



## Inverse modeling for effective dispersal: Do we need tree size to estimate fecundity?

Nikos Nanos<sup>a,1</sup>, Kajsa Larson<sup>b,2</sup>, Matias Millerón<sup>a,1</sup>, Sara Sjöstedt-de Luna<sup>c,\*</sup>

<sup>a</sup> School of Forest Engineering, Technical University of Madrid, Ciudad Universitaria s/n, E-28040 Madrid, Spain

<sup>b</sup> Department of Statistics, Umeå University, SE-901 87 Umeå, Sweden

<sup>c</sup> Department of Mathematics and Mathematical Statistics, Umeå University, SE-901 87 Umeå, Sweden

### ARTICLE INFO

#### Article history:

Received 6 February 2010

Received in revised form 8 July 2010

Accepted 8 July 2010

Available online 13 August 2010

#### Keywords:

EM algorithm

European beech

Dispersal kernel

Recruitment

Reproductive success

### ABSTRACT

The estimation of the dispersal kernel for the seedling and sapling stages of the recruitment process was made possible through the application of inverse modeling to dispersal data. This method uses the spatial coordinates of adult trees and the counts of seedlings (or saplings) in small quadrats to estimate the dispersal kernel. The unknown number of recruits produced by an adult tree (the fecundity) is estimated – simultaneously with the dispersal kernel – via an allometric linear model relating the unknown quantity with a (easily) measured characteristic of the adult tree (usually the basal area). However, the allometric relation between tree size and reproductive success in the sapling (or seedling) stage may not be strong enough when numerous, well-documented, post-dispersal processes (such as safe-site limitation for recruitment) cause large post-dispersal seedling mortality, which is usually unrelated to the size of the tree that dispersed them. In this paper we hypothesize that when tree size and reproductive success in the seedling/sapling stage are not well correlated then the use of allometry in inverse modeling is counter-productive and may lead to poor model fits. For these special cases we suggest using a new model for effective dispersal that we term the *unrestricted fecundity (UF) model* that, contrary to allometric models, makes no assumptions on the fecundities; instead they are allowed to vary freely from one tree to another and even to be zero for trees that are reproductively inactive. Based on this model, we examine the hypothesis that when tree size and reproductive success are weakly correlated and the fecundities are estimated independently of tree size the goodness-of-fit and the ecological meaning of dispersal models (in the seedling or sapling stage) may be enhanced. Parameters of the UF model are estimated through the EM algorithm and their standard errors are approximated via the observed information matrix. We fit the UF model to a dataset from an expanding European beech population of central Spain as well as to a set of simulated dispersal data where the correlation between reproductive success and tree size was moderate. In comparisons with a simple allometric model, the UF model fitted the data better and the parameter estimates were less biased. We suggest using this new approach for modeling dispersal in the seedling and sapling stages when tree size (or other adult-specific covariates) is not deemed to be in strong relation to the reproductive success of adults. Models that use covariates for modeling the fecundity of adults should be preferred when reproductive success and tree size guard a strong relationship.

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### 1. Introduction

Seed dispersal is a key ecological process that determines plant migration and community structure and diversity (Hubbell, 2006), while its respective models are useful tools for discussing colonization-competition hypothesis (Clark et al., 2004) and genetic structure in forest stands (Gonzalez-Martinez et al.,

2006). Recently, the estimation of dispersal models is considered crucial for predicting the invading potential of exotic species (Higgins et al., 2003) or transgenic organisms (Andow and Zwahlen, 2006) but, traditionally, it has been used for discussing species' life-history traits (Lambers and Clark, 2005) and colonization of new habitats in the general ecological setting (Wada and Ribbens, 1997) or in the more applied setting of stand regeneration after silvicultural treatments or forest fires (Hammill et al., 1998; Medjibe and Hall, 2002). More interestingly, the dispersal kernel has received particular attention for the estimation of long distance dispersal events with major implications to our understanding of past massive migrations of plant populations (Clark et al., 1998) or to the development of future plans for conservation of species threat-

\* Corresponding author. Tel.: +46 90 786 51 29; fax: +46 90 786 52 22.

E-mail address: [sara@math.umu.se](mailto:sara@math.umu.se) (S. Sjöstedt-de Luna).

<sup>1</sup> Tel.: +34 91 336 71 13; fax: +34 91 336 55 56.

<sup>2</sup> Tel.: +46 90 786 51 11; fax: +46 90 786 66 14.

ened by global change (Higgins et al., 2003; Pearson and Dawson, 2005).

Dispersal models for forest tree species may be divided into models for primary and effective dispersal. The former predict the initial displacement of seeds from the adult canopy to the location where they are first deposited on the ground, while the latter encompass the additional post-dispersal processes that take place after the seed is deposited on the soil surface until it is transformed into a sapling. Dispersal models, regardless of their type, are fitted to data from mapped field plots where the offspring (either seedlings/saplings or seeds) dispersed by the conspecific adult trees are counted in a number of quadrats (or seed traps). The actual dispersal distances separating adults from their offspring cannot be directly measured in the field since seedling (or seed) shadows of neighboring trees typically overlap. Additionally, the number of offspring produced by each adult of the experiment (fecundity) is unknown. The estimation of the dispersal distance distribution and the fecundity of adult trees have been made possible with the Inverse Modeling (IM) approach (Ribbens et al., 1994). In IM, maximum likelihood methods are used to estimate the parameters of the dispersal kernel and (simultaneously) the fecundity of adults based upon the spatial pattern of offspring and the adults that dispersed them.

Inverse modeling was initially based on a linear deterministic relationship between fecundity and tree size (Ribbens et al., 1994). However, Clark et al. (2004) have noticed that the use of adult size to model fecundity (in the seed stage) may be insufficient due to the great tree-to-tree and interannual variability in the fecundity schedule of forest tree species. They therefore suggested enhancing the model performance by adding a random tree component into the fecundity model. The model is embedded into a hierarchical Bayesian structure that, furthermore, takes in to account interannual variation in the fecundity schedule. Other attempts to make the fecundity model more flexible include this of Schurr et al. (2008), who proposed embedding local environment factors (i.e. stem density) to the fecundity model and Uriarte et al. (2005) who introduced the minimum diameter to maturity as an additional parameter of their fecundity model.

Tree size is likely to be an inefficient predictor of a trees' reproductive success in the sapling (or seedling) stage due to variable post-dispersal mortality rates for the seed-to-seedling and the seedling-to-sapling transition or due to predispersal seed predation by vertebrates and insects (Nilsson and Wastljung, 1987). Undoubtedly, the distribution of safe-sites for seedling establishment and survival plays a central role in shaping the reproductive success of adults through several environmental factors such as light environment or unsuitable substrate (LePage et al., 2000; Uriarte et al., 2005). Additionally, negative density-dependent mortality has been shown to be driving post-dispersal seedling dynamics. De Steven and Wright (2002), for example, report for *Trichilia* sp. that adults with higher reproductive success in the seed stage did not recruit more seedlings, suggesting that negative density-dependent mortality regulated the recruitment success. Finally, the higher rates of natural enemies' occurrence close to parent trees is also a well-known factor that shapes the recruitment pattern by reducing drastically the seedling densities (Augsburger, 1984).

Additional information on the relation between tree size and reproductive success in the seedling and sapling stages has been made available after a series of parental assignment studies that use molecular markers to detect the unknown parent trees of the analyzed offspring. According to these findings, the female reproductive success in the seedling or sapling stage is largely unequal across adults. Piotti et al. (2009), for instance, working in an expanding spruce population, point out that the significant relationship found between reproductive success and tree size was sustained

by just one adult individual (out of 23 genotyped adults). Furthermore, Schnabel et al. (1998) report that 50% of the genotyped *Gleditsia triacanthos* L. adults were reproductively inactive while Gonzalez-Martinez et al. (2006) found that 2% of their genotyped *Pinus pinaster* Ait. adults were responsible for 32% of the natural regeneration.

Occasionally, when modeling primary seed dispersal, ecologists conduct direct seed counting/observations on the tree crown instead of using tree size as a proxy to fecundity. Although time-consuming and imprecise, visual assessment of the seed set of adults provides more accurate fits when compared to allometric fecundity models (LePage et al., 2000; Sagnard et al., 2007). Observations on the tree crown are also used in the Bayesian model of Clark et al. (2004) who classify adults into mature or not depending on whether individual trees bear any seeds. Similar approaches for effective dispersal have not been reported; since there is no virtually feasible method to make direct observation on the number of successfully established seedlings (or saplings) dispersed by an adult.

In this study we present a model for effective dispersal termed the unrestricted fecundity – UF – model. Instead of using an allometric assumption to estimate the effective fecundity of adults, the UF model allows fecundities to vary freely from one tree to another and even to be zero in cases of reproductively inactive trees. We are using this model to examine whether the effective fecundity can be estimated without building a model on covariates. We hypothesize, furthermore, that when the estimation of fecundity is based on a loose relationship with tree size (or other covariates) then numerical maximum likelihood may not succeed in identifying correctly the shape parameter of the dispersal kernel (a usual practice in such cases consists in fixing the shape parameter of the dispersal kernel to a logical guess (Ribbens et al., 1994; Clark et al., 1999; Snäll et al., 2007)). We fit the UF model to a dataset from an expanding European beech population of central Spain as well as to simulated data and derive maximum likelihood parameter estimates through the EM algorithm (Dempster et al., 1977). We also present approximate formulas for the standard errors of the parameter estimates derived via the observed information matrix. Comparisons with a classical allometric model show that the UF model fits the data better and that parameter estimates are less biased. Additionally, we show that the output of the UF model fit is more meaningful from an ecological viewpoint when adjusted to the dispersal data from the European beech population. We suggest using this model when reproductive success is weakly or moderately related to tree size (or other covariates). In all other cases models with (fixed) covariate effects or a combination of fixed and random effects (as in Clark et al., 2004) should be preferred.

## 2. Methods

### 2.1. Model specification

Our main goal is to estimate the distribution of dispersal distances separating seedlings or saplings (hereafter we use the term recruits to refer either to seedlings or saplings) from their parent trees, but at the same time we estimate the adult tree's effective fecundities (i.e. the number of recruits produced by an adult). Data are derived by registering the locations of  $i = 1, \dots, N$  adult trees in a given region and counting recruit abundance on  $j = 1, \dots, M$  sites (small non-overlapping regions). The observed sample  $(n_{11}, \dots, n_{mN})$  consists of the number of recruits in each site. The UF model assumes that the fecundity of tree  $i$  follows a Poisson distribution with expected value  $S_i$ . The allometric seed-shadow model (hereafter referred to as the BA model) assumes that fecundity is proportional to the basal area such that  $S_i = \beta \times b_i$ , where  $b_i$  is

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