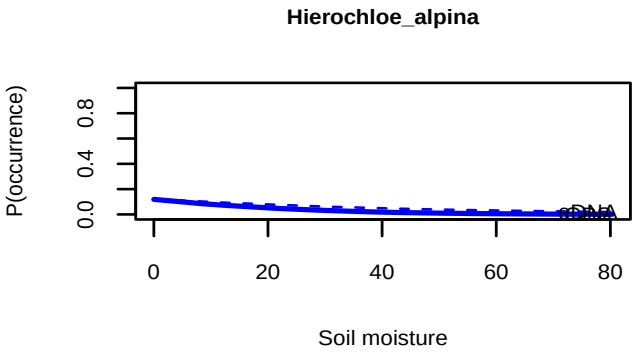

Carex_bigelowii
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
OBS
eDNA

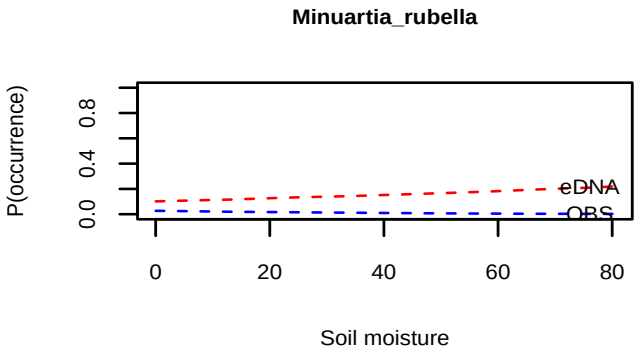

Carex_rupestris
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture

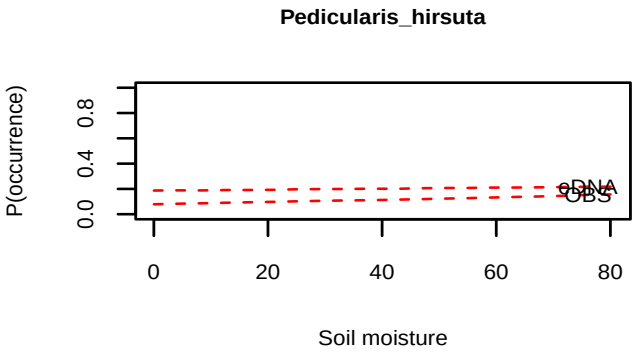

Carex_saxatilis
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
eDNA
OBS


Cassiope_tetragona
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
eDNA
OBS

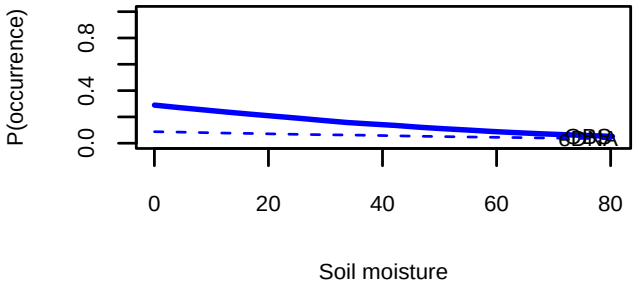

Dryas_octopetala
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
eDNA
OBS


Hierochloe_alpina
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture

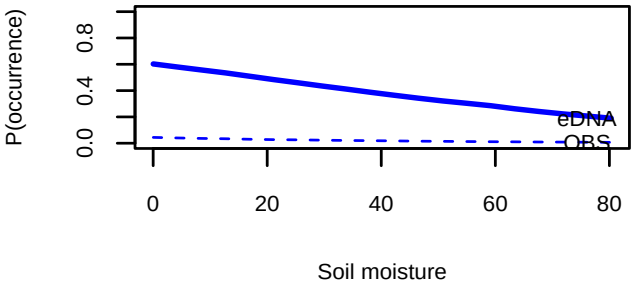

Minuartia_rubella
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture
eDNA
OBS


Pedicularis_hirsuta
P(occurrence)
0.0
0.4
0.8
0
20
40
60
80
Soil moisture

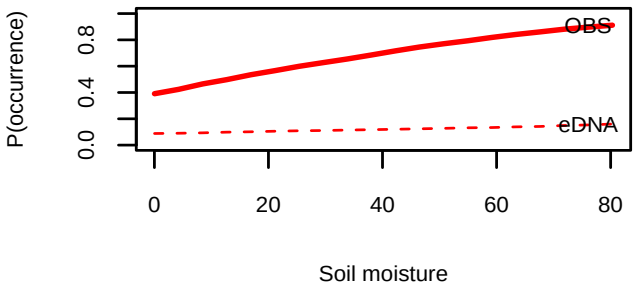
Poa_arctica



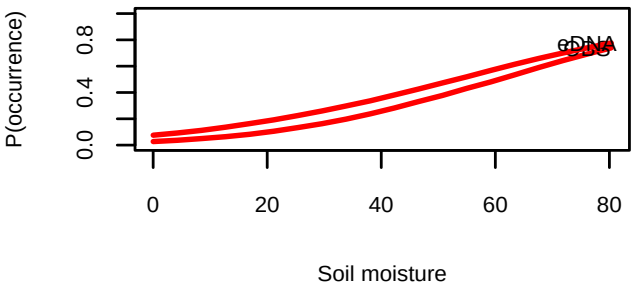
Polemonium_boreale



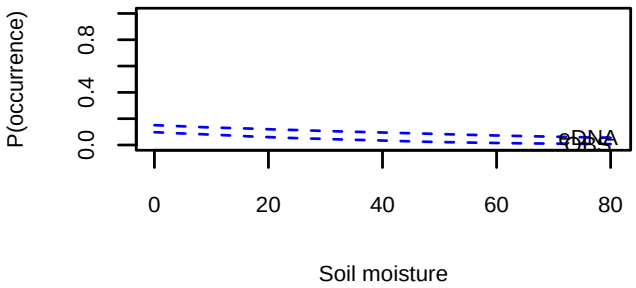
Salix_arctica



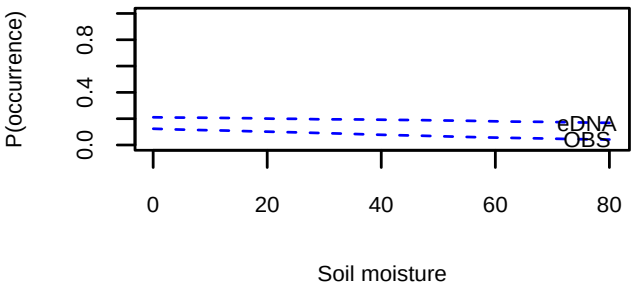
Saxifraga_cernua



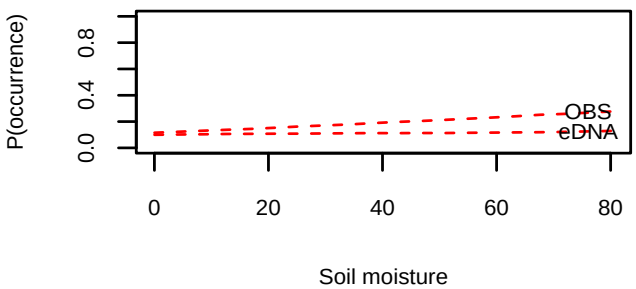
Saxifraga_oppositifolia



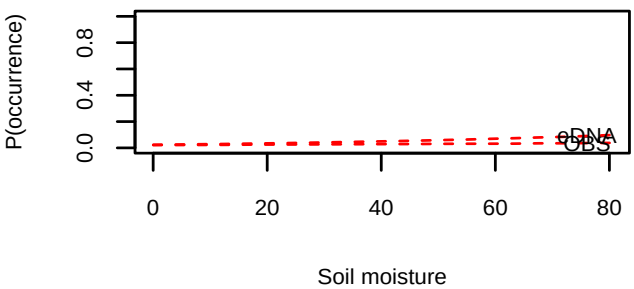
Silene_acaulis



Stellaria_longipes



Trisetum_spicatum



Vaccinium_uliginosum

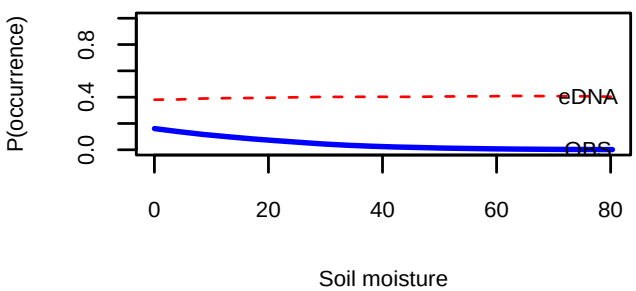


Fig. S10. Numerical summary of associations detected between taxa. The top panel (A) summarizes all possible associations between taxa included in our model. Proportions are calculated from the numbers in brackets, as based on the number of statistically supported associations out of all possible taxon-pairs between each group. The bottom panel (B) summarizes the number of associations detected between taxa, as visually represented in Fig. 5 of the main text and in Fig S11-A&B (below). Proportions are calculated from the numbers in brackets, as based on the number of statistically supported associations out of all possible taxon-pairs for each type of association.

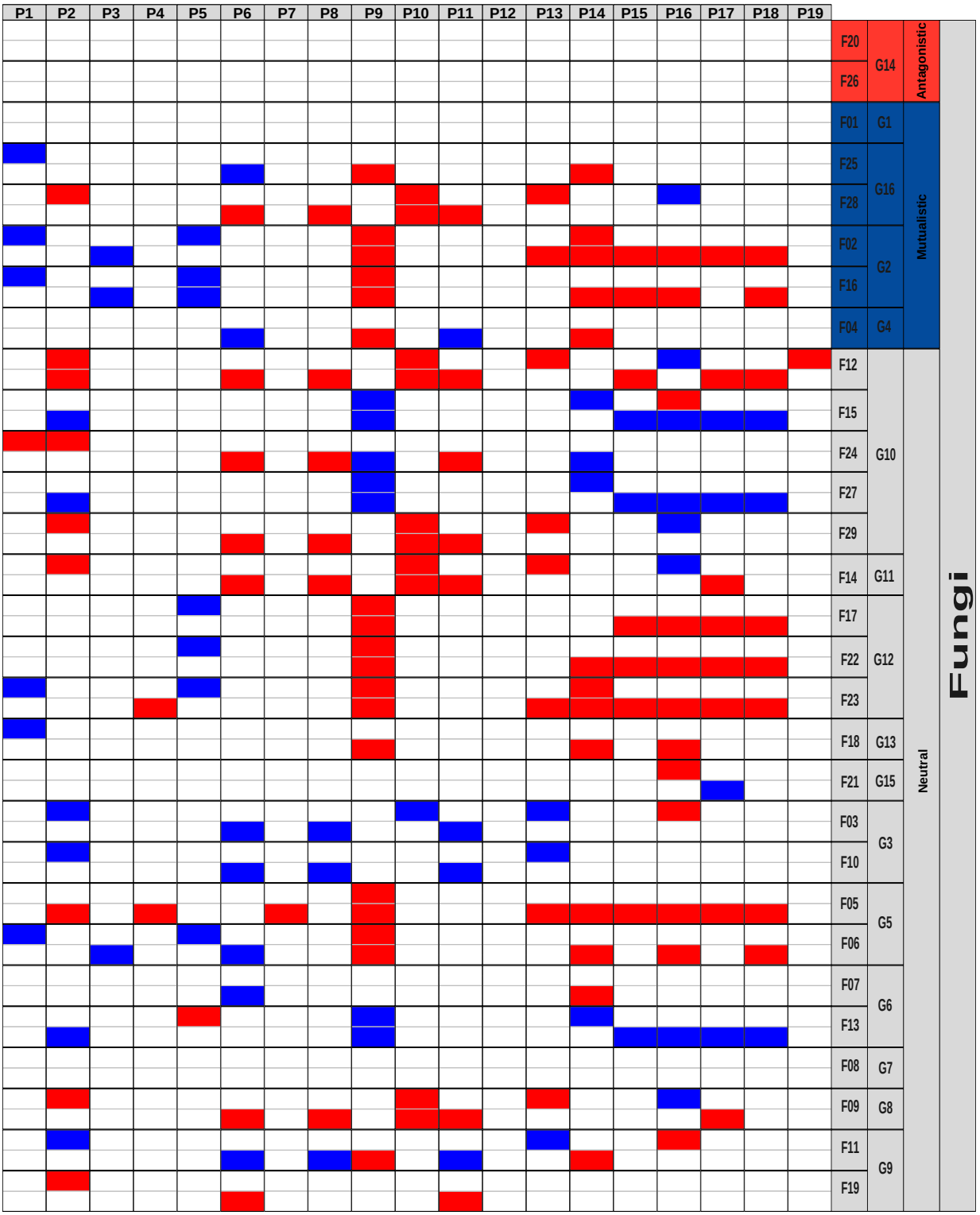
A)

		Plant_OBS (n=44)	Plant_eDNA (n=37)	Bacteria (n=222)	Fungi (n=29)
Plant_OBS (n=44)	Total	21% (406/1936)	6% (103/1628)	33% (3236/9812)	27% (343/1276)
	Negative	5% (104/1936)	2% (32/1628)	14% (1369/9812)	9% (122/1276)
	Positive	16% (302/1936)	4% (71/1628)	18% (1867/9812)	17% (221/1276)
Plant_eDNA (n=37)	Total		6% (87/1369)	15% (1276/8251)	13% (137/1073)
	Negative		1% (16/1369)	7% (575/8251)	5% (55/1073)
	Positive		5% (71/1369)	8% (701/8251)	8% (82/1073)
Bacteria (n=222)	Total			59% (29203/49729)	44% (2866/6467)
	Negative			28% (13912/49729)	20% (1286/6467)
	Positive			31% (15291/49729)	24% (1580/6467)
Fungi (n=29)	Total				38% (317/841)
	Negative				16% (132/841)
	Positive				22% (185/841)

B)

		Proportion of supported associations between the subset of 19 plant taxa and other organism groups					
		Bacteria (n=222)			Fungi (n=29)		
		Antagonistic	Mixed	Mutualistic	Antagonistic	Mixed	Mutualistic
Plant_OBS (n=19)	Total	29.7% (192/646)	24.7% (913/3705)	27.3% (166/608)	0% (0/38)	24.8% (99/399)	22.8% (26/114)
	Negative	9.9 %(64/646)	9.5% (351/3705)	11.2% (68/608)	0% (0/38)	8.3% (33/399)	5.3% (6/114)
	Positive	19.8% (128/646)	15.2% (562/3705)	16.1% (98/608)	0% (0/38)	16.5% (66/399)	17.5% (20/114)
Plant_eDNA (n=19)	Total	14.2% (92/646)	13% (481/3705)	14.7% (89/608)	0% (0/38)	12.8% (51/399)	10.6% (12/114)
	Negative	4.6% (30/646)	6.1% (227/3705)	6.6% (40/608)	0% (0/38)	6% (24/399)	5.3% (6/114)
	Positive	9.6% (62/646)	6.9% (254/3705)	8.1% (49/608)	0% (0/38)	6.8% (27/399)	5.3% (6/114)

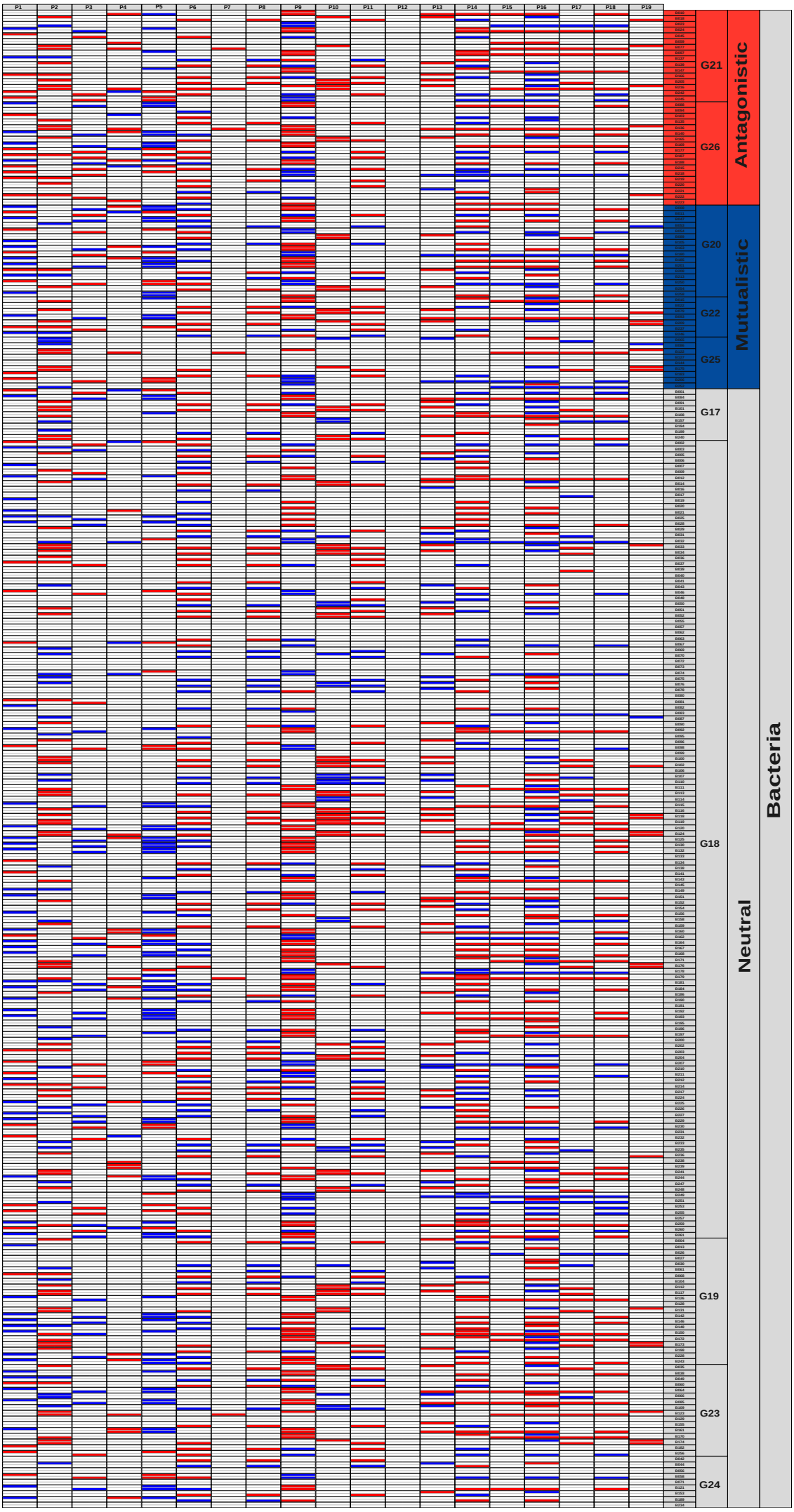
Fig. S11A. Estimated pairwise residual associations among plants and different functional groups of fungi. Here, each plant species is shown as a column, including the 19 plant species identified by both direct observation and eDNA and thus allowing direct comparisons between methods. Rows correspond to individual microbial genera, as sorted by functional groups. Red fields indicate presumptively antagonistic relationships,, as based on the functional classification of taxa, blue fields presumptively mutualistic associations , and grey fields indicate neutral or mixed interactions (i.e. the same genus being associated with several different functions). For visual comparison, each cell is divided in two, with the upper part describing the association estimated when plant occurrence was detected by eDNA and the bottom part describing the association estimated when plant occurrence was detected by Observation. G corresponds to the functional group, F to the Fungal taxon, and P to the plants taxon. For the identity of individual taxa, see key in Supplementary Information 3. For a numerical summary of figure contents, see Fig S10-B



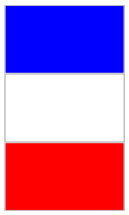
Sign of association

Method

eDNA
OBS



Sign of association



Method

eDNA
OBS