**Detecting exceptional temporal neutral genetic changes in resampled landscapes.**

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Running title: Unique spatio-temporal genetic change

**INTRODUCTION**

Global change, including climate change but also habitat destruction and fragmentation, have caused biodiversity to quickly decline in many parts of the world in the last century (Fischer & Lindenmayer, 2007; Butchart et al., 2010; Dirzo et al., 2014). The future of biodiversity could be bleak (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012), and thus there is an ever-increasing demand from ecosystem managers to evaluate and mitigate biodiversity loss, but also to assess current and proposed management plans (Brondizio, Settele, Díaz, & Ngo, 2019).

Global change ecology is still an emerging field and improvements are being made at a fast pace (Rands et al., 2010). Among the main axes of improvement followed by researchers are increasing our understanding of synergies between drivers of ecosystem services and biodiversity loss, covering previously poorly described biodiversity (including genetic diversity) and resampling to evaluate temporal change and increase our predictive abilities. Although global change trends, and associated uncertainty, have long been closely monitored and described (Sala et al., 2000; IPCC, 2014), more local information about within-landscape temporal changes is needed to further our ability to predict change (Randin et al., 2009; Potter, Arthur Woods, & Pincebourde, 2013; Yates et al., 2018). For example, new local information may substantially decrease the uncertainty plaguing short-term ecological forecasting of global change (Pereira et al., 2010; Mouquet et al., 2015).

Landscape genetics approaches are, and will continue to be, widely used for conservation biology purposes (Allendorf, Hohenlohe, & Luikart, 2010; Segelbacher et al., 2010; Harrisson, Pavlova, Telonis-Scott, & Sunnucks, 2014). Indeed, landscape genetics bridges an important gap in the field of molecular ecology: providing information about the interaction between micro-evolutionary processes and landscape features (Manel, Schwartz, Luikart, & Taberlet, 2003; Manel & Holderegger, 2013; Wagner & Fortin, 2013; Balkenhol, Cushman, Storfer, & Waits, 2015). Landscape genetics can therefore help us address a wide array of questions, such as how gene flow, and therefore effective dispersal (Bohonak, 1999; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009), is affected by environmental heterogeneity (e.g. Wittische et al. 2019), how local landscape characteristics explain the spatial distribution of neutral and adaptive genetic information (e.g. Janes et al., 2014), or even how to locate genetic boundaries.

One of the main ongoing challenges for landscape geneticists, is to detect and predict where and when extraneous disturbance events influence the ecological dynamics and the evolution of species. Changes in genetic diversity can be the result of natural or anthropogenic disturbance at any temporal scale, from a local and abrupt change like a wildfire to a global and gradual change like climate warming (Manel & Holderegger, 2013). However, it is rarely possible to observe the effects of these events instantaneously and researchers are often left with their spatial legacies which may not be readily observable from demographic data alone. When a disturbance does not constitute a selective pressure, alleles are randomly transferred from a generation to the next and genetic drift happens leading to a loss of diversity. Common examples of situations where genetic drift occurs include geographic isolation, population bottleneck and massive migrations from previously isolated populations, which would substantially reduce or alter local genetic variation. The result of such events in a local population tend to alter the genetic distance of this population with surrounding populations (Segelbacher et al., 2010). Detecting changes in the genetic make-up of a population through time, including the nature of those changes, may describe what is happening at the demographic level, and therefore serve as an alarm for managers.

While the development of tools to identify loci putatively under selection (Frichot & François, 2015; Luu, Bazin, & Blum, 2017; Duruz et al., 2019) or classify population samples in genetically coherent clusters (Pritchard, Stephens, & Donnelly, 2000; Jombart, Devillard, & Balloux, 2010; Caye, Deist, Martins, Michel, & François, 2016; Verity & Nichols, 2016) is thriving, options offering to test whether a sample has truly changed relative to others, are less visible. Indeed, the relevance and performance of traditional approaches (e.g. PCA-based) to test change using temporal genetic datasets, where the objective is to find which population has indeed changed more significantly than others in the landscape, has not been evaluated. With the

A permutation-based statistical inference method for the analysis of spatial-temporal changes in community composition have recently been proposed (Legendre & Gauthier, 2014; Shimadzu, Dornelas, & Magurran, 2015). A number of applications of the method on composition data have been made on a range of systems (Legendre & Salvat, 2015; Winegardner, Legendre, Beisner, & Gregory-Eaves, 2017; Kuczynski, Legendre, & Grenouillet, 2018; Legendre & Condit, 2019) and its power and type 1 errors have recently been thoroughly tested through simulations (Legendre, 2018). Temporal Beta-diversity Indices (TBI; Legendre 2018) were designed to asses whether there are sites where the difference in community composition between survey times seems exceptionally large and it was suggested that one could use TBI on gene frequency data. The method involves estimating temporal change in each sampling site between two dates using a dissimilarity index/distance, testing the significance of each change through permutations, and partitioning the change into losses and gains. Comparing genetic data at two different dates separated by a known event may help us understand more about the ecological processes shaping the system. It would also indicate the parts of the landscape where an event had the strongest effects, or highlight which sites should be investigated if managers are not aware of an *a priori* known event.

Our paper seeks to describe how to find out which parts of a landscape have undergone atypical and substantial genetic change, for example after a disturbance event. We simulated scenarios where part of the landscape is affected by non-selective demographic changes mimicking the effects of common disturbance events. We then used TBI to measure changes in the gene pool of our populations, and evaluated the power and error rates associated with this approach. Finally, we illustrated the possibilities of this approach through applications on two real genetic datasets.

**METHODS**

*Simulation framework*

To model the variation of genetic information through time, we used the spatially-explicit gene flow simulation software CDMetaPOP (Landguth, Bearlin, Day, & Dunham, 2017). CDMetaPOP simulates dispersal and mating of individuals across a landscape, and allows to define the initial genetic structure, spatial distribution of individuals, dispersal characteristics, and life history traits of the population.

Loci were modelled after single nuclear polymorphism and therefore are bi-allelic. The mutation rate was set as to reflect empirically-derived mutation rates found in many taxa (REF I gave to Ryan). There was no selective pressure in the virtual landscape and so all loci were considered neutral. Simulated individuals each carried a genome of 100 loci without linkage disequilibrium. Each simulated population had a maximum carrying capacity of 50 individuals and each simulated landscape comprised 25 (5 by 5) interconnected populations with structural connectivity only reflecting geographical distance. That corresponds to a maximum of 1250 individuals in the landscape. Each simulation was run for 100 before an event happened and disturbed the landscape. 10 more generations were simulated after the event.

We simulated 180 replicates for each scenario, with the new allocation of allelic frequencies for each replicate. Those parameters were chosen as a compromise between realism and computational time limitations. While the number of individuals in our metapopulation may be smalled than that of some actual systems, we believe it was large enough to produce the complex evolutionary dynamics necessary to create noisy and realistic genetic data.

With 3 dispersal regimes, 2 different disturbance types and 5 different numbers of populations affected, we have 30 different scenarios giving us a total of 5400 simulations. In the next sections, we detail how we modelled the aforementioned three factors. Additional material concerning the use of the simulator can be found in Supplementary Materials.

*Dispersal regimes*

The dispersal of individuals was controlled through a dispersal kernel based on a negative exponential distribution from which the distance realised by an individual () is sampled (sup. Fig.X showing the rescaled kernels). This distribution transforms the cost distance of travel (CD) between cells according to a single parameter (*B*): . Cost distances used here are simply the geographical distances between the centroids of the populations. The values created through the use of the negative exponential distribution can then be rescaled using the maximum and the minimum distance possible in the landscape, which gives us the probability that an individual goes beyond a specific distance:

When is randomly sampled as being higher than 1, the target population to which an individual travels, was selected randomly from the set of populations available at the distance selected in the previous step. Otherwise, the, individual stays within its original population. We chose this way of modelling dispersal so that most individuals stay within their original population, that is more individuals randomly travel a distance below 1 than higher, while keeping opportunities for occasional long distance dispersal. This holds advantages compared to simpler approaches such as nearest neighbours or linear probability (REF).

In order to investigate the effect of different levels of dispersal, we changed the dispersal kernel by choosing values of *B* which would give us low, intermediate and high dispersal. We considered the % of individuals leaving their original populations as an indicator of the intensity of dispersal. We therefore respectively chose 1% (*B* = 2), 5% (*B* = 1.301), and 25% (*B* = 0.60185).

*Disturbance design*

The first disturbance we considered involves modelling a massive extraneous migration from a previously isolated 26th population otherwise sharing the same characteristics. This population was simulated during the same number of generations and the cost distance between the disturbed population(s) and the 26th (isolated) populations was set to 0 between the 200th and 201st generations, mimicking a mass migration event between the two. The cost distances are then set back to normal.

The second scenario involves modelling a demographic bottleneck through massive mortality. To do that, the carrying capacity of the disturbed population was set to 10% of its original value between the 200th and 201st generations.

*Number and position of disturbed populations*

Beyond the dispersal intensity and the disturbance type, we wanted to evaluate how the number of populations which are disturbed affected the performance of our testing procedure. To achieve this, we disturbed from 1 to 5 populations among the 25. When only 1 population was disturbed we partitioned the 180 replicates of that scenario equally among 6 populations in the landscape. Because our landscape is homogenous and symmetric, only 6 positions need to be assessed (sup Fig YYY). When *k* (>1) populations were disturbed, we randomly sampled 6 combinations among the 25 choose *k* possible combinations for that *k* (30 replicates per combination).

*Genetic dissimilarity*

Chord distance has been commonly used in both community ecology (Orlóci 1967; Legendre & Borcard 2018) and population genetics (Cavalli-Sforza & Edwards 1967; Balkenhol et al. 2016). We chose chord distance because it has already been tested for use with TBI with non-genetic data (Legendre 2019) and because it may be more appropriate than other indices of genetic dissimilarity when most of the variation among populations is due to recent changes (Takezaki & Nei 1996; Kalinowski 2002) as it does not assume populations are in drift-mutation equilibrium.

*Statistical performance*

We use the False Positive Rate and False Negative Rate frameworks to assess statistical performance of the TBI testing procedure

a) Permutation approach

b) Threshold,

**RESULTS**

Table 1. Mean and standard deviation of FPR and FNR associated with TBI permutation tests using three different permutation approaches, at two adjusted p-values thresholds.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Tests** | **FPR** | | **FNR** | |
| 1 year/0.001/permute 1 | 0 (-+ 0) | | 1 (-+ 0) | |
| 1 year/0.01/permute 1 | 0 (-+ 0) | | 1 (-+ 0) | |
| 1 year/0.025/permute 1 | 0.007 (-+ 0.018) | | 0.162 (-+ 0.369) | |
| 1 year/0.05/permute 1 | 0.009 (-+ 0.020) | | 0.160 (-+ 0.368) | |
| 1 year/0.1/permute 1 | 0.012 (-+ 0.021 | | 0.101 (-+ 0.301) | |
| 1 year/0.15/permute 1 | 0.015 (-+ 0.023) | | 0.094 (-+ 0.288) | |
|  | |  | |  | |
| 1 year/0.025/permute 1 | | 0.007 (-+ 0.018) | | 0.162 (-+ 0.369) | |
| 1 year/0.025/permute 2 | | 0 (-+ 0) | | 0.971 (-+ 0.17) | |
| 1 year/0.025/permute 3 | | 0 (-+ 0) | | 1 (-+ 0) | |
| 1 year/0.1/permute 1 | | 0.012 (-+ 0.021 | | 0.101 (-+ 0.301) | |
| 1 year/0.1/permute 2 | | 0 (-+ 0) | | 0.937 (-+ 0.256) | |
| 1 year/0.1/permute 3 | | 0 (-+ 0) | | 1 (-+ 0) | |

From Table 1 we can see that only the first permutation approach, that is permuting a locus in the same way in Chord distance matrices from both samplings, gives useful FNR and FPR. This is true regardless of the threshold value chosen for the adjusted p-value.

Table 2. Mean and standard deviation of FPR and FNR associated with TBI permutation tests using four different lags, at an adjusted p-values threshold of 0.1. The first permutation approach was used.

|  |  |  |
| --- | --- | --- |
| **POST 0 year/0.1/permute 1** | **0.012** (-+ 0.021) | **0.101** (-+ 0.301) |
| POST 1 year/0.1/permute 1 | 0.0125 (-+ 0.023) | 1 (-+ 0) |
| POST 2 year/0.1/permute 1 | 0.0125 (-+ 0.022) | 0.975 (-+ 0.158) |
| POST 3 year/0.1/permute 1 | 0.016 (-+ 0.023) | 0.975 (-+ 0.158) |

As shown in Table 2, it seems that so far, in our high-dispersion bottleneck simulations, we miss the right population where the event occurred after 1 generation of random mating.

Table 3. Mean and standard deviation of FPR and FNR associated with TBI permutation tests using six different time lags between samplings, at an adjusted p-values threshold of 0.025. The first permutation approach was used.

|  |  |  |
| --- | --- | --- |
| **1 year/0.025/permute 1** | **0.007** (-+ 0.018) | **0.162** (-+ 0.369) |
| 2 year/0.025/permute 1 | 0.006 (-+ 0.018) | 0.154 (-+ 0.362) |
| 3 year/0.025/permute 1 | 0.007 (-+ 0.015) | 0.191 (-+ 0.394) |
| 4 year/0.025/permute 1 | 0.007 (-+ 0.017) | 0.233 (-+ 0.423) |
| 5 year/0.025/permute 1 | 0.010 (-+ 0.019) | 0.287 (-+ 0.451) |
| 6 year/0.025/permute 1 | 0.012 (-+ 0.019) | 0.33 (-+ 0.473) |

We can see in Table 3 that the longest the pre-event sampling is from the event, the less power and the more false positives we get. In 6 years the performance as measured by FPR and power has almost been halved. The increase in mean FPR does not seem to be associated with a similar increase in variation, whereas the increase of FNR is associated with an increase in variation.

Table 4. Mean and standard deviation of FPR and FNR associated with TBI permutation tests at different adjusted p-values thresholds. The first permutation approach was used.

|  |  |  |
| --- | --- | --- |
| **Tests** | **FPR** | **FNR** |
| 1 year/0.001/permute 1 | 0 (-+ 0) | 1 (-+ 0) |
| 1 year/0.01/permute 1 | 0 (-+ 0) | 1 (-+ 0) |
| 1 year/0.025/permute 1 | 0.007 (-+ 0.018) | 0.162 (-+ 0.369) |
| 1 year/0.05/permute 1 | 0.009 (-+ 0.020) | 0.160 (-+ 0.368) |
| 1 year/0.1/permute 1 | 0.012 (-+ 0.021 | 0.101 (-+ 0.301) |
| 1 year/0.15/permute 1 | 0.015 (-+ 0.023) | 0.094 (-+ 0.288) |

Stricter values for the adjusted p-value threshold (0.001 and 0.01) expectedly bring a better FPR but also bring a pathological FNR (no power). From 0.025 and up, the FPR increases, eventually reaching the value of the higher adjusted p-value thresholds (0.1 and 0.15), whereas the power increases continuously. The increase in mean power is accompanied by a decrease of the associated standard variation, whereas the increase in mean FPR concurrent with an increasing of its variation.

**DISCUSSION**

*(provided I have not made a mistake and given the limited [only one scenario/one dispersal] set of simulations I have)*

**TBI is applicable to genetic data under certain conditions.**

* The first permutation approach (same line swap across both genetic distance matrices) is the only suitable approach when using gene frequency data.
* Although signal of a past disturbance can be kept in richer genomic data (e.g. probability of mutational configurations in sequence blocks), gene frequency data in a high-dispersion species and connected landscape will not keep the signal beyond a year. To be investigated for non-SNP gene frequency data.
* Provided the landscape was resampled the year of the event, the closer the date of the first sampling, the better performance-wise. However, reasonable performance can be expected even if the first sampling was a few years before the event.
* Given adjustment TBI permutation-derived p-values according to the number of populations, liberal thresholds should be used in order to obtain reasonable statistical power, while keeping the FPR low.

**Paragraph discussing how we were able to use TBI to test and illustrate temporal change** (results not ready yet)**.**

**Paragraph discussing the limits of TBI use on genetic data, including the fact that it may need to be parameterized based on landscape or taxa characteristics.**

**Paragraph discussing further investigation of the relative importance of genetic drift, gene flow and other forces, in shaping temporal variation.**

**Paragraph discussing the importance of LTER, exhaustive sampling, and the need to move beyond single-time snapshot studies of landscape genetics.**

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