

Geographic distribution and ecological niche divergence of the Palaearctic petrophilous pikas (*Ochotona*, Lagomorpha, Mammalia) of the subgenus *Pika*

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ABSTRACT. The comparison of species distribution models and hyperspaces of ecological predictors was carried out in four species of petrophilous pikas of the subgenus *Pika*: *Ochotona alpina*, *O. turuchanensis*, *O. hyperborea* and *O. mantchurica*. All tests show significant differences between species, indicating good niche divergence. One of the species, *O. hyperborea*, lives in sympatry with two other species: *O. alpina* and *O. turuchanensis*; this is most likely due to different ecological preferences. The important role of geographical barriers in realising the potential distribution of these four species is demonstrated. The occurrence of *O. hyperborea* in China is reported for the first time.

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Географическое распределение и дивергенция экологических ниш у палеарктических петрофильных пищух (*Ochotona*, Lagomorpha, Mammalia) подрода *Pika*

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РЕЗЮМЕ. Сравнение экологических моделей и гиперпространств экологических факторов проведено для четырёх видов петрофильных пищух подрода *Pika*: *Ochotona alpina*, *O. turuchanensis*, *O. hyperborea* и *O. mantchurica*. Все тесты показали значимые различия между видами, что свидетельствует о хорошей дивергенции экологических ниш. Один из видов, *O. hyperborea*, живет в симпатрии с двумя другими видами: *O. alpina* и *O. turuchanensis*; скорее всего, это возможно, благодаря разным экологическим предпочтениям. Показана важная роль географических барьеров в реализации потенциальных ареалов этих четырёх видов. Впервые сообщается об обитании *O. hyperborea* в Китае.

КЛЮЧЕВЫЕ СЛОВА: пищухи, *Ochotona*, географическое распределение, экологическая ниша.

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Introduction

The subgenus *Pika* comprises 11 species of pikas that occupy stony habitats in Asia and North America (Lissovsky *et al.*, 2007, 2016; Lissovsky, 2014). Six of these species, namely *Ochotona alpina* (Pallas, 1773), *O. turuchanensis* Naumov, 1934, *O. hyperborea* (Pallas, 1811), *O. mantchurica* Thomas, 1909, *O. coreana* Allen et Andrews, 1913, *O. hoffmanni* Formozov, Yak-

hontov et Dmitriev, 1996 are obligate rock-dwellers, living in the cavities under large rocks mainly in the talus and are distributed in Asia. At first sight, the habitats of these 6 species are very similar, however there has never been a detailed study of the habitats.

Ochotona alpina and *O. turuchanensis* are sister species, their distribution is allopatric (Lissovsky *et al.*, 2007). The remaining 4 species form the second group of sisters (phylogenetic position of the less stud-

ied *O. coreana* is ambiguous) with allopatric ranges. One of the species from this group, *O. hyperborea*, has the largest distribution among pikas — it lives from the Ural Mountains to the Kamchatka Peninsula and from the Arctic Ocean coast to Mongolia. *Ochotona hyperborea* is sympatric with *O. alpina* and *O. turuchanensis* in the south and in the north of its distribution respectively. In sympatry zones, two species may live closely together in the same patch of stony ground, although more often the habitats of two species are somewhat separated by altitude or stone size (Formozov, 1986; Formozov & Yakhontov, 2003). The Manchurian pika *O. mantchurica* is distributed in the Manchurian region and is separated from *O. hyperborea* by the Amur River. The other two pikas, *O. coreana* and *O. hoffmanni*, have very small, isolated distribution ranges, limited by a mountain and a mountain range respectively. In summary, most petrophilous pikas of the subgenus *Pika* have isolated ranges, except for *O. hyperborea*, which is sympatric with distant relatives: *O. alpina* and *O. turuchanensis*.

According to the traditional point of view, speciation leads to the divergence of ecological niches. Treating the ecological niche according to Hutchinson (1957), we can measure niche divergence. Complete overlap of clouds of measured ecological preferences can be interpreted as niche identity. Increasing of the distances between the clouds, as well as decreasing of the clouds overlap should reflect the process of niche divergence. Such an approach can be tested in the subgenus *Pika*, where we have a set of species with different genetic divergence and similar ecological preferences.

Materials and methods

The initial dataset of species occurrences was obtained from the website <https://rusmam.ru> and from museum labels. Petrophilous pikas inhabit sparsely distributed colonies, frequently situated at distances of tens of kilometres from one another. The majority of these settlements are located in remote mountainous regions, distant from human infrastructure. It is therefore unlikely that a comprehensive dataset on the pikas under discussion will be collected in the near future. A total of 663 occurrence points of *O. hyperborea*, 42 of *O. mantchurica*, 109 of *O. alpina* and 121 of *O. turuchanensis* were gathered. The distribution areas of *O. hoffmanni* and *O. coreana* are so limited (approximately the first few thousand square kilometres) that they were not subjected to analysis. The data exhibited an irregular spatial distribution, with notable local aggregations, primarily attributable to the pikas' colonial habits and the limited number of accessible sites for data collection. The data underwent two filtering processes. The initial stage of the process involved the selection of one data point was selected for each square measuring 50 × 50 kilometres. This procedure allowed removing of closely situated points. Nevertheless, aggregations at a larger scale (corresponding to regions with better human infrastructure) were not removed. To address this,

the number of occurrence points within larger squares, measuring 280 × 280 kilometres (arbitrarily selected value), was examined. Outlier values (too many occurrences within a square) were corrected by random selection of the number of points corresponding to the upper quartile (0.75) threshold (Tab. 1).

In order to investigate spatial heterogeneity of study efforts, we selected species that can be detected using the same methods as pikas (visually and with snap trap) and live wider than pikas. Thus this data set included the occurrence points of all pikas, as well as those of the chipmunk (*Eutamias sibiricus* (Laxmann, 1769)) and red-backed vole (*Craseomys rufocanus* (Sundevall, 1846)).

The spatial frame of the analysis comprised a grid of 2 km resolution in Mollweide equidistant projection. A total of 58 environmental variables were employed in the analysis. The CHELSA "bioclimatic" variables, *chelsa_gsl*, *chelsa_gsp*, *chelsa_gst*, *chelsa_scd*, *chelsa_swe* (Karger *et al.*, 2017; Brun *et al.*, 2022), altitude, slopes inclination, global river density (Hengl, 2019; Ouellet Dallaire *et al.*, 2019), percentage of the forest cover (Global forest watch, 2024) and 42 MODIS generalised average monthly data layers (comprising six months of 2004 data across seven spectral bands; <http://glcf.umd.edu/data>) were employed as model predictors.

We used the ENMeval 2.0.3 R package (Muscarella *et al.*, 2014; Kass *et al.*, 2021) to build Maxent models with the "maxent.jar" algorithm. The modelling process was iterative. Each step involved the evaluation of a set of models with different parameters. The varying parameters were: regularisation multiplier ranging from 0.75 to 3, three combinations of feature classes (L, LQ and LQH, where L = linear, Q = quadratic and H = hinge) (Warren & Seifert, 2011; Merow *et al.*, 2013) and a set of coefficients influencing the background sample selection (Merow *et al.*, 2013; Guillera-Aroita *et al.*, 2015). The background sample is the critical unit in the analysis. We selected background points with a probability proportional to the level of sampling effort in the area. The background sample was restricted to a certain buffer area around the occurrence points (600 km) in order to exclude territories with definitely different ecological conditions. The expansion of the range of predictor variation results in the generalization of models (Lissovsky *et al.*, 2020). The probability of selection was changed in the provisional 'distribution area' of the species — a buffer of 30–120 km, depending on the species (the buffer size was selected in order to ensure that the set of buffers accurately reflects the distribution). The degree of this reduction (0.1–1) as well as the diameter of the buffer (200–5000 metres corresponding to selection of 1 raster cell or one or two cell layers around it) around the occurrence points during the background sample selection (selection of some surrounding points also in case of larger buffers) varied and the optimal value was chosen in each analysis. The training sample was excluded from the background sample. Optimality was assessed using the corrected Akaike's information criterion.

The first step was calculated with all environmental predictors included. The second step was carried out on the basis of those predictors whose permutation importance was above 5% in the first step. Environmental predictors were included in the analysis as is, without removing of multicollinearity, since Maxent algorithm address such issues (Elith *et al.*, 2011).

The general concept of comparing models is consistent with the methodology proposed by Warren *et al.* (2010) and Brown & Carnaval (2019). Terms used below follow these two papers. The methods are implemented in R package “humboldt” (Brown & Carnaval, 2019), but the package functions are not flexible enough (for example, one cannot compare models with different parameters or use geographic projections other than longitude/latitude), so we use our own code (Appendix).

The concept was to evaluate the similarity between two models (evaluated using Schoener’s D) with 100 models, calculated on the basis of randomly selected samples of the same size and the same model parameters, taken from the united sample. The ‘background test’ calculates a comparative array as the similarity between one of the species and a randomly selected sample around the occurrence points of the second species. This process can be described as searching for habitats that are suitable for one species in areas where the other species is present.

Two comparative analyses were conducted. The initial comparative analysis was conducted in geographical or G-space. In this instance, a comparison was conducted between rasters obtained following a MaxEnt analysis. Thus, an investigation was conducted to ascertain the degree of similarity in the spatial distribution of suitable habitats. It was not feasible to conduct a direct comparison of the models, given the significant discrepancy in the spatial extent of the species ranges. Therefore, we examined the degree of similarity in

sympatry or parapatry zones, limiting the spatial extent of our analysis to a rectangle circumscribed around the occurrence points of the species with the more limited distribution, with a 60-kilometre buffer. In the case of allopatric but closely distributed *O. alpina* and *O. turuchanensis*, both species distributions were included in the extent of the analysis.

The second analysis was carried out within the space of environmental predictors, or E-space. In this instance, the sets of environmental data corresponding to the occurrence points were processed. These sets were subjected to factor analysis, with the objective of maximizing inter-species differences. The first two axes (which explained the greatest interspecies differences) of the factor analysis were transformed into a rectangle raster comprising seven columns and six rows, with the number of occurrence points serving as the raster values. Consequently, the comparison of these rasters indicated the degree of similarity between the distributions of occurrence points in the space of predictor values.

Results

The distribution models of all four species appear to be accurate (Figs. 1–4). The high AUC values (Tab. 1) indicate a strong correspondence between the models and the occurrence points. The suitable habitats in the models of three species (*O. mantchurica*, *O. turuchanensis* and *O. alpina*) do not overlap in terms of Figs. 2–4, therefore comparison of *O. mantchurica* with *O. alpina* and *O. turuchanensis* in geographical space was not conducted (Tab. 2).

The northern pika model is the most expansive, encompassing the ranges of all other species. To provide further detail, the range of the northern pika covers the Altai Mountains, where only the *O. alpina* is found; the Great Khyngan Mountains and part of the Lesser

Table 1. Parameters of final optimal models for four pika species.

	<i>n</i> points	AUC	Regularisation multiplier R	Features	Parameters N
<i>O. alpina</i>	37	0.98	3	linear + quadratic + hinge	22
<i>O. turuchanensis</i>	22	0.89	0.75	linear + quadratic	8
<i>O. hyperborea</i>	117	0.87	3	linear + quadratic	23
<i>O. mantchurica</i>	19	0.98	0.75	linear + quadratic	8

Table 2. Similarity (Schoener’s D) of four pika species calculated on the basis of environmental predictors, measured in occurrence points (E-space, below diagonal) / species distribution models (G-space, above diagonal). All values significantly (< 0.05) differ from the sample, calculated on the basis of randomly selected data.

	<i>O. alpina</i>	<i>O. turuchanensis</i>	<i>O. hyperborea</i>	<i>O. mantchurica</i>
<i>O. alpina</i>	—	0.17	0.68	—
<i>O. turuchanensis</i>	0.03	—	0.65	—
<i>O. hyperborea</i>	0.26	0.3	—	0.61
<i>O. mantchurica</i>	0.03	0.06	0.15	—

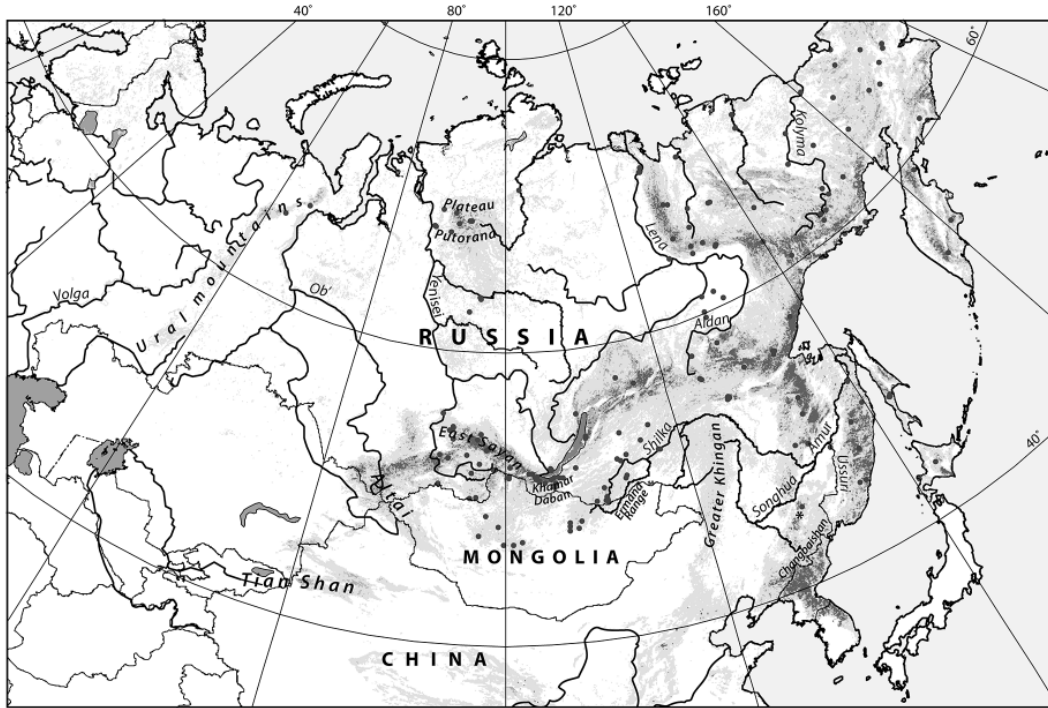


Fig. 1. The geographical pattern of distribution of suitable habitats for the northern pika *Ochotona hyperborea*. Known occurrences are shown with dots. The three grades of grey scale reflect three diapasons of relative suitability: maximum training sensitivity plus specificity threshold–0.75 (light); 0.75–0.9 (medium); 0.9–1 (dark). The Zhangguangcai Ling Mountains are indicated with an asterisk.

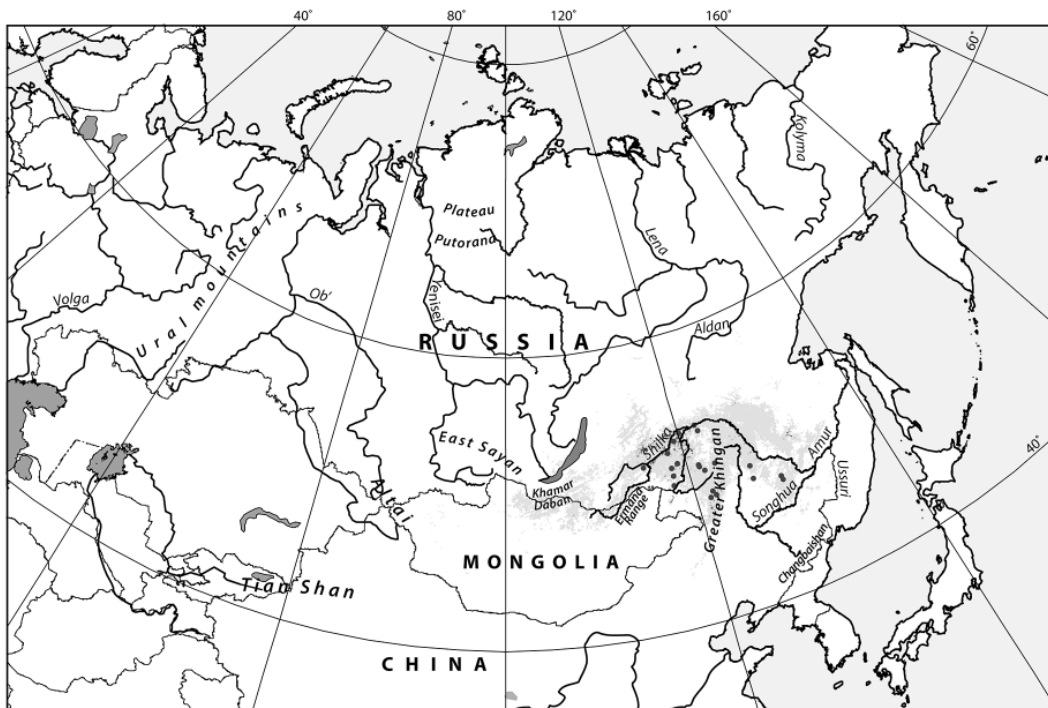


Fig. 2. The geographical pattern of distribution of suitable habitats for the Manchurian pika *Ochotona manchurica*. Known occurrences are shown with dots. The three grades of grey scale reflect three diapasons of relative suitability: maximum training sensitivity plus specificity threshold–0.75 (light); 0.75–0.9 (medium); 0.9–1 (dark).



Fig. 3. The geographical pattern of distribution of suitable habitats for the Altai pika *Ochotona alpina*. Known occurrences are shown with dots. The three grades of grey scale reflect three diapasons of relative suitability: maximum training sensitivity plus specificity threshold–0.75 (light); 0.75–0.9 (medium); 0.9–1 (dark).



Fig. 4. The geographical pattern of distribution of suitable habitats for the Turukhan pika *Ochotona turuchanensis*. Known occurrences are shown with dots. The three grades of grey scale reflect three diapasons of relative suitability: maximum training sensitivity plus specificity threshold–0.75 (light); 0.75–0.9 (medium); 0.9–1 (dark).

Khingan Mountains, where only the *O. mantchurica* is found; the Ermana Range, which is the distribution range of the *O. hoffmanni* and the Changbaishan Mountains, which is the distribution range of the *O. coreana*.

In contrast, the distribution model of *O. turuchanensis* appears to be additive to that of *O. hyperborea*. The Turukhan pika's suitable habitats encompass Middle Siberia, specifically the interfluvium of the Yenisei and Lena Rivers, the upper and middle Lena Basin, and the interfluvium of the Lena and Aldan Rivers, where northern pika habitats are either absent or scarce.

The distribution model of *O. mantchurica* is relatively local in comparison to the two previous species, and broadly aligns with the actual distribution of the species. However, it also encompasses the Ermana Range (the distribution range of *O. hoffmanni*) and the Khentei-Chikoy Highlands (which are inhabited by *O. hyperborea*). Suitable habitats of *O. mantchurica* do not extend to the Changbaishan Mountains.

The distribution model of *O. alpina* is also relatively local, covering the species' actual distribution range. However, there is a discrepancy between the model and the actual distribution, with the Khamar-Daban Range being an exception. This mountain range is separated from the main distribution of *O. alpina* by a band of unsuitable habitats.

The predicted potential distribution of all four species indicates the presence of suitable habitat in remote, uninhabited areas. The species *Ochotona alpina* and *O. hyperborea* exhibit suitable habitats in the Tibetan region and its surrounding areas. Models of the same species have potentially suitable regions in the Scandinavian mountains (not shown in the Figures), the Tian Shan Mts, and the isolated mountains of the Tarbagatai and Saur to the north of them. A substantial proportion of the suitable habitats for *O. turuchanensis* are situated in the north-east of Eurasia and in the Ural Mountains.

In the context of environmental variables, the degree of intersection between species pairs is lower than in G-space (Tab. 2). The values of inter-species similarity are marginally higher when comparing *O. hyperborea* with *O. alpina* and *O. turuchanensis*, which is to be expected given that these pairs of species are partially sympatric. All background tests conducted on the pairs of species yielded insignificant results.

Discussion

Petrophilous pikas are found in stony habitats that exhibit considerable similarity in different sites across Asia. Talus formations can vary considerably in terms of the size and type of stone comprising them, as well as in relation to factors such as depth, slope exposition and inclination, the presence or absence of water sources, and the extent of projective cover afforded by vegetation. Such parameters frequently depend on the geological structure of the mountains in question. In light of the considerable diversity of habitats within each species, it is difficult to formulate any provisional hypotheses regarding the similarities or differences in

ecological preferences between different species. Our investigation provides a potential basis for formulating such a hypothesis.

Our results demonstrate that all four pika species exhibit considerable niche divergence. This assertion is supported by the minimal overlap observed between species in the ecological predictor space (Tab. 2), coupled with the lack of statistical significance in the background tests (Tab. 2). The analysis of shared E-space recommended by Brown & Carnaval (2019) is not applicable in this case due to the absence or limited extent of this shared space.

The degree of similarity between distribution models in geographical space (maps of suitable habitats) in areas of species sympatry or distribution junction is also low (Tab. 2). Furthermore, in areas where two or more species coexist or are potentially capable of coexisting, the predicted spatial distribution of each pair of species is not identical. A straightforward comparison of the distribution of *O. hyperborea* and *O. mantchurica* in Manchuria, *O. alpina* and *O. hyperborea* in the Altai and Sayan Mountains, for instance, reveals notable discrepancies. It is well documented that *O. hyperborea* occupies different habitats than *O. alpina* and *O. turuchanensis* in sympatric zones (Formozov, 1986; Formozov & Yakhontov, 2003). However, the segregation of habitats between two species can be caused not only by different ecological preferences, but also by a shift in individual choice due to interspecies competition. The results demonstrate that different ecological preferences may be a significant factor in determining the potential for sympatry.

The dataset comprises two pairs of species that are closely related. The first pair is that of *O. alpina* and *O. turuchanensis*, while the second consists of *O. hyperborea* and *O. mantchurica*. It can be proposed that the degree of similarity observed within these pairs is less pronounced than that observed between members of different pairs (Tab. 2). Turukhan pika occupies the most distinct niche in both E- and G-space. It occupies habitats and ecological space that are unsuitable for other species (Fig. 4, Tab. 2), and exhibits the lowest degree of similarity to *O. alpina*. We hypothesise that the marked divergence of the ecological niches of this pair of sister species is a result of the recent process of speciation. It is likely that the shift in the ecological niche of *O. turuchanensis* led to the expansion of its range to the north, resulting in the separation of its distribution. The second pair did not require a significant alteration in its ecological preferences, as the distribution of *O. hyperborea* and *O. mantchurica* is separated by the Amur River. It seems plausible to suggest that the primary driver of speciation in this pair of species was the isolation of the Manchurian portion of their distribution range.

Particular issues. Our analysis indicates several new issues in the distribution of *Pika* species that had been never discussed before. First of all, we can say that potential distribution of all four species under discus-

sion is not realised in full. Every species has some areas that can be settled, if our models are true, but some barriers prevent the invasion of these areas. Leaving aside the remote areas, such as Tibet or Tian Shan, there are some areas adjacent to the main range in all cases.

In the case of *O. alpina*, the unsettled patch in question is the Khamar-Daban Range. The mountain range is geographically isolated from the East Sayan Mountains, which are inhabited by this species of pika, by the wide valley of the Irkut River. It is currently unknown whether *O. alpina* ever crossed the Irkut River valley in the past. However, our analysis indicates that this was a feasible possibility.

The potential distribution of the Turukhan pika is the least realised. The Ural Mountains offer suitable habitats for this species, which is isolated from the main distribution range by a considerable distance. The Ural Mountains are inhabited by *O. hyperborea*, and the genetic distance between the Ural population and that of the Putorana Plateau is minimal (Lissovsky *et al.*, 2021). It can therefore be concluded that the northern pika has recently reached the Ural (at least, the last time). It remains unclear whether suitable habitats for the Turukhan pika existed along the route from the Putorana to the west at the time in question, or whether *O. turuchanensis* was absent in the Putorana region at the time the route to the west was opened. In any case, the Turukhan pika is currently absent in the Urals.

The *O. turuchanensis* model displays a considerable proportion of suitable habitats to the east of the Lena River, an area where the species has never been registered, with the exception of the upper part of the Lena basin. It is hypothesised that additional attention needs to be paid to the area of the Lena and Aldan Rivers interfluvium. Only a few individuals from this vast area have been the subject of study (Lissovsky, 2003; Lissovsky *et al.*, 2021), with identification based solely on morphology. Nevertheless, the region in question is suitable for *O. turuchanensis* but presents a low suitability rating for *O. hyperborea*.

The distribution of suitable habitats for *O. hyperborea* displays a number of distinct areas, which are discussed in further detail below. The first area is the Altai Mountains, where the northern pika is currently absent. It can be hypothesised that the Yenisei River acts as an effective barrier in this instance. The colonisation of Altai from the south of the Yenisei (through Tuva) is unlikely due to the disjunction of suitable habitats. Altai was inhabited by *O. hyperborea* during the Pleistocene (Lissovsky & Serdyuk, 2004), indicating that the barrier of the Yenisei is not absolute.

The second location is the Changbaishan Plateau, as defined by the broader geographical context. The *O. hyperborea* model encompasses the entire Plateau, including the Changbaishan Mountain, which is the sole location where *O. coreana* has been found. Additionally, a region of suitable habitat is present within the Zhangguangcai Ling Mountains, situated between the Songhua and Mudanjiang Rivers. No information was available regarding the presence of pikas in this area.

A recent publication (Zhang *et al.*, 2020) described the mitogenome of a pika from this location. The authors incorrectly identified the specimen as *O. coreana*, however, the mitogenome (GenBank ID MT017929) belongs to *O. hyperborea*. Therefore, our distribution model is confirmed to be accurate in this location. The specimen with mitogenome MT017929 represents the first record of *O. hyperborea* in China. This is the first evidence to indicate that the distribution ranges of *O. manchurica* and *O. coreana* are separated by the territory inhabited by *O. hyperborea*. Furthermore, we can now conclude that the distribution ranges of *O. manchurica* and *O. hyperborea* are separated by the Amur and Songhe Rivers.

The potential distribution of *O. manchurica* includes not only the southern bank of the Amur (and Shilka) River, but also the northern bank and the Khentei-Chikoy Highlands, where the species is absent. Therefore, the absence of Manchurian pikas to the north and east of the current distribution is not a consequence of the absence of suitable habitats.

It can be concluded that the implementation of ecological models that predict potential distribution is of significant importance in demonstrating the influence of geographical barriers on the distribution of *Pika* species. All four species have uninhabited territories in close proximity to the main range, but separated by river valleys. In all cases, these territories are occupied by another species. Thus, the Altai region is suitable for *O. hyperborea* and is currently inhabited by *O. alpina*. Conversely, the Khamar-Daban Range is suitable for *O. alpina* and is currently inhabited by *O. hyperborea*. The eastern bank of the Lena River is suitable for *O. turuchanensis* and is currently inhabited by *O. hyperborea*. Both banks of the Amur River are suitable for *O. hyperborea* and *O. manchurica*, but the river serves as a natural barrier, dividing the distribution of these two species. It is evident that rivers act as barriers to the distribution of these species. Nevertheless, it is not yet possible to determine whether the rivers themselves act as barriers or whether the presence of different species prevents pikas from penetrating the territory over the rivers.

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Appendix. R-code of our calculations.

```

#G-space
library(dismo)
library(raster)
base_dir <- "/var/www/rusmam/modeling/data/119/"
pdf(file = paste(base_dir, 'Rplots.pdf', sep=""))
Nreps <- 101
csv1.file <- "/var/www/rusmam/modeling/data/120/species.csv"
csv2.file <- "/var/www/rusmam/modeling/data/52/species.csv"
bias.file <- "/var/www/rusmam/modeling/data/120/bias.csv"
env.file <- list.files(path="/var/www/rusmam/modeling/coverage/tmp", pattern = ".asc$", full.names = T, include.dirs = F)
proj.file <- list.files(path="/var/www/rusmam/modeling/coverage/tmp", pattern = ".asc$", full.names = T, include.dirs = F)
buffer1.val <- c(5000)
buffer2.val <- c(5000)
Rs1 <- 3
Rs2 <- 0.75
Pred1.fs <- "LQ"
Pred2.fs <- "LQ"
range1.buf <- 120000
range2.buf <- 85000
bias1.range <- 0.1
bias2.range <- 1
cut1.buf <- 600000
cut2.buf <- 950000
env.proc <- "predictors"
max.bckg <- 10000
max.pc <- 10000
pc.threshold <- c(0.99995)
NCores <- 2
dist.threshold <- 45000
meth.bg <- 'maxent-like'
project.res <- 'no'
control_bckg <- 'no'
mask_train_sample <- 'yes'
result_type <- 'cloglog'

prj <- CRS("+proj=moll+lon_0=30+x_0=3335846.22854+y_0=-336410.83237 +ellps=WGS84 +datum=WGS84 +units=m +no_defs")
prj_ll <- CRS("+proj=longlat +ellps=WGS84 +datum=WGS84 +no_defs")
meth <- 'maxent.jar'
max.par <- 0
num.pc <- 0

time_start <- Sys.time()
csv1.dat <- read.csv(paste(csv1.file, sep=""))
names(csv1.dat) <- c("sp", "x", "y")
csv2.dat <- read.csv(paste(csv2.file, sep=""))
names(csv2.dat) <- c("sp", "x", "y")
model1.name <- csv1.dat[1,1]
model2.name <- csv2.dat[1,1]
cat("\n****", model1.name, " and ", model2.name, " G-Niche Equivalency Test****", date(), "\n")
csv1.spp <- SpatialPoints(cbind(csv1.dat[,2], csv1.dat[,3]), prj)
csv2.spp <- SpatialPoints(cbind(csv2.dat[,2], csv2.dat[,3]), prj)

env.stack <- lapply(env.file, raster)
env.stack <- stack(env.stack)
crs(env.stack) <- prj
one.ras <- env.stack[[1]]/env.stack[[1]]
if(project.res == 'yes')
{
  proj.stack <- lapply(proj.file, raster)
  proj.stack <- stack(proj.stack)
  crs(proj.stack) <- prj
}

csv.out <- extract(one.ras, csv1.spp)
csv1.spp <- csv1.spp[which(csv.out>0)]
csv.out <- extract(one.ras, csv2.spp)
csv2.spp <- csv2.spp[which(csv.out>0)]
csv2.ext <- extent(buffer(csv2.spp, width=60000, dissolve=F))
bias.dat <- read.csv(paste(bias.file, sep=""))
bias.spp <- SpatialPointsDataFrame(cbind(bias.dat[,2], bias.dat[,3]), as.data.frame(cbind(bias.dat[,1], bias.dat[,4])), proj4string = prj)

test.dat <- bias.dat[bias.dat$Species == model1.name,]
test.spp <- SpatialPoints(cbind(test.dat[,2], test.dat[,3]), prj)
env.temp <- one.ras
env.temp[cellFromXY(env.temp, csv1.spp@coords)] <- NA
if(mask_train_sample=="yes")
{
  test.out <- extract(env.temp, test.spp)
  test.spp <- test.spp[which(test.out>0)]
} else {
  test.out <- extract(one.ras, test.spp)
  test.spp <- test.spp[which(test.out>0)]
}

bias.buf <- buffer(bias.spp, width=buffer1.val, dissolve=F)
bias_strict.buf <- buffer(bias.spp[which(bias.spp$V1 == model1.name)], width=range1.buf)
distmat <- pointDistance(csv1.spp@coords, csv1.spp@coords, type='Euclidean', lonlat = F, allpairs = TRUE)
vec.min.dist <- apply(distmat, 1, function(x) min(x[which(x>0)]))
crop.buf <- buffer(SpatialPoints(csv1.spp)[which(csv1.spp@coords[,1]<3000000 | vec.min.dist < 400000)], width=cut1.buf)
env.temp <- env.temp*0.01
env.temp <- rasterize(crop.buf, env.temp, 1, update = T, updateValue = 'NA')
bg.ras <- rasterize(bias.buf, env.temp, "V1", fun='count', update = T, updateValue = 'NA')
bg2.ras <- rasterize(bias.buf, env.temp, "V1", fun=function(x,...){length(unique(x))}, update = T, updateValue = 'NA')
bg3.ras <- rasterize(bias_strict.buf, env.temp, field=bias1.range, update = T, updateValue = 'NA')
bg.ras <- bg3.ras*log(bg.ras*0.1 + bg2.ras)
bg.ras[which(values(bg.ras)<0)] <- 0
bg.num <- length(bg.ras[bg.ras > 0])
if (bg.num > max.bckg) bg.num <- max.bckg
bg1 <- as.data.frame(randomPoints(bg.ras, bg.num, prob = T, lonlatCorrection = F))
plot(one.ras, main=paste("Background points for species 1"))
plot(bg.ras, add=T)
bg1.spp <- SpatialPoints(cbind(bg1[,1], bg1[,2]), prj)
plot(bg1.spp, add=T)

```

```

if(grepl('L', Pred1.fs)==TRUE) { Lf <- 'linear=true'
} else { Lf <- 'linear=false' }
if(grepl('Q', Pred1.fs)==TRUE) { Qf <- 'quadratic=true'
} else { Qf <- 'quadratic=false' }
if(grepl('P', Pred1.fs)==TRUE) { Pf <- 'product=true'
} else { Pf <- 'product=false' }
if(grepl('H', Pred1.fs)==TRUE) { Hf <- 'hinge=true'
} else { Hf <- 'hinge=false' }
if(grepl('T', Pred1.fs)==TRUE) { Tf <- 'threshold=true'
} else { Tf <- 'threshold=false' }
Rf <- paste("betamultiplier=", Rs1, sep="")
If <- 'maximumiterations=5000'
args1.max <- c(Lf, Qf, Pf, Hf, Tf, Rf, If)

test.dat <- bias.dat[bias.dat$Species == model2.name,]
test.spp <- SpatialPoints(cbind(test.dat[,2], test.
dat[,3]),prj)
env.temp <- one.ras
env.temp[cellFromXY(env.temp, csv2.spp@coords)] <- NA
if (mask_train_sample=="yes")
{
  test.out <- extract(env.temp, test.spp)
  test.spp <- test.spp[which(test.out>0)]
} else {
  test.out <- extract(one.ras, test.spp)
  test.spp <- test.spp[which(test.out>0)]
}

bias.buf <- buffer(bias.spp, width=buffer2.val, dissolve=F)
bias_strict.buf <- buffer(bias.spp[which(bias.spp$V1 ==
model2.name),], width=range2.buf)
distmat <- pointDistance(csv2.spp@coords, csv2.spp@
coords, type='Euclidean', lonlat = F, allpairs = TRUE)
vec.min.dist <- apply(distmat, 1, function(x)
min(x[which(x>0)]))
crop.buf <- buffer(SpatialPoints(csv2.spp)[which(csv2.
spp@coords[,1]<3000000 | vec.min.dist < 400000)],
width=cut2.buf)
env.temp <- env.temp*0.01
env.temp <- rasterize(crop.buf, env.temp, 1, update = T,
updateValue = 'NA')
bg.ras <- rasterize(bias.buf, env.temp, "V1", fun='count',
update = T, updateValue = 'NA')
bg2.ras <- rasterize(bias.buf, env.temp, "V1",
fun=function(x,...){length(unique(x))}, update
= T, updateValue = 'NA')
bg3.ras <- rasterize(bias_strict.buf, env.temp, field=bias2.
range, update = T, updateValue = 'NA')
bg.ras <- bg3.ras*log(bg.ras*0.1 + bg2.ras)
bg.ras[which(values(bg.ras)<0)] <- 0
bg.num <- length(bg.ras[bg.ras > 0])
if (bg.num > max.bckg) bg.num <- max.bckg
bg2 <- as.data.frame(randomPoints(bg.ras, bg.num,
prob = T, lonlatCorrection = F))
plot(one.ras, main=paste("Background points for species 2"))
plot(bg.ras, add=T)
bg2.spp <- SpatialPoints(cbind(bg2[,1],bg2[,2]),prj)
plot(bg2.spp, add=T)

if(grepl('L', Pred2.fs)==TRUE) { Lf <- 'linear=true'
} else { Lf <- 'linear=false' }
if(grepl('Q', Pred2.fs)==TRUE) { Qf <- 'quadratic=true'
} else { Qf <- 'quadratic=false' }
if(grepl('P', Pred2.fs)==TRUE) { Pf <- 'product=true'
} else { Pf <- 'product=false' }

```

```

if(grepl('H', Pred2.fs)==TRUE) { Hf <- 'hinge=true'
} else { Hf <- 'hinge=false' }
if(grepl('T', Pred2.fs)==TRUE) { Tf <- 'threshold=true'
} else { Tf <- 'threshold=false' }
Rf <- paste("betamultiplier=", Rs2, sep="")
If <- 'maximumiterations=5000'
args2.max <- c(Lf, Qf, Pf, Hf, Tf, Rf, If)

if(project.res == 'yes')
{
  env.pc <- proj.stack
} else {
  env.pc <- env.stack
}
l1 <- length(csv1.spp)
l2 <- length(csv2.spp)
csv.spp <- bind(csv1.spp, csv2.spp)
Drandom <- vector()
for (i in 1:Nreps)
{
  if(i>1) cat("\nIteration ", i-1, "\n")
  modm1 <- maxent(env.stack, csv1.spp@coords,
a=bg1, args=args1.max)
  modm2 <- maxent(env.stack, csv2.spp@coords,
a=bg2, args=args2.max)
  result1.ras <- predict(modm1, env.pc,
args=c(paste0("outputformat=", result_type)),
progress='text')
  result2.ras <- predict(modm2, env.pc,
args=c(paste0("outputformat=", result_type)),
progress='text')
  result1.ras <- crop(result1.ras, csv2.ext)
  result2.ras <- crop(result2.ras, csv2.ext)
  D <- nicheOverlap(result1.ras, result2.ras, stat='D',
mask=FALSE, checkNegatives=FALSE)
  if(i==1)
  {D0 <- D
  plot(result1.ras, main=model1.name)
  plot(result2.ras, main=model2.name)
  } else Drandom[i-1] <- D
  x3 <- sample(x = c(1:(l1+l2)), size = 11, replace =
FALSE)
  csv1.spp <- csv.spp[x3]
  csv2.spp <- csv.spp[-x3]
}

hist(Drandom, main="D", xlim=c(0,1), include.lowest =
TRUE, nclass = 10)
abline(v = D0, col = "red", lty = 2)
p.D <- (1-pnorm(D0, mean(Drandom), sd(Drandom), lower.
tail = FALSE))
cat("D-index", D0)
cat("p-value: ", p.D)
write.table(D0, file=paste(base_dir, "result", ".csv", sep=""),
append = FALSE, row.names = F, col.names = "D0", sep =
",")
write.table(Drandom, file=paste(base_dir, "result", ".csv",
sep=""), append = TRUE, row.names = F, col.names = "Dran-
dom", sep = ",")
write.table(p.D, file=paste(base_dir, "result", ".csv", sep=""),
append = TRUE, row.names = F, col.names = "p-value", sep
=",")

time_diff <- difftime(Sys.time(), time_start, units='mins')
cat ("\nTime elapsed:", round(time_diff,2), "minutes\n")

```

```

#E-space
library(dismo)
library(raster)

base_dir <- "/var/www/rusmam/modeling/data/119/"
pdf(file = paste(base_dir, "Rplots.pdf", sep=""))
Nreps <- 101
csv2.file <- "/var/www/rusmam/modeling/data/52/species.csv"
csv1.file <- "/var/www/rusmam/modeling/data/120/species.csv"
env.file <- list.files(path="/var/www/rusmam/modeling/coverage/rf", pattern = ".asc$", full.names = T, include.dirs = F)
e.dist <- 10000 #distance for Background Test

rotate.between.groups <- function (X, groups)
{
  if (is.data.frame(X))
    X <- as.matrix(X)
  else if (is.matrix(X))
    stop("'X' must be a matrix or a data frame")
  if (!all(is.finite(X)))
    stop("'X' must contain finite values only")
  if (is.na(match(",groups")) == FALSE)
  {
    X1 <- X[-(which(groups == ",")),]
  } else {
    X1 <- X
  }
  groups <- factor(groups)
  glev <- levels(groups)
  nlev <- length(glev)
  gsizes <- as.vector(table(groups))
  if (1 %in% gsizes) {
    warning("group with one entry found")
  }
  p <- ncol(X1)
  Gmeans <- matrix(NA, nrow = nlev, ncol = p, dimnames = list(glev, colnames(X1)))
  for (i in 1:nlev) {
    Gmeans[i, ] <- apply(X1[which(groups == glev[i]), ], 2, mean)
  }
  B <- cov(Gmeans)
  dimnames(B) <- list(colnames(X1), colnames(X1))
  EV <- eigen(B)
  Factor.res <- as.matrix(X) %>% EV$vectors
  RES <- list()
  RES$eigen.values <- round(EV$values, 6)
  RES$factors <- Factor.res
  return(RES)
}

prj <- CRS("+proj=moll+lon_0=30+x_0=3335846.22854+y_0=-336410.83237+ellps=WGS84+datum=WGS84+units=m+no_defs")

time_start <- Sys.time()
csv1.dat <- read.csv(paste(csv1.file, sep=""))
names(csv1.dat) <- c("sp", "x", "y")
csv2.dat <- read.csv(paste(csv2.file, sep=""))
names(csv2.dat) <- c("sp", "x", "y")
model1.name <- csv1.dat[1,1]
model2.name <- csv2.dat[1,1]
cat("\n****", model1.name, " and ", model2.name, " Niche Overlap and Niche Divergence Tests****", date(), "\n")

csv1.spp <- SpatialPoints(cbind(csv1.dat[,2], csv1.dat[,3]), prj)
csv2.spp <- SpatialPoints(cbind(csv2.dat[,2], csv2.dat[,3]), prj)
env.stack <- lapply(env.file, raster)
env.stack <- stack(env.stack)
crs(env.stack) <- prj
one.ras <- (env.stack[[1]]+env.stack[[2]])/(env.stack[[1]]+env.stack[[2]])

csv.out <- extract(one.ras, csv1.spp)
csv1.spp <- csv1.spp[which(csv.out>0)]
csv.out <- extract(one.ras, csv2.spp)
csv2.spp <- csv2.spp[which(csv.out>0)]
csv.spp <- bind(csv1.spp, csv2.spp)
points.ext <- extent(buffer(csv.spp, width=1000))
env.stack <- crop(env.stack, points.ext)
one.ras <- crop(one.ras, points.ext)

env1.temp <- one.ras
env1.temp[cellFromXY(env1.temp, csv1.spp@coords)] <- NA
env2.temp <- one.ras
env2.temp[cellFromXY(env2.temp, csv2.spp@coords)] <- NA

bckg1 <- extract(env1.temp, csv1.spp, cellnumbers=T, buffer=e.dist)
bckg2 <- extract(env2.temp, csv2.spp, cellnumbers=T, buffer=e.dist)

cat("Preparation is finished, start of analysis.\n")
dat1 <- cbind(sp = rep(model1.name, length(csv1.spp)), data.frame(extract(env.stack, csv1.spp)))
dat2 <- cbind(sp = rep(model2.name, length(csv2.spp)), data.frame(extract(env.stack, csv2.spp)))
dat <- rbind(dat1, dat2)
dat[,2:ncol(dat)] <- scale(dat[,2:ncol(dat)])

factors <- rotate.between.groups(dat[,2:ncol(dat)], dat[,1])
plot(x=factors$factors[,1], y=factors$factors[,2], )
points(x=factors$factors[which(dat[,1] == model1.name),1], y=factors$factors[which(dat[,1] == model1.name),2], col = "blue")
points(x=factors$factors[which(dat[,1] == model2.name),1], y=factors$factors[which(dat[,1] == model2.name),2], col="red")
legend("bottomright", legend = c(model1.name, model2.name), col = c("blue", "red"), pch = c(1, 1))
write.table(cbind(dat[,1], factors$factors[,1:2]), file=paste(base_dir, "result", ".csv", sep=""), append = FALSE, row.names = F, col.names = T, sep = ",")
factors$eigen.values
x <- raster(ncol=7, nrow=6, xmn=mean(factors$factors[,1])-1.99*sd(factors$factors[,1]), xmx=mean(factors$factors[,1])+1.99*sd(factors$factors[,1]), ymn=mean(factors$factors[,2])-1.99*sd(factors$factors[,2]), ymx=mean(factors$factors[,2])+1.99*sd(factors$factors[,2]))
sp.names <- dat[,1]
l1 <- nrow(dat1)
l2 <- nrow(dat2)
Drandom <- vector()
sp1 <- cbind(factors$factors[which(sp.names == model1.name),1], factors$factors[which(sp.names == model1.name),2])
sp2 <- cbind(factors$factors[which(sp.names == model2.name),1], factors$factors[which(sp.names == model2.name),2])
for (i in 1:Nreps)
{

```



```

if(i>1) cat("\nIteration ", i-1, "\n")
sp1.ras <- rasterize(sp1, x, fun='count')
sp1.ras <- sp1.ras/sp1.ras@data@max
sp2.ras <- rasterize(sp2, x, fun='count')
sp2.ras <- sp2.ras/sp2.ras@data@max
sp1.ras[is.na(sp1.ras[])] & !is.na(sp2.ras[]) <- 0
sp2.ras[is.na(sp2.ras[]) & !is.na(sp1.ras[])] <- 0

D <- nicheOverlap(sp1.ras, sp2.ras, stat='D', mask=FALSE,
checkNegatives=FALSE)
if(i==1) {
  D0 <- D
  plot(sp1.ras)
  plot(sp2.ras)
} else { Drandom[i-1] <- D }
x3 <- sample(x = c(1:(l1+l2)), size = l1, replace =
FALSE)
sp1 <- cbind(factors$factors[x3,1], factors$factors[x3,2])
sp2 <- cbind(factors$factors[-x3,1], factors$factors[-
x3,2])
sp.names[x3] <- model1.name
sp.names[-x3] <- model2.name
factors <- rotate.between.groups(dat[,2:ncol(dat)], sp.names)
}

hist(Drandom, main="Schoener's D", xlim=c(0,1), include.low-
est = TRUE, nclass = 10)
abline(v = D0, col = "red", lty = 2)
p0.D <- 2*(1-pnorm(D0, mean(Drandom), sd(Drandom), lower.
tail = FALSE))
write.table(D0, file=paste(base_dir, "result", ".csv", sep=""), ap-
pend = TRUE, row.names = F, col.names = "D0", sep = ",")
write.table(Drandom, file=paste(base_dir, "result", ".csv",
sep=""), append = TRUE, row.names = F, col.names = "Dran-
dom", sep = ",")
write.table(p0.D, file=paste(base_dir, "result", ".csv", sep=""),
append = TRUE, row.names = F, col.names = "p-value", sep =
",")
cat("D-index", D0)
cat("p-value: ", p0.D)

for (i in 1:(Nreps-1))
{
  if(i>1) cat("\nIteration ", i-1, "of the Background test sp1 (",
model1.name, ") -> bckg2\n")
  n.list <- vector()
  for (k in 1:l2)
  {
    n <- sample(which(bckg2[[k]][,2]>0), 1, replace = FALSE)
    n.list[k] <- bckg2[[k]][n,1]
  }
  bckg2.sample <- cbind(sp = rep(model2.name, l2), data.
frame(extract(env.stack, n.list)))
  dat <- rbind(dat1, bckg2.sample)
  dat[,2:ncol(dat)] <- scale(dat[,2:ncol(dat)])
  factors <- rotate.between.groups(dat[,2:ncol(dat)], dat[,1])
  factors$eigen.values
  sp.names <- dat[,1]
  sp1 <- cbind(factors$factors[which(sp.names ==
model1.name),1], factors$factors[which(sp.names == model1.
name),2])
  sp2 <- cbind(factors$factors[which(sp.names ==
model2.name),1], factors$factors[which(sp.names == model2.
name),2])
  sp1.ras <- rasterize(sp1, x, fun='count')
  sp1.ras <- sp1.ras/sp1.ras@data@max
  sp2.ras <- rasterize(sp2, x, fun='count')
  sp2.ras <- sp2.ras/sp2.ras@data@max
  sp1.ras[is.na(sp1.ras[])] & !is.na(sp2.ras[]) <- 0
  sp2.ras[is.na(sp2.ras[]) & !is.na(sp1.ras[])] <- 0

  Drandom[i-1] <- nicheOverlap(sp1.ras, sp2.ras, stat='D',
mask=FALSE, checkNegatives=FALSE)
}

hist(Drandom, main="Sp2 -> bckg1 Schoener's D", xlim=c(0,1),
include.lowest = TRUE, nclass = 10)
abline(v = D0, col = "red", lty = 2)
p2.D <- 2*(1-pnorm(D0, mean(Drandom), sd(Drandom), lower.
tail = FALSE))
cat("D-index", D0)
cat("np-value (Equivalency): ", p0.D)
cat("\nSp1 (", model1.name, ") -> bckg2 p-value: ", p1.D)
cat("\nSp2 (", model2.name, ") -> bckg1 p-value: ", p2.D)

time_diff <- difftime(Sys.time(), time_start, units='mins')
cat ("\nTime elapsed:", round(time_diff,2), "minutes\n")

```