

Spatial Demography

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Demographic methods across the tree of life

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Chapter 15: Spatial Demography

Guillaume Péron

Abstract

We can use demographic methods to study the spatial response of individuals and populations to current global changes. The first mechanism underlying range shifts is a change in the spatial distribution of births and deaths. The spatial regression of demographic rates with geostatistical and spatially explicit models documents the intrinsic growth rate across the range of a population. The population distribution is expected to shift towards areas with the largest intrinsic growth rate, both mechanistically and because these areas are attractive to dispersing individuals. The second mechanism is indeed movement, including emigration away from places that recently became inhospitable and immigration into newly available locations. The analysis of dispersal fluxes using movement data, or indirectly by comparing the observed and intrinsic growth rates in integrated population models, documents these fluxes. Combining these two mechanisms in integral projection models or in individual-based simulations is expected to yield major advances in predictive spatial ecology, that is, mechanistic species distribution models.

Keywords

Emigration, geostatistics, immigration, spatially explicit, GIS, spatial demography

15.1 Introduction

Eco-evolutionary processes are rooted in the way fitness varies across space and the way individuals implement dispersal strategies in response to that variation. As climate and land use

changes redistribute the abiotic drivers that influence demography, the importance of spatial aspects in eco-evolutionary dynamics is increasingly obvious (Thuiller et al. 2013). In particular, the balance between extinctions and colonisations contributes to range shifts in metapopulations (Hanski and Gyllenberg 1997; Gandon and Michalakis 1999; McCauley et al. 2013). In the broader community context, the balance between local adaptation (Bohonak 1999; McRae et al. 2008; Burton et al. 2010) and dispersal/movement also creates ways for species and individuals to coexist by implementing different space use tactics (Leibold et al. 2004; Wolf et al. 2007; Péron et al. 2019).

This chapter reviews the analysis of demographic data for inference about spatial variation in fitness components and about dispersal strategies (Table 15.1). It also includes a section about prospective analysis, that is, the study of model properties for predictive inference (section 15.4: the feedback between space use and fitness).

<COMP: INSERT Table 15.1 NEAR HERE>

15.2 Spatial variation in demographic rates

The *intrinsic population growth rate*, the balance between local births and local deaths, documents whether a place acts as a *population source* that contributes to the overall increase in population (Pulliam 1988) or a *population sink* likely to attract more immigrants than it emits emigrants (Novaro et al. 2005). Mapping out the spatial variation in intrinsic population growth rate is thus key to understanding the spatial functioning of populations, pinpoint the areas deserving of conservationists' concerns, infer whether dispersing individuals are using public information or conspecific occurrence to decide where to settle, and determine gene flow from source–sink dynamics. I will first review the generic nonparametric statistical tools to estimate spatial variation in any variable (section 15.2.1) and provide a nonexhaustive review of recent

nonparametric analyses pertaining to spatial demography (section 15.2.2). Parametric approaches will only be briefly discussed (section 15.2.3) because they have been reviewed elsewhere and extensively (Dormann et al. 2007; Beale et al. 2010).

15.2.1 Statistical tools for nonparametric inference about spatial variation

The objective in this section is to provide an overview of often complex statistical techniques and point the reader in the right direction, hopefully.

First, at the data exploration stage, users may want to use Moran's index of autocorrelation to determine whether there is spatial structure in their data (Moran 1950; Cressie 1993). Moran's index detects the presence of a systematic increased level of similarity between data points that are close together compared to data points that are further apart. In practice, one may use the function `Moran` from the `raster` package for R if the data are in raster format and assuming a linear decay in autocorrelation strength with Euclidian distance; or the function `moran` from the `spdep` package to accommodate less regular samples (Bivand et al. 2013).

I will now review the three main options for the analysis of spatial variation in demographic data. Note that these methods can be applied directly to spatially explicit sets of fecundity data or population survey data, but, to apply them to capture–recapture data for inference about survival and lifespan (cf. Chapter 13), they must first be incorporated into the appropriate state-space model that deals with imperfect detection of individuals (Gimenez et al. 2006; Péron et al. 2011).

Random forest algorithms

Also known as hierarchical clustering algorithms, this class of method belongs to the data mining and machine learning movement. It owes its name to its building blocks which are decision trees (Breiman 2001). A decision tree is a sequence of multiple-choice questions based

on clustering criteria or *features* (e.g. 'Is the object red, blue, or green?', 'Is it a square or a circle?'). The *training dataset* is grouped into *bags* according to these features (e.g. bag 1 = 'green squares'). The value of the dependent variable in each bag is computed from the training data (e.g. 'bag 1 was good to eat'). The decision tree is fitted to the training data using traditional statistics (e.g. least square criterion or receiver operating characteristic curve). The interest then lies in the predictive power of the tree, that is, its ability to bin new objects into bags without *a priori* knowledge of the dependent variable and only knowing the features of the object (e.g. 'determine palatability based on colour and shape'). The main issue with this type of approach is overfitting, for example, when the tree uses more features than supported by the training data and identifies small-sample artefacts rather than meaningful trends. To prevent overfitting without losing information, a *random forest* is a group of decision trees each based on a reduced subset of features. The prediction is the consensus between all the trees in the forest. For the random forest to perform better than a single decision tree, we simply need some of the features to be meaningful, that is, related to the predicted variable, and that the predictions made by individual trees have low correlations with each other (Breiman 2001). The latter condition is usually enforced by training each tree in the forest with a different subset of the data and by selecting the features of each tree at random irrespective of their predictive power.

When applied to spatial demography, the key strength of the random forest framework is the ability to input ancillary information in the form of spatial covariates. If the covariates are meaningful and well chosen, the algorithm makes it possible to downscale or disaggregate the demographic data at the resolution of these ancillary covariates (Stevens et al. 2015). However, the random forest algorithm also performs adequately if provided with nothing more than the geographical coordinates of the samples, in which case it will look for clusters of adjacent samples with similar demographic properties (Brickhill et al. 2015; Rushing et al. 2016). In

practice, the random forest algorithm for spatial data is implemented in, for example, the `ranger` package for R (Wright and Ziegler 2017).

Splines

This section is going to be more technical than the rest of the chapter. The principle of this family of techniques is to approximate the spatial variation in a variable *Y* by a sum of *K* unimodal functions with desirable mathematical properties, which are termed the *splines* (Ruppert et al. 2003). The main feature of the splines is their location, that is the position of their *knot* $\boldsymbol{\kappa}_k$, which is typically decided using a data-driven space-filling algorithm (Nychka and Saltzman 1998). The analytical shape of the spline is less influencial. Hereafter, I will consider radial splines denoted $D(\boldsymbol{\kappa}_k, \cdot)$, where *D* is the distance operator. The dependant variable *Y* at location (*x*, *y*), is then modelled through the link function ℓ, as $\ell\left(\hat{Y}\right)(x,y) = \beta_0 + \beta_1 x + \beta_2 y + \sum_{k=1}^{K} b_k \cdot D\left(\boldsymbol{\kappa}_k, (x,y)\right)$. The *b* parameters represent the weights associated to each of the *K* splines. The β parameters represent clinal variation. To fit that model, we need to minimise the least-square criterion $\mathrm{C}(\boldsymbol{b}, \boldsymbol{\beta}) = \| \ell(\boldsymbol{Y}) - \boldsymbol{X} \cdot \boldsymbol{\beta} - \boldsymbol{Z} \cdot \boldsymbol{b} \|^2$, where *Y* contains the *N* observations of the focal variable, $\boldsymbol{X}$ is a *N*×3 matrix containing the coordinates at the sampling locations preceded by a 1 for the intercept, and $\boldsymbol{Z}$ is a *N*×*K* matrix, with $Z_{i,k}$ the value of spline *k* at sampling location *i*.

The main issue with this basic implementation of the spline model is, like in the decision tree case, overfitting. To avoid giving too much weight to idiosyncratic patterns occurring at the sampled locations, one typically incorporates a *penalisation term* designed to force the sum of the squared *b*s to stay below a threshold (Ruppert et al. 2003, p. 65). The criterion to be minimised then becomes of the form $\mathrm{C}(\boldsymbol{b}, \boldsymbol{\beta}, \lambda) = \| \ell(\boldsymbol{Y}) - \boldsymbol{X} \cdot \boldsymbol{\beta} - \boldsymbol{Z} \cdot \boldsymbol{b} \|^2 + \lambda^2 \cdot \boldsymbol{b}^T \cdot \boldsymbol{\Omega} \cdot \boldsymbol{b}$.

Following Ruppert et al. (2003, p. 73), we use for $\boldsymbol{\Omega}$ the $K \times K$ distance matrix with $\Omega_{k,l} = D(\boldsymbol{\kappa}_k, \boldsymbol{\kappa}_l)$. λ is the *smoothing parameter* controlling how much the idiosyncrasies will be smoothed out, to be estimated directly from the data themselves. λ is akin to the bandwidth parameter in kernel density estimators or the penalisation coefficient in lasso regularised regressions. To estimate the parameters, following Ruppert et al. (2003, p. 108ff), we exploit the fact that the criterion $\mathrm{C}(\boldsymbol{b}, \boldsymbol{\beta}, \lambda)$ is the same as that of a linear mixed model with predictor $\boldsymbol{X}$, fixed-effect regression coefficient $\boldsymbol{\beta}$, design matrix $\boldsymbol{Z} = \boldsymbol{Z} \cdot \boldsymbol{\Omega}^{-1/2}$, Gaussian random effects $\boldsymbol{u} = \boldsymbol{\Omega}^{1/2} \cdot \boldsymbol{b}$, and individually and independently distributed Gaussian error term $\boldsymbol{\varepsilon}$ such that $\mathrm{Var}(\boldsymbol{\varepsilon}) = \lambda^2 \mathrm{Var}(\boldsymbol{u})$. This means that we can fit the model using any software designed to fit linear mixed effect models, as long as the software interface allows us to specify a custom design matrix. Implementations using Bayesian software are available (Crainiceanu et al. 2005), including within capture–recapture models that account for imperfect detection of individuals (Gimenez et al. 2006; Péron et al. 2011).

Autoregressive models

This section is also going to be more technical than the rest of the chapter. Note, however, that autoregressive models are readily available in R packages `spdep` and `nlme` (Pinheiro et al. 2013) and are extensively used in ecology (Dormann et al. 2007). The underlying assumption of this class of model is that the value of the target variable *Y* at location (*x*, *y*) can be predicted from the value at any nearby location (*x*+*dx*, *y*+*dy*) and inversely. There are two nonexclusive options to implement that principle (Cressie 1993).

- In a *spatial lag* model, the observations are directly regressed against each other:

  $\ell(\boldsymbol{Y})(x, y) = \boldsymbol{\mu}(x, y) + \rho \boldsymbol{W} \ell(\boldsymbol{Y}) + \boldsymbol{\varepsilon}(x, y)$, where $\boldsymbol{\mu}$ is a mean term that usually

depends on spatially explicit linear predictors, ρ is the autocorrelation coefficient, $\boldsymbol{W}$ is a weight matrix typically corresponding to the Euclidian distances between samples, and $\boldsymbol{\varepsilon}$ contains individually and independently distributed (IID) error terms.

- In a *spatial error* model, the spatial autocorrelation affects the error term only: $\ell(\boldsymbol{Y})(x,y) = \boldsymbol{\mu}(x,y) + \boldsymbol{e}(x,y)$ with $\boldsymbol{e}(x,y) = \lambda \boldsymbol{W}\boldsymbol{e} + \boldsymbol{\varepsilon}(x,y)$. This type of model is typically used when the sampling noise is spatially autocorrelated. If this autocorrelation in the sampling error was not accounted for, the estimation of $\boldsymbol{\mu}$, that is, the ecological process of how the dependent variable *Y* depends on environmental covariates at location (x,y), would be biased, sometimes severely (Beale et al. 2010). Importantly, however, spatial error models work under the assumption that only the sampling error is autocorrelated. If it is not the case, that is, there is a biological process of spatial autocorrelation, using a spatial error model will assign too much spatial variance to the error and not enough variance to the mean.

In terms of R implementation, one may use the functions `lagsarlm` for the spatial lag model and `errorsarlm` for the spatial error model, both from package `spdep`. The spatial lag and spatial error models can also be merged together to obtain the simultaneous autoregressive models (SAR) that features both autocorrelation structures. There is also the conditional autoregressive model (CAR) or autologistic model, a variant of the spatial lag model. CAR is often preferred in ecological applications because of its flexibility and ability to accommodate missing data (Yackulic et al. 2012; Péron et al. 2016). CAR is obtained by designing the weight matrix according to user-specified lists of 'neighbours' for each sample, for example, the adjacent cells in a raster. We specify $\boldsymbol{W}$ as the adjacency matrix with a 1 if two

samples are neighbours and 0 otherwise, and $\boldsymbol{D}$ is the normalisation matrix, a diagonal matrix with $D_{ii} = \sum_j W_{ij}$. Then the CAR model is a Gaussian random field (Gelfand and Vounatsou 2003), of mean $\boldsymbol{\mu}$ and variance $\sigma^2 \left(\boldsymbol{D} - \rho \boldsymbol{W} \right)^{-1}$ (Cressie 1993). Following Besag (1974), there is an analytical solution under some constraints. In practice, implementations like the function `spautolm` from the `spdep` package rely on numerical optimisation to offer more flexibility regarding what goes in $\boldsymbol{\mu}$ and how the $\boldsymbol{W}$ matrix is defined, at the cost of increased risk of numerical errors and optimisation failures. Many ecological applications furthermore include the CAR structure within a more complex hierarchical structure, for example, a partially observed colonisation/extinction process (Yackulic et al. 2012; Péron et al. 2016).

15.2.2 Recent implementations in spatial demography

Spatially explicit matrix population models

By 'spatially explicit matrix population model' I mean an array of grid cell-specific matrix population models (cf. Chapter 9), parameterised using the nonparametric estimation techniques outlined above in section 15.2.1. They describe the spatial variation in intrinsic population growth rate but do not account for dispersal. Actually, I will only review the studies of spatial variation in survival rate, not in intrinsic population growth rate *per se*. This is because I could not locate any study of the spatial variation in fecundity that used a nonparametric technique. However, see data sets of passerine clutch size and nest fate (Baillie 1990; Brickhill et al. 2015; Eglington et al. 2015), acorn production in oak (*Quercus* sp.) forests (Koenig and Knops 2013; Touzot et al. 2018), and egg or foetus mass in harvested individuals from exploited species like commercial fish (Bell et al. 1992; Kraus et al. 2000; Stige et al. 2017) and game (Karns 2014; Gamelon et al. 2018).

Even survival studies are quite rare to the best of my knowledge. Saracco et al. (2010) used autoregressive models to generate maps of survival probability for the wood thrush (*Hylocichla mustelina*), a migratory passerine. The way survival increased in the northern and especially northwesternmost sections of the range is congruent with the observed increase in abundance in the northwestern part of the range (Rushing et al. 2016) and aligns with predictions from climate change. The particularity of the Saracco et al. study is that they accommodated transience at the bird ringing locations, that is, an excess of individuals captured only once (Pradel et al. 1997)—an important nuisance parameter to accommodate when individuals are not site-faithful.

Péron et al. (2011) used the spline method to delineate population sinks as areas where the predicted overwinter survival probability of Eurasian woodcocks (*Scolopax rusticola*) fell below the population renewal rate, itself a function of spatially invariant fecundity and summer survival rates. Their results confirm the additive nature of hunting mortality (Péron 2013) and imply that the dispersal of juveniles into population sinks is critical to the persistence of the species in the sinks.

Campbell et al. (2018) also used the autoregressive method to perform a spatially explicit population viability analysis of the Sonoran desert tortoise (*Gopherus morafkai*) based on spatially explicit survival rates. In this desert-adapted species, their results provide a demographic explanation for the 'abundant centre hypothesis' (Péron and Altwegg 2015b), that is, demographic performance was best at the core of the species' range and worst near the edge of the species' range. Interestingly, a decrease in the age at maturity near the edge of the range failed to compensate for the decreased survival rates.

To my knowledge, there is no study to date using the random forest method to estimate spatial variation in survival rates. This is because the cross-validation part of the random forest

algorithm is not straightforwardly compatible with the state-space modelling framework required to estimate survival from capture–recapture data with imperfect detection.

Modelling the population growth rate from count data

When the vital rates themselves are not available, and if time-specific and spatially-explicit population count data are available, these counts may be interpolated both spatially and temporally to compute the spatial variation in the population growth rate directly (Renner et al. 2013; Rushing et al. 2016). However, in most cases, data sets have proven too sparse and authors have either estimated the spatial and temporal components separately (i.e. using additive effects) or they pooled the data at a coarse ecoregion level. In the latter case, random forest algorithms appear well suited to delineate these ecoregions based on the demographic data themselves (Brickhill et al. 2015; Rushing et al. 2016). In any case, as reviewed further in section 15.3 on dispersal, in vertebrates it is extremely rare to collect exact population counts at a fine spatial resolution and over large geographical areas. What is typically available instead is crowd-sourced, rasterised presence/absence or minimum count data (e.g. Péron and Altwegg 2015a). Using the link between the overall abundance in the landscape and the probability that any given location is occupied, or alternatively the link between the local abundance and the probability that at least one individual is detected (Royle and Nichols 2003), we may use these data as a proxy for the local abundance (Williams et al. 2017) and compute the spatial variation in the population growth rate that way.

15.2.3 Discussion

Empirical discrepancies between the three nonparametric regression methods

Empirically, the outputs of the three nonparametric methods are often significantly different (e.g. ‘RF’ vs. ‘MARS’ in Figure 6 in Renner et al. 2013). This is in part because of differences

in the amount of smoothing. As illustrated by Kie (2013) in the context of kernel density estimators, the smoothing parameter is of paramount importance (see also 'GAM' vs. 'MARS' in Figure 6 in Renner et al. 2013; and 'KDE' vs. 'KDEr' and vs. 'AKDE' in Figure 1 in Péron 2019b). Therefore, the fact that the three methods are not strictly equivalent in terms of the amount of smoothing that they apply is critical. If the noise/signal ratio is large, that is, if nonspatial variance exceeds spatial variance in the data, the random forest is the most likely to overfit the data, and researchers should therefore prefer either the spline or the autoregressive method. But by contrast, if there are discontinuities or locally sharp gradients in the focal variable, the random forest method is the most relevant because other methods will smooth out these discontinuities, and this might lead to lack of fit.

What about fully parametric approaches?

Instead of a nonparametric, descriptive approach, researchers are often keen on using spatial covariates to predict spatial demography and infer the underlying ecological mechanisms (Beale et al. 2010; Germain et al. 2018). This is especially the case when extrapolating mortality factors from telemetry data which have a natural spatial component to them (Schwartz et al. 2010; Basille et al. 2013; Péron et al. 2017). However, researchers should be acutely aware that, especially in our data-rich times, it is often possible to find combinations of climate and vegetation covariates that adequately predict the observed spatial variation in demography, but without capturing any significant biological mechanism, in other words, only by coincidence (Journé et al. 2019). Such correlations are therefore potentially great for interpolating gaps in coverage, but they should not be overinterpreted or used for predictions and extrapolations. For example, within a population of red-billed chough (*Pyrrhocorax pyrrhocorax*), the between-site variation in survival probability was caused by the different natal origin of the individuals in the different sites, not by the environmental attributes of the

sites (Reid et al. 2006). In an archipelago population of great tits (*Parus major*), the spatial variation in demography was driven by an evolutionary 'island syndrome', not directly by the variation in climate between islands and the continent (Postma and van Noordwijk 2005). To avoid the pitfall of overinterpreting correlations, one may define broad ecoregions and compute spatial variation in demographic rate at this resolution. Alternatively, all the nonparametric approaches described in section 15.2.1 can be made into semiparametric tools that combine a regression against spatial covariates and a nonparametric spatial structure in the error term of the regression (Gimenez et al. 2006).

On spatial capture–recaptures

In the context of spatial demography, beware that the phrase 'spatial capture–recaptures' (Borchers and Efford 2008; Royle et al. 2013) usually refers to a type of model that is indeed spatially explicit but does not typically yield an estimate of spatial variation in survival. Spatial capture–recapture models are designed to improve the estimation of the population size by accommodating the decrease in individual capture probability with the distance between the home range centroid of the animal and the capture locations. They thereby provide a better fit to the capture–recapture data. They can inform spatial variation in population density (Gardner et al. 2010), but spatial variation in survival probability remains largely out of bounds for this type of model and data.

15.3 Estimating dispersal fluxes

Dispersal is defined as movement that has the potential to lead to gene flow (Clobert et al. 2001). Movements within individual home ranges and seasonal migrations are not considered dispersal. In many taxa, adults are site-faithful either by constraint (plants, sessile animals) or

due to philopatric behaviour (Greenwood 1980), and thereby gene flow mostly occurs through *natal dispersal*, that is, the movements of immatures or propagules (Greenwood 1980). Importantly, especially with a vertebrate focus, dispersal is the result of a series of decisions—from the decision to leave the current location to the choice of the new location among the locations that were explored (Grosbois and Tavecchia 2003). These different decisions may use different environmental cues, and different individuals may make different decisions based on the same cues. These decisions, summed over time and across individuals, yield the dispersal kernel: the probability that an individual in location (x_1, y_1) at time t_1 will disperse to location (x_2, y_2) at time t_2. One often also refers to 'dispersal fluxes' when the population is spatially structured (the number of individuals dispersing from one site to another site, per unit of time) or to 'dispersal rates' (number of individuals dispersing from one site to another, per unit of time and per individual in the site of origin) (Table 15.1). Dispersal may be recorded directly by documenting the changes in individual locations from one breeding attempt to the next or from the place of birth to the first breeding attempt (Doligez et al. 2002; Ducros et al. 2019). But this type of data remains rare and therefore I will also review less direct methodologies.

15.3.1 Integrated population models

In this method, the target variable is the net flux of individuals that exit or enter a given study region over a given period of time. The net flux is the difference between the number of emigrants and the number of immigrants. That flux is estimated as the difference between the overall population growth (ΔN) minus the intrinsic population growth ($b - d$, where b is the number of births and d is the number of deaths). In practice, the best approach is to jointly analyse capture–recapture data, fecundity survey data, and population survey data in an integrated population model (Abadi et al. 2010), as described in Chapter 14. Because it remains extremely challenging to collect these three types of data together and at the same time,

examples are still rare in the literature (Millon et al. 2019). Importantly, however, several less-data-hungry approaches have been proposed for special cases. For example, Nichols and Pollock (1990) described how to use a 'robust design' of the capture–recapture protocol for voles (*Microtus pennsylvanicus*) that relies on the precise ageing of the juveniles upon capture to separate local recruits from immigrants during the post-dispersal capture events of the same year. Peery et al. (2006) combined the observed rate of recruitment of locally born chicks of marbled murrelets *Brachyramphus marmoratus* and Pradel's (1996) estimate of anteriority within the breeding adults to compute the immigration rate as the difference between local and total recruitment. Note that both of the latter approaches only quantify immigration; emigration is confounded with mortality in these two approaches. Potential users should furthermore carefully consider the model assumptions and the fieldwork requirements that the above authors listed.

15.3.2 Multisite capture–recapture models and integrated metapopulation models

In these methods, individuals are monitored over discrete population units or 'sites', such as seabird colonies or forest fragments. When an individual is recorded to move from one site to another, this represents a recorded dispersal event. The data are processed through a multisite capture–recapture model to allow for missing observations of some individuals in some years (Lebreton et al. 2009), as described in Chapter 13, yielding an estimate of dispersal rates. To further study the dispersal decision process, the dispersal rates may be decomposed into the probability of site-fidelity and the site selection conditioned on the lack of site-fidelity (Grosbois and Tavecchia 2003). The model may feature a 'memory effect' of the location of birth (Péron et al. 2010b) or of the previous dispersal decision (Lagrange et al. 2014).

In addition, to accommodate the fact that researchers in the field may not be able to monitor all the sites in a metapopulation, a 'ghost' population unit may be incorporated in the model,

representing unmonitored population units where an individual may temporarily reside and therefore temporarily escape detection (Schaub et al. 2004). Statistical inference in this case may be facilitated if the unmonitored population units that form the ghost state can be surveyed for population size. These data may be jointly analysed with the capture–recapture data in an 'integrated metapopulation model' (Péron et al. 2010a). The key benefit of the integrated approach is improved accuracy of parameter estimates and the ability to extrapolate the dispersal information from a subset of sites where marked individuals are monitored to a larger ensemble of sites where only population count data are collected (Péron et al. 2010a). Lastly, when the interest lies only in the decision to leave or stay in the current site (Schmidt 2004), the dispersal information may be simplified into a binary variable—site-faithful or site-unfaithful—thereby discarding the information about the site identities (Lagrange et al. 2014).Lastly, note that the dispersal rates in these models do not account for permanent emigration out of the survey area, which is confounded with death but may be age-specific.

In practice, multisite capture–recapture models are best implemented using dedicated software as described in Chapter 13. Integrated metapopulation models are best implemented in the Bayesian framework (e.g. Péron et al. 2012 and references therein), although initial implementations were in the frequentist framework using the Kalman filter to compute the likelihood of the population count data (Péron et al. 2010a and references therein).

15.3.3 Dispersal as a diffusion process along resistance surfaces

The main drawback of the two previous methods is that they require clear boundaries delineating population units. In most cases, these do not exist. The population is instead distributed in a continuous manner along ecological gradients. The dispersal process is then more akin to a diffusion process than to a discrete state-switching process (Ovaskainen et al. 2008; Jongejans et al. 2011; Foltête and Giraudoux 2012; Williams et al. 2017). Nevertheless,

dispersal may still be spatially structured by landscape features (McRae et al. 2008; Spear et al. 2010; Berthier et al. 2013; Hanks and Hooten 2013) or by the social cues that the individuals use to decide where to move, such as conspecific population density and conspecific breeding success (Doligez et al. 2002; Péron et al. 2010b).

Traditionally, this type of ecological landscape structure is documented either by *landscape genetics*, whereby the genetic structure of the population is compared to a landcover map, mostly to infer the barriers to dispersal but also the dispersal corridors that promoted genetic homogenisation (McRae et al. 2008; Spear et al. 2010; Hanks and Hooten 2013), or by *movement data analysis*, whereby the tracked movements of focal individuals are extrapolated to infer the barriers to movement and the corridors that would facilitate the movements of potential dispersers (Ovaskainen 2004; Panzacchi et al. 2016; Scharf et al. 2018; Zeller et al. 2016; Wang 2020). The result is a *resistance surface*.

The resistance surface may also be estimated from demographic data. The spatial and temporal variation in the rasterised population abundance $\boldsymbol{N}$ may be modelled as a *partial differential equation* or *diffusion equation* (Skellam 1951; Okubo and Levin 2001; Ovaskainen et al. 2008; Foltête and Giraudoux 2012; see also Neubert and Caswell 2000; Jongejans et al. 2011). That framework allows an elegant partition of the local population growth rate $\frac{d\boldsymbol{N}}{dt}$ into the intrinsic population growth on the one hand and on the other hand a diffusion term representing the flux of individuals from or into neighbouring locations:

$$\frac{d\boldsymbol{N}}{dt} = \overbrace{\boldsymbol{R} \cdot \boldsymbol{N} \cdot \left(1 - \frac{\boldsymbol{N}}{\boldsymbol{K}}\right)}^{intrinsic} + \overbrace{\nabla^2(\boldsymbol{D} \cdot N)}^{diffusion}$$

The diffusion parameters in $\boldsymbol{D}$ directly quantify the resistance surface. $\boldsymbol{R}$ and $\boldsymbol{K}$ represent the population growth rates and carrying capacities, and ∇^2 is the Laplace operator that computes

the sum of the second partial derivatives relative to geographical coordinates. In practice the diffusion term is approximated by its rasterised formulation, with adjacency matrix $\boldsymbol{W}$ and raster grid resolution h:

$$\nabla^2\left(\boldsymbol{D}\cdot\boldsymbol{N}\right) \approx \sum_{j \mid W_{ij}=1} \frac{\left(\boldsymbol{D}\cdot\boldsymbol{N}\right)_j - \left(\boldsymbol{D}\cdot\boldsymbol{N}\right)_i}{h^2}$$

The rasterisation transforms the diffusion equation into a set of ordinary differential equations, making it solvable within any numerical solver that can manage large systems of equations. As formulated above, the dispersal kernel does not feature a preferential dispersal direction. In wind-dispersed plants (Jongejans et al. 2011), and in the theoretical situation where individuals would have been selected by climate change to systematically disperse in a particular direction, the contributions to the sum over j in the above equation could be weighted according to the dispersal direction.

Another major caveat, which is not always recognised, is that the diffusion equation as written above assumes that movements are most likely between adjacent grid cells. The framework does not really accommodate long-distance dispersal. Depending on the behaviour of the species at stake, this model may therefore grossly misrepresent the biological process. This may explain some apparent lack of fit of that model to the patterns that occur along the colonisation front of species that routinely perform long-distance dispersal (Louvrier et al. 2019). Alternative formulations of the diffusion term in the above equation therefore appear warranted. Avenues of research in this direction include the Riesz fractional derivatives, as used to represent the infamous (for movement ecologists) 'Lévy flight' (Mandelbrot 1982; Sims et al. 2008; Çelik and Duman 2012).

Eventually, the main issue with this approach is going to be the data requirements, but a new era seems to have opened in that respect. Recently, Williams et al. (2017) proposed to leverage the link between the abundance of a species and the probability that it is detected

during any one visit to a location of occurrence (Royle and Nichols 2003). This makes it possible to fit the above model to presence/absence data, which are much easier to obtain nowadays by crowd-sourcing than population survey data which would require an intense professional field effort. The parameters of the dynamic occupancy model (colonisation rates, extinction rates, and detection probabilities; Yackulic et al. 2012; Péron et al. 2016) are expressed as functions of ***R***, ***K***, and ***D***, allowing the estimation of the latter. Recent examples include the description of the colonisation of a newly ice-free bay by sea otters (*Enhydra lutris*) (Williams et al. 2019) and the recolonisation of south-eastern France by wolves (*Canis lupus*) (Louvrier et al. 2019). The main limiting assumption of that presence–absence framework is that the population must remain well below carrying capacity. In other words, the framework applies to rare species or species that are currently expanding. When the population enters the density-dependent regime, most of the study area is occupied, the detection of at least one individual does not depend on abundance anymore (Royle and Nichols 2003), and the intrinsic growth rate is mostly influenced by ***K*** rather than ***R***. This makes the model unidentifiable, that is, the parameters cannot be separately estimated in this biological configuration. This is called *weak identifiability*.

In conclusion, the diffusion equation approach to the estimation of resistance surfaces currently rests on several strong assumptions. Although this represents a limit to its applicability today, the framework nevertheless appears extremely promising as an approach to analyse crowd-sourced data and therefore warrants more attention from mathematically inclined ecologists.

15.4 The feedback between space use and fitness

In the previous sections, I described how to estimate the link between the geographic location of an individual, its demographic performance, and its dispersal kernel. Now I will outline how

to use this information to parameterise an integral projection model (IPM) to forecast the future distribution of the population based on its spatial demography.

15.4.1 Principles of integral projection models as pertaining to spatial demography

In IPM parlance (cf. Chapter 10), natal dispersal corresponds to 'inheritance' and adult or breeding dispersal corresponds to 'growth'. Besides that, spatial IPMs are not conceptually very different from unidimensional IPMs designed to study the dynamics of quantitative traits like body mass (Lewis et al. 2006; Jongejans et al. 2011; Merow et al. 2014). The basic principle is to define a kernel function *k* representing the probability that an individual at location (x_1, y_1) at time t_1 will yield an individual at location (x_2, y_2) at time t_2. The kernel function combines all the information about how the individual survived, where it moved, whether it reproduced, and where the offspring moved. Further defining the *function to function operator* $K(\boldsymbol{v})(x_2, y_2) = \iint_{\Omega} \boldsymbol{v}(x_1, y_1) k(x_1, y_1, x_2, y_2) dx_1 dy_1$, where $\boldsymbol{v}$ represents a distribution function, the IPM equation becomes $\boldsymbol{n}(t_2) = K(\boldsymbol{n}(t_1))$, where $\boldsymbol{n}(t)$ denotes the population distribution at time *t*. In the following I will outline how to analyse the properties of *K*, but first I will review a lingering question in spatial ecology, that is, the fundamental difference between contingency and agency.

15.4.2 Space use or resource selection?

One of the critical decisions that eventual applications of the above principles will have to make is whether to model space use *per se*—for example, the focal variable is the geographical coordinates of the individual (Lewis et al. 2006; Jongejans et al. 2011)—or whether to model a behavioural trait that governs space use—for example, resource selection coefficients, personality traits, or 'movement syndromes'. 'Movement syndromes' refer to covariations

between movement rates and between movement rates and other behavioural traits, often labelled as personalities, for instance explorative or competitive personality (Wolf et al. 2007; Spiegel et al. 2017). Species- and individual-specificity in these syndromes is known to enhance coexistence (Vanak et al. 2013; Péron et al. 2019) and population viability in fragmented landscapes (Zheng et al. 2009; Zera 2017).

In the first case, the model describes the interaction between geographical coordinates and fitness. For geographical coordinates, one may use the centroid of an animal's home range. One may also replace the coordinates with the proportion of a given landcover in the home range (Péron 2019b) or the environmental covariates where a plant is growing (Merow et al. 2014), thereby swapping the geographic coordinates for the ecological coordinates. In this type of application, the IPM will become a relatively phenological model, forecasting the population distribution if current reaction norms are maintained into the future (Neubert and Caswell 2000; Lewis et al. 2006; Merow et al. 2014). However, the spatial variation in demography will just get described, not explained.

In the second case, one first estimates behavioural traits and in a second step links these traits to spatial demography. But in this case, researchers may need to incorporate plastic reaction norms describing how the behavioural trait changes depending on the context. For example, resource selection coefficients depend on what is available for selection, often in a nonlinear way (Forester et al. 2009). A typical example is roe deer (*Capreolus capreolus*), which today are commonly found in open agricultural landscapes but will revert to selecting forest edges if given the opportunity. The realised resource selection coefficients may therefore need to be interpreted with caution and may perhaps best be replaced by alternative behavioural metrics that capture the plasticity of resource selection by each individual (Bonnot et al. 2018). Importantly, the two approaches (geographical coordinates and behavioural traits) are not mutually exclusive. They are opposed here to reflect on the underlying philosophy and lingering

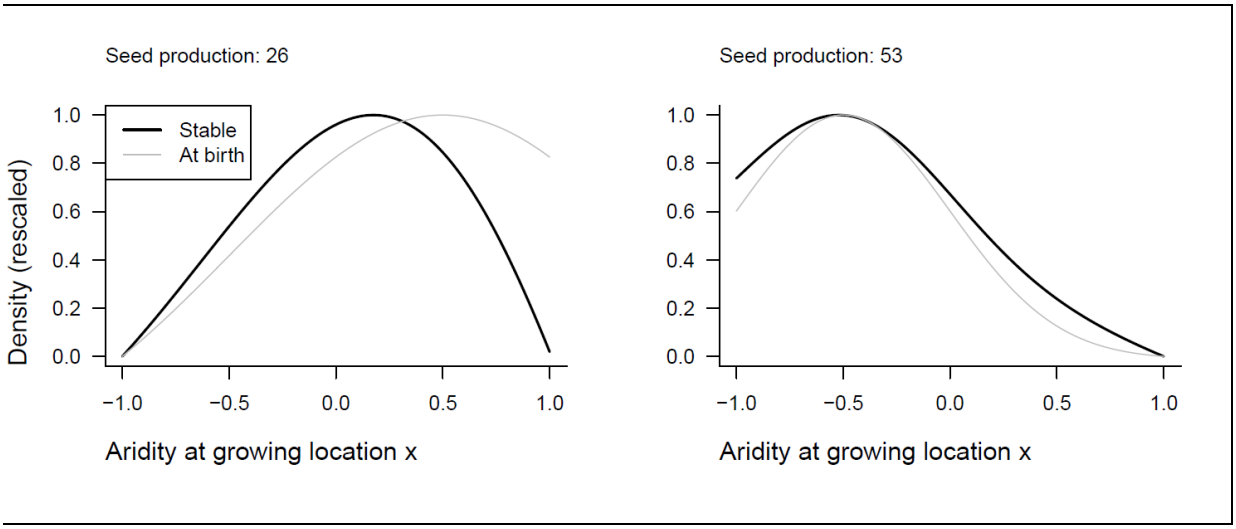
challenges in terms of data acquisition. Lastly, the interpretation of spatial IPMs in terms of evolutionary dynamics is not always straightforward. Similar to the way that offspring may inherit the large or small body mass of their mother because they feed on the same resource, not because they share the same genotype, the inheritance parameter in spatial IPMs combines true heritability and nongenetic inheritance. The nongenetic inheritance stems from the fact that offspring are expected to settle closer to their parents than expected at random, due to physical constraints on movement distance..

15.4.3 Formal analysis of IPMs

IPMs, once parameterised with field data, can be formally analysed for inference about equilibrium distribution, spatially explicit population growth, sensitivity of the population growth rate to variation in model parameters, individual variation, transitory dynamics (Ellner and Rees 2006), and the speed of the range shift under some additional conditions (Lewis et al. 2006). As an illustration, I will focus on a well-worked example that pertains to monocarpic perennial plants (Rose et al. 2005; Ellner and Rees 2006; Rebarber et al. 2012). The keys to this model are that (1) the distribution of the focal trait among propagules is independent from the trait value of their parents; and (2) density dependence occurs among seedlings/propagules only, meaning that the recruitment rate declines with the number of candidates to recruitment, not the number of adults. There is usually a stable distribution of the trait in such a system (Ellner and Rees 2006; Rebarber et al. 2012) which can be computed as a function of the trait-specific survival function *s*, the trait distribution at birth *b*, the trait-specific fecundity function *c*, and the density-dependent recruitment term *g* (Figure 15.1; Appendix 1; please go to www.oup.com/companion/SalgueroGamelonDM).

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Figure 15.1 Simulation inspired by Rebarber et al. (2012) of a perennial plant population with no seed bank and random seed rain, faced with two scenarios of aridity. Left: a drier scenario. Seeds are more likely to fall in an arid spot (cf. grey curve). Compared to the distribution among seedlings (grey curve), the stable population distribution is shifted towards wetter locations (black curve), mostly because the seedlings that grow in the driest locations fail to survive. This means that over time the population is expected to shift its range centroid towards wetter locations, at a pace that can be estimated, but that there will always be a few individuals growing in arid locations because that is where they fell as a seed. Right: a wetter scenario. The stable population distribution is barely different from the expectation from the seed rain. This means that the population range is not expected to change much over time. Note also among the model outputs the forecast of the average population fitness and reproductive rates. In detail, the model was specified by the survival function $s(x)=logit^{-1}(2-2x)$, the fecundity function $c(x)=exp(2-2x)$, and the density-dependent recruitment $g(C)=C^{-0.33}$. The code is freely available and can be modified to accommodate any other analytical form for these functions (Appendix S1; please go to www.oup.com/companion/SalgueroGamelonDM).



Now, to make this model a model of spatial demography, the trait may, for example, represent the aridity at the specific location where the plant is growing. Then, *b* represents the

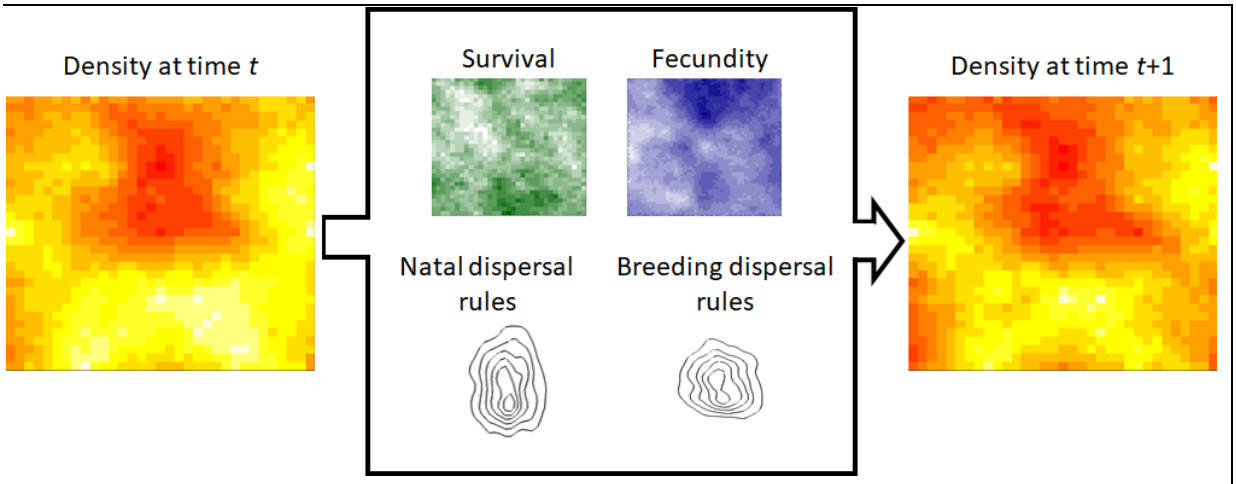
relative frequency of arid and wet places in the landscape where seeds are randomly dispersed by wind, for example; that is, *b* represents the environmental constraints. The stable distribution represents the eventual population distribution along the aridity gradient, as caused by the demographic performance of the individuals (Figure 15.1). There is, however, no evolution involved: at each generation the seedlings are redistributed at random along the aridity gradient (using the grey curves in Figure 15.1). As a side note, the complex mathematics underlying the formal analysis of density-dependent IPMs (Rebarber et al. 2012) render the framework somewhat costly to tailor to specific situations, which might restrict the type of study systems for which it is relevant and the type of evolutionary questions that can be tackled with it.

15.4.4 Individual-based simulation approach

As highlighted in section 15.4.3, the formal analysis of IPMs may not offer enough flexibility in practice to accommodate the complexity of ecological processes and to easily tailor the IPMs to specific case studies. In the context of spatial demography, a more flexible alternative is individual-based modelling (Chapter 12). The simulation focuses on individual movement decisions and their consequences in terms of survival and reproduction. The simulation parameters are informed by analyses from section 15.2 about spatially explicit survival and fecundity and from section 15.3 about dispersal kernels. The IPM properties are then computed as emergent properties of the individual-based simulation (e.g. Wiens et al. 2017). The movement model do not need to be more complex than a step selection model (Signer et al. 2017; Péron 2019a). However,the interest of the framework lies in its flexibility, for example, to incorporate interactions between individuals, to take into account the cost of movement (Péron 2019b), to add heritable individual covariates that influence dispersal decisions, and to outfit the individuals with the ability to gather information about the spatial variation in fitness (Doligez et al. 2002) (Figure 15.2).

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Figure 15.2 Principles of the simulation approach to analyse complex IPMs. The simulated animals are drawn from the density distribution at time *t*, made to perform and move according to the IPM kernel function, yielding the density distribution at time *t*+1. The process may be iterated a large number of times to obtain the asymptotic behaviours of the system. The kernel function may incorporate more complex rules than depicted, for example, dependency on nonstationary environmental covariates and interactions between the model individuals. Importantly, the kernel functions may depend on heritable individual traits that govern the spatial behaviour, rather than directly on the geographical coordinates. For example, data permitting, the trait under study could be the preferential direction of the natal dispersal kernel, and the model would provide inference about the selection pressure on dispersal direction.



Technical bottlenecks that currently hamper the more widespread empirical implementation of spatial IPMs to vertebrates include the need to track the movements and demographic performance of a large number of individuals with known parentage and over long enough periods of time that the repeatability, reaction norms, and age specificity of their space use patterns and fitness components can be estimated. Despite the democratisation of geotracking technologies, these conditions remain hard to meet.

15.5 Conclusions

Although spatial demography is firmly located at the core of eco-evolutionary thinking, it does not appear to have given rise to a rich empirical literature yet, even if many methods are now readily available. The reasons include on the one hand the prohibitive data requirements and on the other hand the relative lack of communication between method-heavy 'quantitative ecology' projects and concept-heavy theoretical initiatives. This overall makes it challenging to adopt a comprehensive empirical outlook on spatial demography. The increasing availability of crowd-sourced species distribution data and the democratisation of geotracking technologies represent exciting opportunities. The fact that spatial demography bridges some currently isolated subfields like movement ecology and evolutionary biodemography may also open fruitful interfaces.

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Table 15.1 List of the spatial demography methods reviewed in this chapter. Note, that this chapter does not consider movement tracking data or genetic data, only demographic data in the sense of information about vital rates and population abundance.

Spatial variation in demographic rates		
Method name	Objectives	Section
Splines	Continuous spatial variation in a demographic rate, nonparametric (no environmental predictor needed)	15.2.1
Autoregressive models	Continuous variation, nonparametric	15.2.1
Random forest algorithm	Continuous variation, nonparametric	15.2.1

Spatial variation in demographic rates		
Method name	Objectives	Section
Linear models	Continuous or discrete variation, parametric (environmental predictor needed)	15.2.3
Multisite capture–recapture model	Discrete spatial variation in survival probability (i.e. analysis of the differences between predefined population units)	15.3.2
Integrated metapopulation model	Same as above but ability to estimate fecundity too	15.3.2
Dispersal fluxes		
Method name	Objectives	Section
Integrated population model	The net flux of individuals into or outside of a focal population	15.3.1
Multisite capture–recapture model	The rates at which individuals disperse between discrete population units	15.3.2
Integrated metapopulation model	Same as above but increased statistical power and spatial extent	15.3.2
Diffusion equation	Landscape resistance to population homogenisation in a continuously distributed population	15.3.3