Lag phases of virtual species (EDITED, Kwizera Jean)

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This initial report outlines the methodological approach and the aims of this study.

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# Abstract

**Aim:** Lag-phases are commonly portrayed in plant invasions, and assessment methods range from field observations literature-based studies to statistical analysis. Recent methodological developments reduce the number of assumptions related to occurrence data. Still, they cannot address the organic nature of the data itself (changing survey effort and focus over time, sparse collections in early invasion stages, inaccessible herbaria). Therefore, comparing the results of real herbaria data to simulated occurrence data will advise the suitability of the (Hyndman et al., 2015) lag assessment method.

**Location**: Australia

**Methods:** I use the RangeShiftR package to simulate a species dispersal on the Australian landmass, supposing introductions at four different ports. We use artificially generated landscapes that contain cell-based habitat suitability and a climate suitability map generated by BCCVL (Hallgren et al., 2016) with varying dispersal distances. We later fit a generalized linear model to the virtual species occurrence records of Australia’s identifying simulations with significant lag-phase and compare those to the existing results using statistical tests for lag length values.

**Results**:

# Introduction

Invasion ecologists and population biologists entertain themselves by investigating species, populations and habitat characteristics determining invasiveness and invasibility. Set aside their ecological and economic harm, invasive species inherit excellent reproductive characteristics facilitating experimentation to determine a species’ invasiveness. In addition, contemporary invasion events present a challenging opportunity to understand ecological and evolutionary processes driving populations to deploy their invasive potential. Four phases describe population dynamics during biological invasions (Kolar and Lodge, 2001; Theoharides and Dukes, 2007) and a frequently reported phase of quiescence with stagnant population growth is one of the crucial stages before a naturalised population becomes invasive (Bock et al., 2015). Context-dependent studies describe species (Liu et al., 2013) and habitat-specific causes for lag-existence and length (Wangen and Webster, 2006), but little is known about generic processes releasing a population from the phase impeding population growth and spread (Bock et al., 2015). This lag phenomenon, depicted as the time required by an invader to reach a point with a significant increase in abundance (Crooks and Soulé, 1999; Shigesada and Kawasaki, 1997; Williamson and Fitter, 1996) after naturalisation or spontaneous occurrence in an area (Hobbs and Humphries, 1995; Pyšek and Prach, 1995), is witnessed in the majority of invasion events (Kowarik, 1995; Larkin, 2012; Mack, 2000).

Various plausible explanations are described (Crooks and Soulé, 1999; Shigesada and Kawasaki, 1997; Williamson and Fitter, 1996), as biotic and abiotic resistors hindering reproduction and dispersal (Chapin et al., 2011), but biological invasions depend on the geographic and environmental context, making it difficult to assign a single cause to an invasion event and to identify factors responsible for the transition between different invasion stages of plants (Crooks, 2005; Daehler, 2009; Kattge et al., 2020; Kowarik, 1995).

Whereas the environment of the native and invaded range is similar, plasticity, an essential driver of the naturalisation process (Sexton et al., 2002), may be sufficient for the invader to establish a self-sustaining population. Genetic mechanisms include evolutionary adaption from standing genetic variation and mutations resulting in increased adaptation or dispersal capability. High propagule pressure provides opportunities for gene recombination fitting the novel environmental conditions (Kolbe et al., 2004) along with the introduction of individuals of the missing sex in dioeciousspecies (Baker and Stebbins, 1965), or mutualists. *Resulting adaptation facilitates spread into secondary habitats after successful establishment in an area* (Colautti and Barrett, 2013; R. D. Holt et al., 2005; Prentis et al., 2008)(Colautti and Barrett, 2013; Robert D. Holt et al., 2005; Prentis et al., 2008)*, as opposed to being responsible for the release from the lag-phase* (Sexton et al., 2002)*.*

# Methods

## Herbarium Data

We expect herbarium data of early stages of invasion to be of poor quality inheriting a high variance and spatial and temporal gaps. We acknowledge that the collection effort varies over time and across different invasion stages, especially whereas changes in awareness, environmental protection policies and invasive species management may lead to structured surveys and management efforts of individual species.

## Dispersal simulation

Therefore we simulate dispersal of a virtual species on the Australian landmass based on *Cakile edentula* using the RangeShiftR package (Malchow et al., 2021). We assume introductions at four ports to simulate dynamics over landscape and climate using a process-based model. RangeShiftR includes modules for demography, dispersal, and genetics whereas we ignore the genetic evolution as part of the model.

*Cakile edentula* has been observed to have high mortality rates during storms and harsh winter conditions, but is resistant to salt spray. It is therefore adapted to complete its lifecycle in short periods of time when shores are free from disturbance through early germination, rapid growth rates and high fecundity. In less harsh conditions such as the pacific coast of California, some of the individuals survive to the 2nd breeding season but with diminished productivity as well (Maun, Boyd and Olson, 1990). The RangeshiftR package considers a non-stage structured dispersal model for non-overlapping generations. We define a less restrictive settlement parameter for *Cakile edentula* such thatan individual that lands in an unsuitable cell can move to one of the eight neighbouring cells in the case that at least one of them is suitable.

### Climate suitability

### We define a Landscape map using Australia’s climate suitability probabilities obtained from BCCVL. Global presence data on *Cakile edentula* was modelled on global climate data at a 1 km resolution, using the MAXENT model on the BCCVL platform to obtain the suitability probabilities for each cell. We filter the data to Australia’s extent and create a raster map file in the ascii format; as specified in the RangeShiftR package documentation. The steps we took to obtain the results from BCCVL were:

* All data required for the climate suitability model must be present in BCCVL to be used. We first log into the platform, navigate to the datasets and upload the global *Cakile edentula* presence dataset in a *csv* file.
* Under “experiments”, we “Start a new experiment”, select “Species Distribution modelling Experiment” and give a name and a description to the experiment.
* We then select the species occurrence data we uploaded, and since we do not have an absence dataset for *Cakile edentula*, configure parameters for the Pseudo Absence model.
* BCCVL provides a set of climate and environmental datasets that can be used in species distribution modelling. We use the “WorldClim, current climate (1950-2000), 2.5 arcmin (~5 km)” dataset, which was the most suitable at the time of this analysis. The data had the lowest resolution and it overlapped with both the occurrence locations (making it possible to estimate a species distribution model model) and target locations (allowing for prediction of suitability probabilities)
* Finally we constrained our model to the occurrence and target locations , ignoring the regions outside the scope of this analysis, selected model to use (MAXENT), and run the experiment.

### Species Distribution Map

### We define a Species Distribution map to initialise the simulation with 100 *Cakile edentula* individuals in each of the 4 port locations of introduction. The map is a raster map file in the ascii format and its resolution is equal to that of the Landscape map (1 km). The coordinates in both the climate suitability and species distribution maps are expressed in longitude-latitude.

Simulation

We use the RangeShiftR package to simulate the dispersal of *Cakile edentula* in Australia. We define the simulation model by providing the landscape, demography, dispersal, initialisation and simulation parameters. The landscape parameters include the Landscape map created from the climate suitability probabilities (LandscapeFile), the maximum number of individuals that can occupy a single cell with a suitability probability (K\_or\_DensDep), the species distribution map (SpDistFile ) and the maps’ resolutions (Resolution and SpDistResolution ). We also define a parameter (HabPercent ) which indicates that the landscape map are cells with suitability probabilities rather than unique habitat codes characterising each cell’s habitat.

We define Demography by the maximum number of offsprings an individual can have in a single reproduction season (Rmax = 1000), the species competition coefficient in its habitat (bc ) given a non-stage structured model with non-overlapping generations (StageStruct ). We also define the species’ reproduction type (ReproductionType ) representing *Cakile edentula’s* asexual reproduction.

We define dispersal by 3 parameters; the emigration probability (EmigProb ), settlement which defines the behaviour of the dispersed species when it arrives in an unsuitable cell (Settle i.e the species moves to a nearby suitable cell) and the movement process for an individual departing from its natal cell towards a potential new cell. *Cakile edentula’s* movement is defined with a double dispersal kernel, providing for the specification of short () and long () range dispersal distances and their probabilities () respectively.

We use the Initialisation parameters to specify that the simulation starts with a species distribution map (InitType) and the parameter (InitDens) which then allows us to specify the number of individuals to be introduced in each cell (IndsHaCell). We simulate *Cakile edentula’s* dispersal with 10 replicates over 1000 years and record the range, population and occurrence at intervals.

## Lag-phase Analysis

Recently Hyndman et al. (2015) have developed a new statistical method which accounts for the variation in sampling efforts when using herbarium time series data to test for lag-phase in biological invasions. To detrend the inter-annual variation in collection effort, they used the total number of herbarium specimens collected in each year , as a measure of the collection rate. If the number of specimens of the focal species, , is Poisson distributed then changes in as a function of time can be described by the following generalized linear model:

. (1)

where ) describes changes in the number of specimens over time. A lag is justified if ) is constant until a given time () and takes a positive slope thereafter (Aikio et al., 2010). The lag year (), the number and position of the knots, are selected by minimizing the Akaike information criterion ((Burnham and Anderson, 2004). We fitted the above model to time series of invader species in Australia and New Zealand using the R (R Development Core Team, 2009) with codes provided by (Hyndman et al., 2015).

# Results

## Simulations

## Lag-phase analysis

## Constancy

Species introduced to more than one region can serve as experimental replicates and provide insights into spatio-temporal invasion trajectories.

# Discussion

TBD

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