

Environmental suitability throughout the late Quaternary explains population genetic diversity.

Norma Hernandez, Angel Robles Nathan Upham

2023-06-27

Abstract

Genetic variation among populations is known to exhibit biogeographic patterns in many species, but general rules of spatial genetic variation have not been established. In this paper, we establish a theoretical framework based on projecting environmental Grinnellian niches back through time to relate the present geographic distribution of population genetic structure to a given species' historical evolutionary context.

Thanks to the advance of next-generation sequencing technologies, as well as more accurate climate models and an enormous amount of information stored in biological collections, it is possible to implement this theoretical framework directly. We use as a case study the Tassel-eared Squirrel (*Sciurus aberti*) to jointly analyze spatial, environmental, and genetic data to predict the historical endemic area of this species. Our results reveal that in cases of genetic isolation by geographic distance, the prevalence of environmental suitability over time corresponds to the genetic fixation index of populations with respect to a source population. Populations closer to the historical endemic area present a higher genetic diversity and a lower F_{st} value.

This empirical example fits into a theoretical framework, which allows us two advances: (i) we can now add a biogeographic explanation to the results obtained with population genetic methods; and (ii) we can generate maps of this genetic structure as predictive tools to support biodiversity conservation efforts. Overall, this work advances a perspective that integrates population genetics with historical patterns of species distribution.

Introduction

Current species distributions do not always correspond to their historical distributions over evolutionarily significant periods. Often they differ substantially, such as in the case of postglacial range expansion in high latitude environments (e.g., Lessa, Cook, and Patton (2003)). This is because environmental conditions are highly dynamic over time, and species tend to track those environments, distributing where conditions are most favorable. That is, species environmental niches tend to be conserved (Peterson (2011)).

It follows from this relationship between environment and species distribution that population size also varies with time. This variation in population size is related to the effective population size N_e (Karlin 1968), so that an index reflecting changes in environmental conditions in geography might be expected to be related to N_e and thus to indicators of population structure such as the fixation index F_{st} . It should therefore be possible to relate patterns of change in the distribution of species to the genetic structure of their populations using a statistical model that explains this relationship.

With this approach we expect to predict the geographic pattern of population-genetic structure from abiotic environmental information alone. This approach is strongly driven by advances in currently available climate simulations (Leonardi et al. 2023; Krapp et al. 2021), as well as next-generation sequencing data, and supported by both ecological niche (Thorup et al. 2021; Nogués-Bravo 2009; Lira-Noriega and Manthey 2014) and population genetics theories (Walsh and Lynch 2018). Importantly, these predicted patterns of population structure will serve as a type of *a priori* hypothesis for the influence of abiotic factors alone, with

the empirical detection of deviations from this hypothesis indicating that biotic factors such as competition or predation from other species have also impacted the observed population structure.

In this work, we propose a method to find an index that we call the Suitability Prevalence Area (SPA) that is the area of highest environmental suitability for a given species over a historical time period. The SPA is an index with a double purpose: 1) identifying areas of greatest likelihood for the historical distribution of a target species (i.e., historical endemism); and 2) to explain the expected patterns of genetic diversity given the species' inferred history of population stability and connectivity.

As a case study, we consider Tassel-eared Squirrels (*Sciurus aberti*), a species of rodent that is currently distributed in disjunct patches from the southern Rocky Mountains in the United States to the northern Sierra Madre Occidental in Mexico for which it is possible to find reliable information on both the genetic structure of its populations and its current distribution (Bono et al. 2018; Burgin et al. 2018). To obtain the SPA for *S. aberti*, we overlapped historical reconstructions of the species' geographical distribution estimated every 2,000 years from the present day until 120,000 years ago, recording the environmental suitability in each time interval at each modeled site.

Subsequently, we calculated the fixation index (F_{st}) of the genetic relatedness among populations and compared that to the SPA index of historical endemism, constructing a statistical model of the fixation index as a function of the SPA. With this explanatory model, the F_{st} values were projected to the current geographic distribution of *S. aberti* to obtain a predictive map of expected F_{st} values over space.

Theoretical basis

Environment, fitness and suitability We define $\vec{e}_i = (e_1, e_2, \dots, e_i)$ as a vector of environmental variables, that is, a point in the space of v environmental variables. Then $R_i(\vec{e}_i)$ is a function that relates evolutionary fitness to environment. That is, for a species with non-overlapping generations, the population's net reproductive rate R_i is a measure of evolutionary fitness that depends on environmental conditions.

In other words, \mathbf{G}_o is the set of sites in the geography that present positive growth rates related to favorable conditions. If we take the set of places in environmental space where these values are greater than a threshold, we can define a volume in multidimensional space such that $R(\vec{e})$ is always positive and greater than this threshold, that is $\mathbf{N}_F(t) = \{\vec{e} | R(\vec{e}(t)) > k\}$.

This is a way of expressing the fundamental niche \mathbf{N}_F as a function of environmental conditions. Thus, for each site in the geography there will correspond a site in the environmental space with different environmental conditions and different growth rates. However, all sites within the region defined by \mathbf{N}_F will have viable populations and positive growth rates. Nonetheless, we assume that the environment is dynamic and each geographic point is static, so for each site in geographic space this growth rate depends on the environmental conditions and therefore growth rate changes in value at each time interval.

Locally, the growth rate will be related to the local population size as long as it is within the boundary defined by \mathbf{N}_F . Therefore, the local population size as a function of the intrinsic growth rate, which depends on the change in environmental conditions over time, can be expressed as: $N_i(t+1) = R(\vec{e}_i(t))N_i(t)$. That is, the locally population size is a function of ideal environmental conditions.

We start by considering this defined volume of the set of R as a set of trajectories for each point from geographic space to environmental space. Considering this rate fixed \mathbf{R} when the population grows, that is, $\mathbf{N}_F(t) = \{\vec{e} | R(\vec{e}(t)) > 1\}$ and therefore any local population will have a positive growth rate.

This equation was proposed by Soberon and Peterson (2020) to relate demographics to a function of evolutionary fitness and environment. In that study they tested the validity with monthly variables and empirical values on a short time scale. relating life history parameters and the environmental suitability of niche models.

This set can be seen as a convex volume in environmental space and we relate this growth rate to an environmental suitability function bounded between 0 and 1, for example, for a unimodal multivariate probability density function, it would be equivalent to the distance from the maximum of the function. That is, the fitness-related environmental suitability can be any function such that it is 0 if $R_i(\vec{e}_i) > 1$ and 1

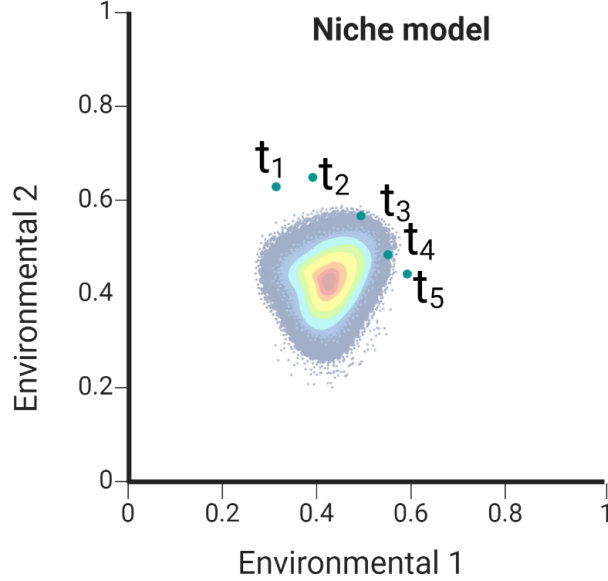


Figure 1: Hypothetical niche in environmental space. An arbitrary point moves within the ambient space entering and exiting the volume (niche) where the intrinsic growth rate is positive.

when R is evaluated at the expected value of \vec{e} for all values of $R_i(\vec{e}_i) > 1$. In a practical way, \mathbf{N}_F is approximated from points of presence in the geography obtained from databases, numerically approximating a convex surface with a surface \mathbf{N}_R of the environmental space.

Once we have an approximation of this volume, we consider that each point in the geography is static and has a trajectory in the environmental space and that for each trajectory, the fitness function changes and, therefore, the suitability function changes but not accordingly, in a homogeneous way, if not more so that each site presents different displacement rates and different demographic rates.

The goal of this theoretical approach is not to know the shape of the function of R but rather to find this local variation relating this value of R and the function \mathbf{N}_F with a function $S_i(\vec{e}_i)$ of environmental suitability that can be estimated from known methods of applied mathematics and machine learning (for example the case of Maxent, (Phillips, Anderson, and Schapire 2006)), i.e. :

$$N_i \propto S_i(\vec{e}_i)$$

Population size locally is a function of environmental suitability, where if suitability is 0 the population is 0 and if suitability is 1 the population has a maximum growth rate $R_i(\vec{e}_i)$ in some point of the environmental space.

Genetic variation and effective population size On the other hand, loss of heterozygosity may be related to the amount of genetic variation present in the absence of mutation and selection, so theoretically, one would expect a strong correlation between effective population size and heterozygosity on the basis of population genetics. We start from the assumption that in the absence of gene flow between subpopulations, the rate of fixation by isolation depends on the effective population size N_e when subpopulations diverge from a common ancestor in t generations. Walsh and Lynch (2018):

$$F_{st}(t) = 1 - e^{-kt/N_e}$$

where we assume, according to Nei (Nei 1986), that genetic drift within each subpopulation causes the average heterozygosity between populations (H_s) to approach zero ($F_{st} = 1 - H_s/H_t$), i.e., for $t = 0$ $F_{st} = 0$

and for very large t the index is 1. that is, for $t = 0$ $F_{st} = 0$ and for very large t the index is 1. We have included a constant k without loss of generalization.

Using $e(x) = \sum_{k=0}^{\infty} \frac{x^k}{k!} = 1 + x + \frac{x^2}{2} + \dots$ and leaving to first order for N_e large enough

$$F_{st} \approx \frac{kt}{N_e} + C$$

Moreover, the effective population can be estimated as the harmonic mean of the population in a demographic time series (Karlin 1968) for τ generations $\frac{1}{N_e} \approx \frac{1}{\tau} \left(\frac{1}{N_1} + \frac{1}{N_2} + \dots + \frac{1}{N_\tau} \right)$. We substitute the harmonic mean into the above equation, considering that although the number of generations is not exactly equal to the time of the fixation index, they are expected to be very close:

$$F_{st} \approx \left(kt \right) \frac{1}{\tau} \sum_{j=1}^{\tau} \frac{1}{N_j}$$

Relationship between the fixation index and environmental suitability We can infer locally for each population N_i in the geography expect to be proportional to the environmental suitability for each time considered, For simplification in the index we select a N_i population in the geography and infer that locally, this population is proportional to the environmental suitability in each time considered, i. e. $N_j \propto S_j(\vec{e}_j)$ (each index j is for the generation time), as we describe above, so we can assume an harmonic mean of suitabilities $\frac{1}{\tau} \sum_{j=1}^{\tau} \frac{1}{S_j} = \frac{1}{\bar{S}}$ and substitute in the previous equation:

$$F_{st} \approx \left(kt \right) \frac{1}{\tau} \sum_{j=1}^{\tau} \frac{1}{S_j(\vec{e}_j)}$$

We call this harmonic mean of environmental suitability *Suitability prevalence index* (S) given between 0 and 1, since it reflects the rate of population growth as a function of environment over a period of time. Thus we have a way to check that the loss of heterozygosity (through the fixation index F_{st}) is inversely proportional to the suitability prevalence for an i site in the geography:

$$F_i^{st} = \frac{\beta_0}{S_i} + \beta_1$$

If we consider all sites in the available geography, we call this harmonic mean *Suitability Prevalence Area* $\mathbf{S} = \{S_i | S_i > k\}$ (SPA) since we expect that areas where the F_{st} is lower are in areas where the prevalence over time is higher, i.e.~environmental conditions remain suitable for a significant period of time and therefore no effects of genetic drift of populations have occurred. Conversely, it is expected that in populations with a high fixation index value, suitability will not have prevailed over the same time interval even though conditions currently exist and populations are present.

Methods

We summarize our 5 steps predictive approach in the figure 2.

We propose a method to find the Suitability Prevalence Area (SPA) as an index with a dual purpose: 1) to find endemic areas to delimit the historical distribution of species and 2) to explain patterns of genetic diversity.

The method for estimating SPA consists of a series of 4 steps:

1. Model the potential distribution of a taxon with present-day environmental conditions and obtain an environmental suitability map.

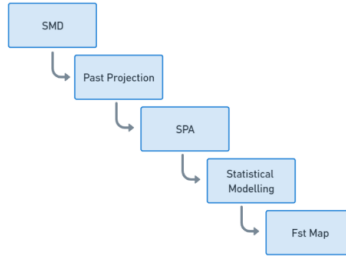


Figure 2: Realized niche in environmental space. A point dynamically moves along different time slices

2. Project the potential distribution model to various environmental scenarios in the past with constant time steps and obtain the environmental suitability for each time scenario.
3. Characterize past analogous climates and retain projections only for sites with climates analogous to the present.
4. Generate a harmonic mean suitability map for all time slices.

Subsequently, one application of the SPA is to explain genetic diversity (the fixation index) as a function of the SPA and project it to the geography. For this it is necessary to perform a series of steps, which consist of:

- Obtain georeferenced points of genetically structured populations with fixation index values.
- Extract values from the SPA map with these points.
- Perform a linear model of the fixation index value with respect to the SPA.
- With the linear model all SPA values of suitability are interpolated.
- Generate a map with all the values interpolated by the model.

As a case study we consider squirrels (*Sciurus aberti*), a species currently distributed in disjunct patches from the southern Rocky Mountains in the United States to the northern Sierra Madre Occidental in Mexico for which it is possible to find reliable information on both the genetic structure of its populations and its current distribution (Bono et al. 2018; Burgin et al. 2018). In order to select this species, we list the following considerations:

As a case study, we consider squirrels (*Sciurus aberti*), a species currently distributed in disjunct patches from the southern Rocky Mountains in the United States to the northern Sierra Madre Occidental in Mexico for which it is possible to find reliable information on both the genetic structure of its populations and its current distribution (Bono et al. 2018; Burgin et al. 2018). In order to select this species, we list the following considerations:

- Since it is a medium-sized mammal (0.5 kg) its identification is easy.
- The subspecies are geographically isolated, since they are found in pine forests surrounded by desert. Therefore we can consider the assumption of isolation by distance (Wright 1943).
- It has low speciation rate (0.25) (Upham, Esselstyn, and Jetz 2019), therefore, we assume that its fundamental niche is stable over time.
- There is fixation index information (Bono et al. 2018) for different populations of the subspecies, which is useful for using SPA as a way to explain genetic differentiation between populations.

Unique occurrence records

We have downloaded geographic information on *Sciurus aberti* from the open access platform Global Biodiversity Information Facility (GBIF). Subsequently, we eliminated duplicate records, those without precise coordinates and those with uncorroborated collection information. Once the unique occurrence records were obtained, we filtered the geographic space in order to avoid overpredictions in the spatial distribution models

caused by the agglomeration of occurrence points. The filtering consisted of superimposing the records in the geographic space, then we made 5 latitudinal slices of 5 degrees of separation between each one, from latitude 20 degrees south to latitude 45 degrees north, taking as criteria the known distribution of the species and the ecoregions of North America, level 1 (downloaded from the US Environmental Protection Agency, 2010). Once the geographic space was segmented, we left the same number of records for each band (30 records per band) obtaining a total of 150 unique records of presence.

Environmental characterization

The environmental information to generate the models, from the present and the reconstruction to the past, was obtained from Pastclim 1.2, an R statistical software package designed to download and manipulate paleoclimatic datasets. In our particular case we chose the Beyer et al. Beyer, Krapp, and Manica (2020) set as it has environmental information available up to 120 000 BE, significantly evolutionary time, at 2000 year time intervals based on Global Circulation Models HadCM3 (Singarayer and Valdes 2010) and HadAM3H (Valdes et al. 2017). The environmental dataset has 17 bias-corrected bioclimatic variables, reduced spatial scale and spatial resolution of 0.5°square cells.

Accessibility region (M).

Species distribution models according to the BAM diagram (Soberon and Peterson 2005) states that the geographic range occupied by a species (\mathbf{G}_o) is the region of appropriate assemblages in terms of abiotic conditions. The region \mathbf{M} represents in geography areas in which the species has access due to its colonization capabilities and the structure of geographic barriers within a specific period of time (Soberón and Nakamura 2009).

In this study we selected a set of North American ecoregions for modeling to delimit our Accessibility region. We took into account ecoregions that overlap with the known distribution of the species and also took into account neighboring ecoregions to increase the potential accessibility in projection scenarios to the past. Thus, regions 5, 6, 9, 10, 12, 13 of the level I ecoregions (<https://www.epa.gov/>) were selected.

Niche models

Current distribution Estimating niche boundaries for species occurrence is called ecological niche modeling (ENM), and when the emphasis is on geographic distribution, it is known as species distribution modeling (SDM) (Guisan and Thuiller 2005; Peterson and Soberón 2012; Saupe et al. 2012). We model the current distribution of *S. aberti* using the MAXENT 3.4.4 algorithm (Phillips, Anderson, and Schapire 2006), which is a correlative model based on the maximum entropy principle used to estimate species distributions. The output of Maxent is a relative occurrence rate (ROR) interpreted as a probability of habitat suitability given observed environmental conditions by presence-only points (Merow, Smith, and Silander Jr 2013).

The parameterization was performed with the default values of the program with the exception of the “extrapolate” and “clamping” options to avoid artificial extrapolations in the extreme values of the climatic variables used in the models. To calibrate the models we used 70% of the records and the remaining 30% to validate them.

In order to give statistical certainty and to consider uncertainty, as well as to reduce overfitting and to have a suitable model to extrapolate to past scenarios, 10 replications were performed for each model using a cross-validation with the training data. In the end, the average model of these replications was considered as the result.

We evaluated the statistical significance of the resulting models for the present using the partial ROC test (Peterson, Papeş, and Soberón 2008), which is a modification of the ROC (receiver Operation Characteristic) test. The results of this test are proportions (ratios) of the area under the curve of the model with respect to a null model, product of repetitions that allow to statistically evaluate the areas under the curve (AUC) in relation to that expected by chance (Peterson, Papeş, and Soberón 2008), where a value derived by chance would be 0 and an acceptable value, according to the proportion of minimum omission errors tolerated in the

model, would be greater than 1. A different set of test data was used on the average model of the replicates and in this way the reduction of overfitting was guaranteed.

Reconstruction to the past The average model obtained from Maxent was extrapolated to environmental conditions into the past. Environmental layers were taken from pastclim (Leonardi et al. 2023) in 2000 year time slices to cover a total of 120 000 years. For each scenario into the past, 10 replicates were cross-validated and averaged. For each projection into the past, as well as the model of the present, we generated a binary map at a suitability threshold of 90% to get an estimate of the area distribution for each time slice in pixels. In addition we fit a locally estimated scatterplot smoothing (loess) model to the time series trend area using the R package stats in order to observe patterns in the area - timeline scatterplot.

Suitability Prevalence Area (SPA)

Finally, to generate the SPA, both the average projection of the present and all the average projections of the past are considered. The output files are read in raster format.

A harmonic mean is performed as follows: For each layer the inverse of each cell value is obtained. Then the inverse values are summed by cells and divided by the number of scenarios. Finally, the inverse of each cell is obtained. It is important to consider that the Maxent outputs may contain very small values close to zero in many cells, for this reason we added a small amount of 0.001 to all the values in all the maps so that when obtaining the harmonic mean we could have an inverse value for values close to zero without altering the biological sense of environmental suitability.

Endemic historic Area

To calculate the historic endemic area, the SPA result is taken and a threshold is applied to generate a binary map according to the $mathbf{f}S$ equation. This threshold is the proportion of time that pixel has had ideal conditions. For our study, we consider the value of 90% since for a period of 120 000 years it is a coverage of 100 000 years, which is a significantly evolutionary time to fix genetic patterns at the population level.

Fixation index as a function of SPA

To test our hypothesis of genetic diversity as a function of environmental suitability prevalence, from a set of genetically structured populations, a matrix of fixation indices between populations is considered. For this work we consider the data from Bono et al. (2018). It considers 10 populations along the known distribution and provides values of F_{st} between this populations in matrix form. The matrix was transformed into a table as pairs between populations with index values between each pair. The values of the population with itself, i.e. 0, were included. Subsequently, georeferences were obtained for each population considered in the fixation index matrix. From this geo-referencing the SPA value for each population was extracted. Finally, the SPA value was aligned in the table of fixation index pairs. In total the table has 4 columns: source population, target population, fixation index and SPA of the target population. This table was separated by source population groups to generate a set of linear models between SPA values and fixation indexes F_{st} . An analysis was performed for each source population with the hypothesis that the correlation between SPA and fixation index exists and is non-zero if a dispersal process has occurred from the historical endemic area of the taxon.

Fixation index projected in geography

The linear model that presents the highest value of R^2 is considered suitable to make a geographic projection of the fixation index and observe genetic diversity in geographic space. To generate this map, the SPA values are taken and a table of coordinates and SPA values is generated for each cell of the raster. The SPA values are then extrapolated to obtain fixation index values from the linear model obtained previously. This column is added to the coordinate table and a raster is generated with the projected F_{st} values. Finally, a cutoff of this raster is performed using a map of the distribution of the species at present with a cutoff threshold of 90% in binary format (where 1 = presence and 0 = absence), since the records of the presence localities were obtained from bases that might contain some errors in the data (Phillips, Anderson, and Schapire 2006).

Results

Current and past distribution

We get the binary maps for all the models in suitability threshold of 0.9 and extract the number of pixels above this threshold in order to get a relative predicted area. Here we show the trend from present (Figure 3A) to past of the the projected area of *Sciurus aberti* along the time line (Figure 3F). The trend pattern exhibits an inverted U-shape, showing that the present area is similar to the 120 000 area, with a maximum in 22 000 coinciding with the Last Glacial Maximum in North America (Figure 3B). We highlight three other notable scenarios, the first local minimum after the interglacial maximum appears in the year 30 000 (Figure 3C) coinciding with a distribution similar to the present but with more suitable regions emerging in New Mexico and Colorado; a local maximum in year 62 000 at the middle of the trend line (Figure 3D), with a more suitable potential distribution towards the south, with conditions disappearing practically everywhere in the United States, except in the border with Sonora, but connecting the area of the Sierra Madre Occidental with Zacatecas, San Luis Potosí and the appearance of a corridor over the Transverse Volcanic Axis (from Jalisco to Tlaxcala); finally we show a minimum area of the whole time series in year 112 000. (Figure 3E), with the disappearance of conditions in practically all the places where there were expansions, preserving conditions only in some places of Chihuahua (Campo Verde and Tutuaca Natural Protected Areas), Durango and Arizona (Prescott and Sedona).

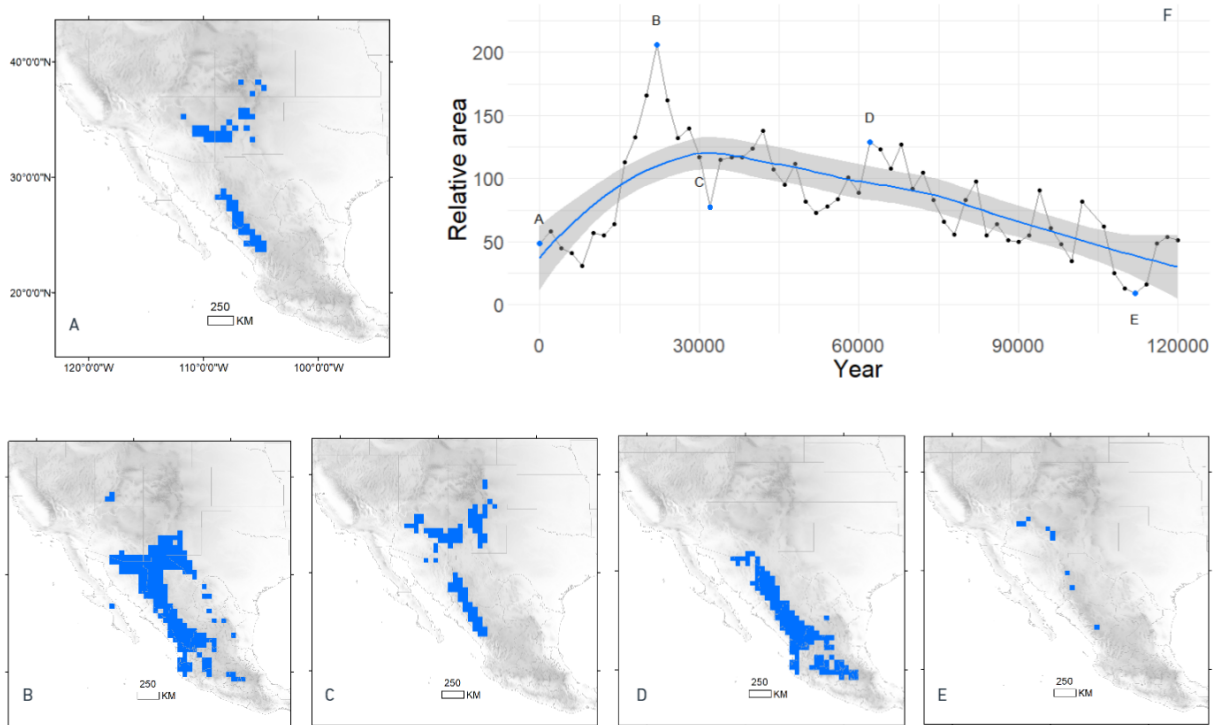


Figure 3: A) Species distribution model for *Sciurus aberti* present distribution. B) Relative projected area for SDM in pixels according a threshold of 0.9 suitability for each past time-sliced environmental conditions. We can observe a maximum area corresponding to the last interglacial era and an inverted U-shape in the trend of the area along the time considered. Also It can be noted that the actual distribution has similar area to the conditions 120 000 years ago. B) and D) corresponds to distribution peaks along the time scale and C) and E) corresponds to minimum

SPA and Endemic Historic Area

We get the suitability prevalence area delimited by a 0.5 and 0.9 threshold (Figure 4). The endemic region where the environmental conditions 90 % of the time is the Sierra Madre Occidental, in the limits of Sonora, Chihuahua, Sinaloa and Durango. We correspond this Area to the *Sciurus aberti barbieri* subspecies. Also is notable that at 0.5 threshold, other regions seems to have stable conditions. We observe the area close to Coronado National Forest as well as Gila National Forest and Mescalero Reservation as suitable areas along time in the United States and some Areas of the Volcanic Belt in Mexico (Puebla, north of Guerrero State and Jalisco).

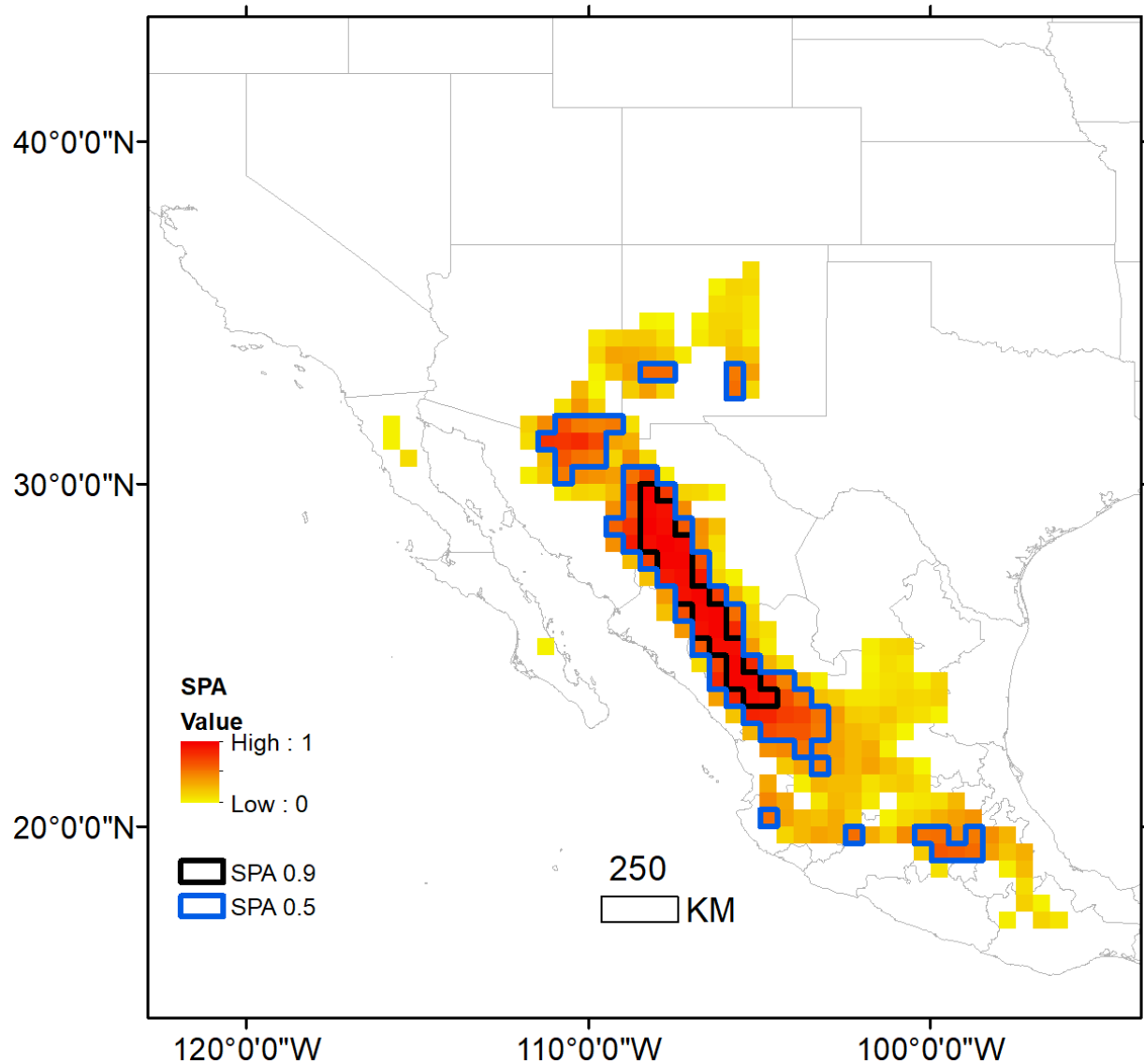


Figure 4: Suitability prevalence area. Here we observe the harmonic mean of suitability for each pixel along the distribution from 0 to 1. The bold lines shows the the area when the harmonic mean es above 0.5 threshold (blud line) and 0.9 threshold (black line)

F_{st} as a function of SPA and Fixation index projected in geography

For all the linear regressions performed (Table 1), the only one that had statistical significance is the one for the *Sciurus aberti barberi* population with an R^2 value of 0.794.

Population	R squared	p value
<i>S. a. aberti Carson-SFW</i>	0	0.962
<i>S. a. aberti Coconino-Gila</i>	0.131	0.304
<i>S. a. aberti MT-Zuni</i>	0.002	0.894
<i>S. a. aberti San Juan</i>	0	0.952
<i>S. a. barberi</i>	0.794	0.001
<i>S. a. chuscensis E</i>	0.002	0.892
<i>S. a. chuscensis W</i>	0.018	0.713
<i>S. a. ferreus Carson E</i>	0.04	0.581
<i>S. a. ferreus Pike</i>	0	0.967
<i>S. a. kaibabensis</i>	0.005	0.841

It can be noted that *S. a. aberti Coconino-Gila* had an R-squared value greater than 0 (0.131) but it is not statistically significant. Furthermore, in our approach we imputed the value of the origin with an F_{st} of zero. To show that the model hypothesis still holds, we performed a regression for *barberi* without the point of origin imposed (Figure 5b), in addition to eliminating the *S. aberti chuscensis* populations due to their low uncertainty in georeference, obtaining an R-squared of 0.72 (p value = 0.016).

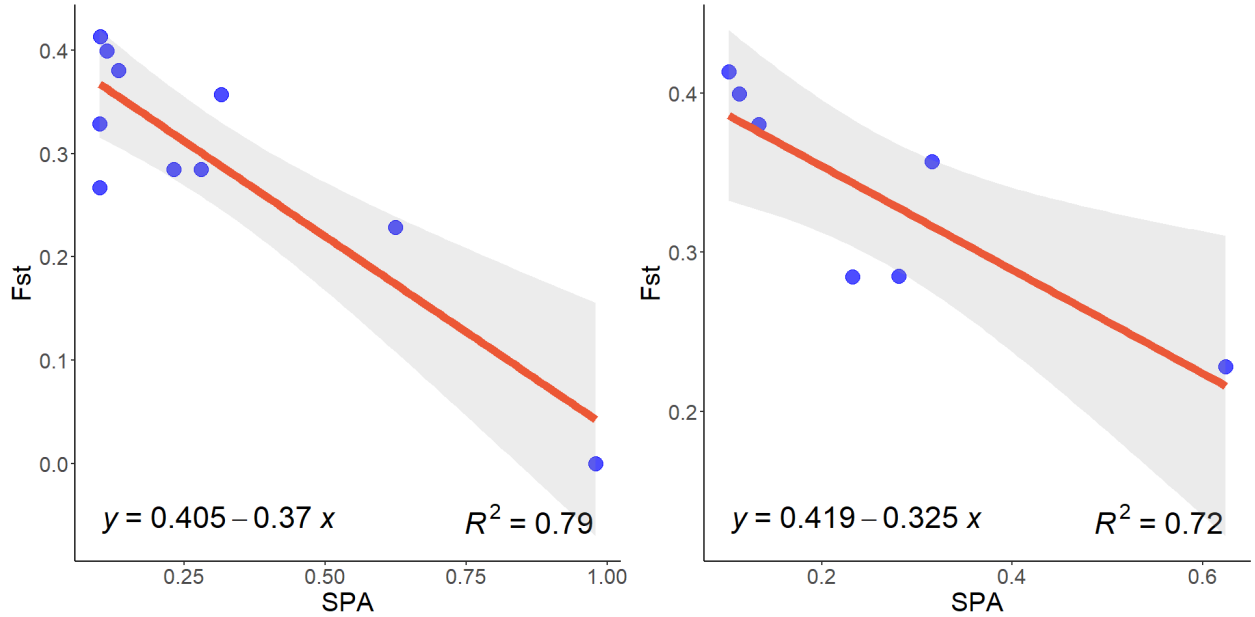


Figure 5: Linear regression for *S. a. barberi* population A) SPA in all populations B) without *barberi* and *chuscensis* populations. We can observe that in both cases the fixation index is explained with the SPA and the hypothesis holds without the imputation of the origin of the population (this means to add a 0 F_{st} value for *barberi* population)

From the model we extrapolated the values from SPA along the geography to new F_{st} values to get a geographical projection of fixation index from *S. a. barberi* population. (Figure 6). The lowest values are close to the Sierra Madre Occidental Area, in the limits of Chihuahua and Sonora States as well as Sinaloa and Durango, score higher near to the Tutuaca Wildlife refuge There is also a hotspot between Sonora And arizona, near to Bisbee Arizona in United States as well as Naco Sonora y Mexico.

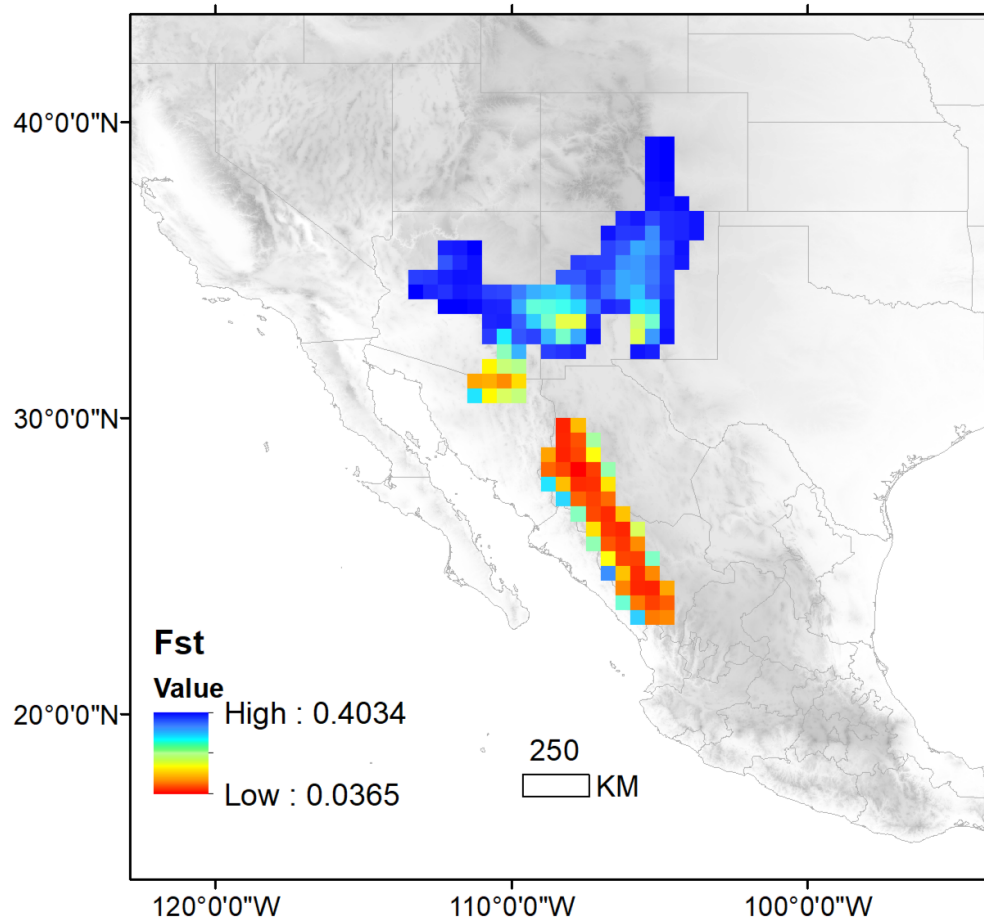


Figure 6: Projection of the F_{st} model to the geography in the actual distribution of *S. aberti*

Discussion

With the current availability of occurrence data and models of potential distribution projected to past climate scenarios it is possible to find geographic patterns of differentiation in populations at an acceptable resolution (half a degree) that allows us to define sites where the species can potentially be found but share different degrees of genetic diversity..

Projections of genetic diversity in geography have been made in previous studies (Van Zonneveld et al. 2012). However in a general way they are extrapolations of observations, without a predictive model, which with some explanatory variable behind can explain in a statistically convincing way the information obtained from population genetics.

We have shown a generalizable protocol for predicting patterns of population genetics in geography. In this way we link information on the evolutionary history of a taxon and its ecology. In addition, we provide a predictive vehicle that generates new geographic information applicable to decision making in both survey conduct and taxon conservation.

Thanks to the theoretical support that we have briefly outlined in this paper, it is possible to explain the explanatory value of the coefficient of determination for our linear model, $R^2 = 0.79$, which is information coming from two completely different sources, but always guided by the premise of the evolutionary process as causal.

These maps represent a turning point in the conception of conservation. With the tool we propose in this study, it is possible to delimit conservation sites based on evidence of current and historical distribution and genetic diversity among different populations.

While many conservation decisions are made on the basis of genetic diversity, studying the genetic structure of populations at a macro-scale is often very complicated, and making conservation decisions based on current distribution without taking into account the historical distribution of taxa can lead to a misguided conservation strategy.

The generalization of our protocol and its implementation in tools widely used by biogeography allow its direct implementation in many case studies with available information, as well as the design of new questions, e.g.~species assemblages under prevalence of environmental suitability. A research path was also established on whether the process of environmental stability over time is related to biodiversity.

It is also noteworthy to mention that in previous taxonomic descriptions, it was taken into account that the distribution of *Sciurus aberti* was only related to the distribution of *Arizona pinus ponderosa*. However, there is a consensus on the range of distribution of this pine, which is limited to the southern United States (Hess and Fulé 2020). Therefore the known distribution of *Sciurus aberti* is in mixed coniferous forests. This plasticity in the squirrel-pine interaction explains the expansion of the species in interglacial periods and its distribution in warmer periods, such as the current one. However, the low genetic diversity found in places where the squirrel species interact with few pine species could put it at greater risk of climate change that constricts the distribution of p. p. Arizona, especially in the Sky Island region of Arizona.

References

- Beyer, Robert M, Mario Krapp, and Andrea Manica. 2020. "High-Resolution Terrestrial Climate, Bioclimate and Vegetation for the Last 120,000 Years." *Scientific Data* 7 (1): 236.
- Bono, Jeremy M, Helen K Pigage, Peter J Wettstein, Stephanie A Prosser, and Jon C Pigage. 2018. "Genome-Wide Markers Reveal a Complex Evolutionary History Involving Divergence and Introgression in the Abert's Squirrel (*Sciurus Aberti*) Species Group." *BMC Evolutionary Biology* 18 (1): 1–17.
- Burgin, Connor J, Jocelyn P Colella, Philip L Kahn, and Nathan S Upham. 2018. "How Many Species of Mammals Are There?" *Journal of Mammalogy*. Oxford University Press US.
- Guisan, Antoine, and Wilfried Thuiller. 2005. "Predicting Species Distribution: Offering More Than Simple Habitat Models." *Ecology Letters* 8 (9): 993–1009.
- Hedrick, Philip W. 2005. "A Standardized Genetic Differentiation Measure." *Evolution* 59 (8): 1633–38.
- Hess, Victoria A, and Peter Z Fulé. 2020. "Is a Mexican Pine Species Better Adapted to the Warming Climate of the Southwestern USA?" *Frontiers in Forests and Global Change* 3: 60.

- Karlin, Samuel. 1968. "Rates of Approach to Homozygosity for Finite Stochastic Models with Variable Population Size." *The American Naturalist* 102 (927): 443–55.
- Krapp, Mario, Robert M Beyer, Stephen L Edmundson, Paul J Valdes, and Andrea Manica. 2021. "A Statistics-Based Reconstruction of High-Resolution Global Terrestrial Climate for the Last 800,000 Years." *Scientific Data* 8 (1): 228.
- Leonardi, Michela, Emily Y Hallett, Robert Beyer, Mario Krapp, and Andrea Manica. 2023. "Pastclim 1.2: An r Package to Easily Access and Use Paleoclimatic Reconstructions." *Ecography*, e06481.
- Lessa, Enrique P, Joseph A Cook, and James L Patton. 2003. "Genetic Footprints of Demographic Expansion in North America, but Not Amazonia, During the Late Quaternary." *Proceedings of the National Academy of Sciences* 100 (18): 10331–34.
- Lira-Noriega, Andrés, and Joseph D Manthey. 2014. "Relationship of Genetic Diversity and Niche Centrality: A Survey and Analysis." *Evolution* 68 (4): 1082–93.
- Merow, Cory, Matthew J Smith, and John A Silander Jr. 2013. "A Practical Guide to MaxEnt for Modeling Species' Distributions: What It Does, and Why Inputs and Settings Matter." *Ecography* 36 (10): 1058–69.
- Nei, Masatoshi. 1986. "Definition and Estimation of Fixation Indices." *Evolution* 40 (3): 643–45.
- Nogués-Bravo, David. 2009. "Predicting the Past Distribution of Species Climatic Niches." *Global Ecology and Biogeography* 18 (5): 521–31.
- Peterson, A Townsend. 2011. "Ecological Niche Conservatism: A Time-Structured Review of Evidence." *Journal of Biogeography* 38 (5): 817–27.
- Peterson, A Townsend, Monica Papeş, and Jorge Soberón. 2008. "Rethinking Receiver Operating Characteristic Analysis Applications in Ecological Niche Modeling." *Ecological Modelling* 213 (1): 63–72.
- Peterson, A Townsend, and Jorge Soberón. 2012. "Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right." *Natureza & Conservação* 10 (2): 102–7.
- Phillips, Steven J, Robert P Anderson, and Robert E Schapire. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190 (3–4): 231–59.
- Saupe, EE, V Barve, CE Myers, J Soberón, N Barve, CM Hensz, AT Peterson, H Lc Owens, and A Lira-Noriega. 2012. "Variation in Niche and Distribution Model Performance: The Need for a Priori Assessment of Key Causal Factors." *Ecological Modelling* 237: 11–22.
- Singarayer, Joy S, and Paul J Valdes. 2010. "High-Latitude Climate Sensitivity to Ice-Sheet Forcing over the Last 120 Kyr." *Quaternary Science Reviews* 29 (1–2): 43–55.
- Soberon, Jorge, and A Townsend Peterson. 2005. "Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas."
- Soberón, Jorge, and Miguel Nakamura. 2009. "Niches and Distributional Areas: Concepts, Methods, and Assumptions." *Proceedings of the National Academy of Sciences* 106 (supplement_2): 19644–50.
- Soberón, Jorge, and A Townsend Peterson. 2020. "What Is the Shape of the Fundamental Grinnellian Niche?" *Theoretical Ecology* 13 (1): 105–15.
- Thorup, Kasper, Lykke Pedersen, Rute R Da Fonseca, Babak Naimi, David Nogués-Bravo, Mario Krapp, Andrea Manica, et al. 2021. "Response of an Afro-Palearctic Bird Migrant to Glaciation Cycles." *Proceedings of the National Academy of Sciences* 118 (52): e2023836118.
- Upham, Nathan S, Jacob A Esselstyn, and Walter Jetz. 2019. "Inferring the Mammal Tree: Species-Level Sets of Phylogenies for Questions in Ecology, Evolution, and Conservation." *PLoS Biology* 17 (12): e3000494.
- Valdes, Paul J, Edward Armstrong, Marcus PS Badger, Catherine D Bradshaw, Fran Bragg, Michel Crucifix, Taraka Davies-Barnard, et al. 2017. "The BRIDGE HadCM3 Family of Climate Models: HadCM3@ Bristol V1. 0." *Geoscientific Model Development* 10 (10): 3715–43.
- Van Zonneveld, Maarten, Xavier Scheldeman, Pilar Escribano, Maria A Viruel, Patrick Van Damme, Willman Garcia, César Tapia, José Romero, Manuel Siguenas, and José I Hormaza. 2012. "Mapping Genetic Diversity of Cherimoya (*Annona Cherimola* Mill.): Application of Spatial Analysis for Conservation and Use of Plant Genetic Resources." *PloS One* 7 (1): e29845.
- Walsh, Bruce, and Michael Lynch. 2018. "59The Genetic Effective Size of a Population." In *Evolution and Selection of Quantitative Traits*. Oxford University Press. <https://doi.org/10.1093/oso/9780198830870.003.0003>.
- Wright, Sewall. 1943. "Isolation by Distance." *Genetics* 28 (2): 114.