TOSSM: an R package for assessing performance of genetic analytical methods in a management context.

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Abstract
TOSSM (Testing of Spatial Structure Methods) is a package for testing the performance of genetic analytical methods in a management context. In the TOSSM package, any method developed to detect population genetic structure can be combined with a mechanism for creating Management Units (MUs) based on the genetic analysis. The resulting Boundary-Setting Algorithm (BSA) dictates harvest boundaries with a genetic basis. These BSAs can be evaluated with respect to how well the MUs they define meet management objectives.

Introduction

An adequate understanding of population structure is frequently crucial to conservation decisions. Many recently developed analytical techniques use genetic data to detect and describe population structure. Although simulation-based comparative performance testing of genetic analytical methods has become more commonplace in recent years (e.g., Chen et al., 2007, Latch et al., 2006, Waples and Gaggiotti, 2006), most studies focus on a narrow range of parameter values relevant to evolutionary questions and fail to address the dispersal rates relevant to the definition of management units (Palsboll et al., 2007, Taylor and Dizon, 1999, Waples and Gaggiotti, 2006). Furthermore, comparison of methods across studies is difficult because each study uses different methods for generating simulated data and evaluating performance. Perhaps most importantly, none of these studies evaluate the performance of methods relative to management goals.

We developed the TOSSM package and datasets (both available from http://swfsc.noaa.gov/tossm.aspx) to facilitate comparative performance testing of analytical methods intended for use in for conservation planning. The TOSSM package, written in the statistical language R (Team, 2006), allows evaluation of methods for detecting genetic structure in a management context. In TOSSM simulations, genetically-structured populations can be divided into management units (MUs) and subjected to managed harvest. The MUs are defined by a Boundary-Setting Algorithm (BSA), which is a combination of 1) an analytical method for detecting spatial genetic structure, and 2) a mechanism for placing MU boundaries based on that spatial structure (Figure 1). Harvest within each MU is set by a management scheme based on catch limits. The performance of a BSA is evaluated using both conservation-based measures (e.g., preventing depletion of populations; Martien and Taylor, 2003) and harvest-based measures (e.g., maximizing catch).

The TOSSM package uses the density-dependent individual-based model implemented in the R package 'rmetasim' (Strand, 2002). A TOSSM simulation is divided into three phases: 1) a historic harvest phase that mimics any past exploitation, and which determines the state of the system when genetic data are collected and managed harvest is first implemented, 2) a phase in which populations are managed according to the management units defined by a BSA and the chosen management scheme, and 3) an optional recovery period in which no harvest occurs. The user has control over the timing of key events during the simulation, including the length of the three phases and the years in which genetic samples are collected, abundances estimated, MUs defined, and catch limits re-calculated. Most of the major aspects of the package (e.g., collection of genetic samples, calculation of catch limits, harvest) are written as independent functions that can be easily replaced by user-defined functions. This modularization of the package allows easy adaptation to specific applications.

A main input to a TOSSM simulation is an initial set of populations with pre-specified population structure. These populations must be represented by a landscape object created within 'rmetasim'. Many such landscape datasets have been generated and are available for download from http://swfsc.noaa.gov/tossm.aspx. These initial datasets, henceforth referred as the TOSSM datasets, represent a variety of population structure scenarios, including different numbers of populations, abundances, and dispersal rates. The objective behind developing these simulated datasets was to provide standard datasets that could be used to test any genetic analytical method.

The user must specify the geographic range of each population in a simulation. Populations can be geographically discrete, contiguous, or overlapping. The user specifies the number, size, and location of sampling sites, and the number of samples per site. Sampling sites can be discrete or contiguous, but may not be overlapping. A contiguous distribution of samples can be achieved by specifying a single sampling site that covers the entire simulated landscape. The default genetic sampler included with the package draws samples at random from all individuals located within a sampling site. However, users could implement other sampling schemes (e.g., sex-biased, spatially clumped, etc.) by writing new sampling functions.

The package supports two methods of simulating historic harvest. The simplest approach is for the user to specify the ratio of current abundance to carrying capacity for each population at the start of the managed harvest phase. Alternatively, the user can divide the landscape into any number of historic harvest areas and specify the number of animals killed in each area in each year of the historic harvest phase. This latter method of specifying historic harvest allows for more realistic simulations for species for which reliable records of past exploitation exist (Archer et al., 2007).

Management units defined by a BSA must be non-overlapping and must cover the entire simulated study area, so that every simulated individual is assigned to exactly one MU. Most genetic analytical methods were not developed specifically to define management units, and will therefore need to be adapted before they can be tested within the TOSSM framework. Methods that work at the level of the sampling site, such as the method we test in the example below, will likely be easier to adapt into BSAs than individual-based methods (Figure 1). A simple utility for converting the output of sampling-site-based methods into valid MUs is included with the package.

The TOSSM package includes two functions for calculating catch limits for each MU. The default function implements the 'Potential Biological Removal' (PBR) scheme used to calculate the allowable human kill of marine mammals under the U.S. Marine Mammal

Protection Act (Wade, 1998). The alternative provided with the package is the catch-limit algorithm, or CLA (IWC, 1994), which is the method used by the Scientific Committee of the International Whaling Commission to calculate the catch limits that would be allowed for large whale species if the moratorium on commercial whaling were lifted (for further details, see Cooke, 1994).

Harvest occurs every year of the managed harvest phase based on the most recent catch limit calculated for each MU. An optional spatial bias in harvest can be implemented to simulate a situation in which the harvesters wish to minimize the distance their travel distance, and so concentrate their effort close to their home base, which is assumed to be the left edge of the study area.

Illustration of package use

We used the TOSSM package to examine the performance of a BSA across a range of datasets that vary in spatial structure (Table 1). The BSA tested was proposed by Waples and Gagiotti (2006), and performs multiple pairwise g-tests between all possible sampling site pairs. The resulting MUs are based on networks of sampling sites connected via non-significant g-tests. After splitting the sampling sites into isolated networks (Figure 1B), the BSA then splits the entire study-area space into non-overlapping MUs (Figure 1D).

The BSA was tested across five population structure scenarios, each of which started with an initial total abundance of 7,500 individuals. The first scenario was a single panmictic population, while the others consisted of two equally-sized populations (initial abundance of each = 3,750) with the annual dispersal rate between them ranging from 5×10^{-6} to 5×10^{-3} (Table 1). For each of these five scenarios, 100 simulations were run, each of which consisted of 100 years of management under the PBR scheme. The two populations were respectively at 0.3 and 0.99 of carrying capacity when managed harvest started and 0.30 in the case of the panmictic population. Harvest was concentrated on the depleted population. Twenty-five individuals were sampled from each of eight sampling sites. G-tests performed by the BSA were based on genotypes at 30 microsatellite loci. BSA performance was evaluated relative to the criteria used in developing the PBR, namely, that a population initially depleted to 0.30 should have a 95% probability of being above Maximum Net Productivity Level (MNPL; defined here as 50% of carrying capacity) after 100 years (Taylor et al. 2000).

The performance of this BSA depended strongly on the magnitude of genetic differentiation between populations (Table 1). A single MU was created in all replicates for scenario 1. Conversely, two MUs were almost always created when simulations were run using two populations when dispersal was 5×10^{-6} or 5×10^{-5}. Performance declined considerably with higher dispersal rates. When the dispersal rate was 5×10^{-4}, the depleted population only achieved MNPL in 23% of replicates. In fact, the initially depleted population went extinct in 39% of the replicates.

Performance actually improved when the dispersal rate increased to 5×10^{-3}, with 72% of replicates achieving MNPL, despite the fact that the BSA failed to detect population structure in any of these replicates (Table 1). Although this is still short of 95%, it is a considerable improvement over the performance when the dispersal rate is 5×10^{-4}. This improvement in performance occurs because over-harvesting of the depleted population is nearly compensated for by immigration from the neighboring population when dispersal is 5×10^{-3}.

The results presented in Table 1 demonstrate that the ability to correctly identify population structure is not always correlated to its performance in a management context, and

that a method often must be able to detect relatively weak population structure to meet management objectives. For these reasons, it is imperative that analytical methods that are being used to inform management decisions be tested in the context of the management questions they are being used to address. The TOSSM package provides a convenient, flexible framework for conducting such performance tests.

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Table 1. Performance of the BSA across the five population structure scenarios examined. Extinction rate and recovery rate both apply to the initially depleted population. Recovery means returning to greater than MNPL (0.5*K).

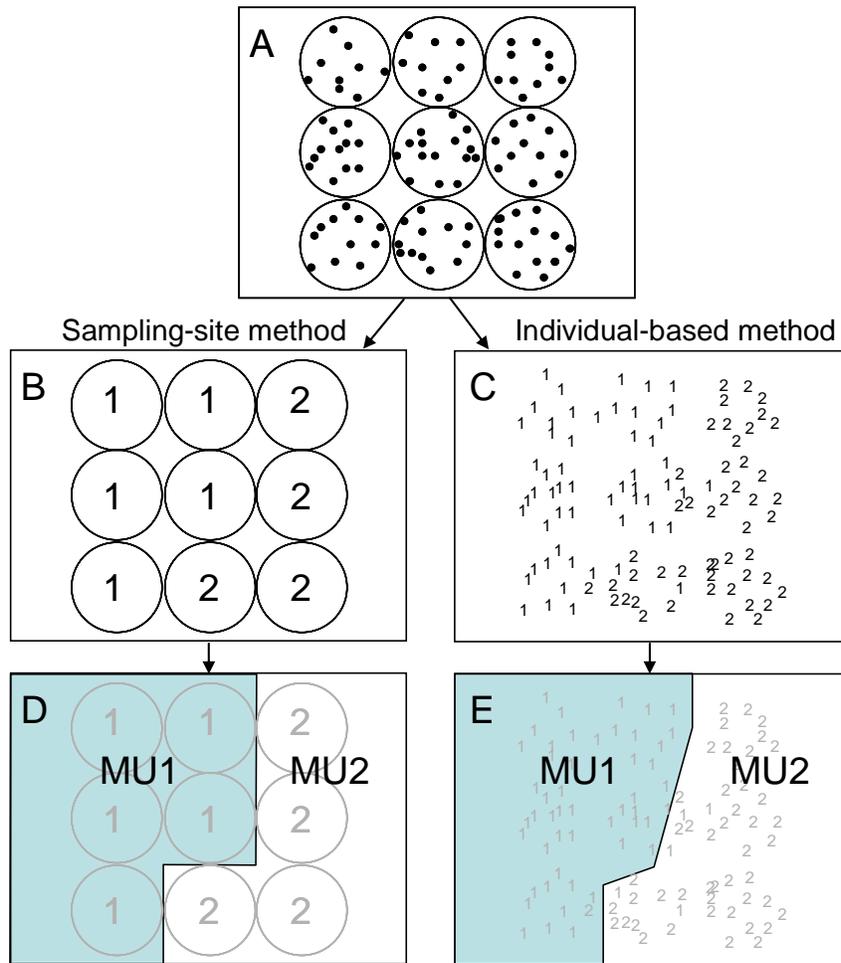| Scenario	# of populations	Dispersal Rate	# of MUs created			Extinction rate	Recovery rate
			1	2	3		
1	1	0	100	0	0	0	1
2	2	5×10^{-6}	0	98	2	0	1
3	2	5×10^{-5}	0	99	1	0	1
4	2	5×10^{-4}	77	23	0	0.39	0.23
5	2	5×10^{-3}	100	0	0	0	0.72

Figure 1. Genetic data from individuals (points) or sampling sites (circles) (A) are analyzed by the BSA and assigned to management units (B,C). The BSA then uses this information to place MU boundaries (D,E).