Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics

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Abstract. The colonization–extinction dynamics of many species are affected by the dynamics of their patches. For increasing our understanding of the metapopulation dynamics of sessile species confined to dynamic patches, we fitted a Bayesian incidence function model extended for dynamic landscapes to snapshot data on five epiphytic lichens among 2083 mapped oaks (dynamic patches). We estimate the age at which trees become suitable patches for different species, which defines their niche breadth (number of suitable trees). We show that the colonization rates were generally low, but increased with increasing connectivity in accordance with metapopulation theory. The rates were related to species traits, and we show, for the first time, that they are higher for species with wide niches and small dispersal propagules than for species with narrow niches or large propagules. We also show frequent long-distance dispersal in epiphytes by quantifying the relative importance of local dispersal and background deposition of dispersal propagules. Local stochastic extinctions from intact trees were negligible in all study species, and thus, the extinction rate is set by the rate of patch destruction (tree fall). These findings mean that epiphyte metapopulations may have slow colonization–extinction dynamics that are explained by connectivity, species traits, and patch dynamics.

Key words: *Bayesian inference; colonization–extinction dynamics; dispersal; incidence function model; lichens; niche breadth; patch-tracking metapopulation; tree age.*

Introduction

The colonization–extinction dynamics of sessile organisms are poorly understood, but known to often be affected by the dynamics of their patches (e.g., Snäll et al. 2003, Verheyen et al. 2004, Jönsson et al. 2008). Empirical studies of their rates of colonization are rare, but many seem to be restricted by dispersal as the summed distance to surrounding occupied patches (henceforth connectivity; Hanski 1999) has been shown to be important (e.g., Verheyen et al. 2004, Snäll et al. 2005, Jönsson et al. 2008). This suggests dispersal limitation of many species in accordance with metapopulation theory (Hanski 1999). The ability to colonize unoccupied patches is expected to be affected by species traits such as habitat preference, dispersal propagule size, or propagule numbers. For example, generalists, with wide niches, should occupy more patches in the landscape compared to specialists with narrow niches (Brown 1984). This results in higher connectivity for generalists than for specialists and, thus, according to metapopulation theory (Hanski 1999), a higher colonization rate. However, we are not aware of any studies of the relationship between niche breadth and colonization rate in sessile species. The dispersal propagule size is a

key trait in explaining the colonization rate in wind-dispersed species. Decreasing propagule size has been suggested to increase the dispersal range (e.g., Okubo and Levin 1989, Kimmerer 1991, Löbel et al. 2009), but decrease the establishment or recruitment (Jakobsson and Eriksson 2000, Löbel and Rydin 2010). Ground-floor vascular plants with small seeds occur more frequently in young forest than large-seeded species that seemingly colonize later (Verheyen et al. 2003), and forest species with small seeds have higher colonization rates than species with large seeds (Verheyen et al. 2004). Moreover, there is a trade-off between propagule size and numbers (Jakobsson and Eriksson 2000), suggesting decreasing establishment or recruitment with increasing numbers. However, increasing numbers of dispersed propagules (emigrants) should also increase the colonization rate.

Local extinctions of sessile organisms that are confined to dynamic patches can either result from demographic or environmental stochasticity in intact patches, or from patch destruction (Snäll et al. 2003). Stochastic extinctions have been shown to be negligible in predicting the metapopulation dynamics of a bryophyte (Snäll et al. 2005) and of wood-decaying fungi (Jönsson et al. 2008). Instead, local extinctions were driven by deterministic patch destruction. In contrast, stochastic extinctions were relatively common in other sessile organisms (e.g., epiphyllous bryophytes [Zartman and Shaw 2006], vascular epiphytes [Laube and Zotz
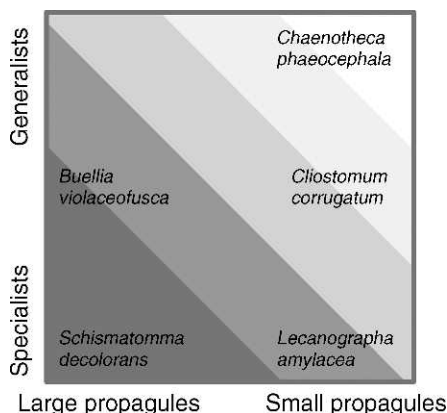
Fig. 1. Conceptual model for the relationship between niche breadth, propagule size, and colonization rates in sessile species. The colonization rate increases from dark to light. The characteristics of the study lichen species according to the literature and independent data (Appendix A: Table A1) are illustrated by the placement of their names.

2007], epixylic lichens [Caruso et al. 2010], a lichen [Öckinger and Nilsson 2010]). Evidently, the importance of local stochasticity in determining the extinction rates of sessile organisms varies, and one reason may be the stability of the patches.

A key problem in studying colonization–extinction dynamics of sessile species is their slow dynamics. Therefore, a model that can be fitted using data from one point in time (henceforth snapshot data) is useful. Verheyen et al. (2004) extended the incidence function model (IFM; Hanski 1994) to dynamic landscapes by including the age of the patches. This meant adding a temporal dimension to the model, a feature that was lacking in the original IFM. We modify and extend this model for answering the questions addressed in the current study.

The tree–epiphyte system is a good model system to explore dispersal and metapopulation processes of sessile species living in dynamic landscapes, as trees are easily defined patches that emerge, grow, and fall, surrounded by an inhospitable matrix. In Europe, pendunculate oak (*Quercus robur* L.) trees constitute a key host for many species groups (Niklasson and Nilsson 2005). One example is epiphytic lichens, of which many depend on the characteristic coarse bark of old oaks (Thor and Arvidsson 1999). The frequency and occurrence of many of these species increase with tree age or with tree characteristics that are correlated with age (Ranius et al. 2008, Johansson et al. 2010). As the tree ages, the abiotic conditions and the substrate suitability changes, and tree age is therefore a suitable, relatively easily measured, niche proxy for epiphytes.

The study aim is to increase the understanding of the metapopulation dynamics of sessile species with slow colonization–extinction rates that depend on the dynamics of their patches. The approach is fitting a modified and extended Bayesian version of the IFM for

dynamic landscapes (Verheyen et al. 2004) using snapshot data on a set of epiphytic lichens. Specifically, we investigate whether the colonization–extinction dynamics are explained by metapopulation theory: are colonizations explained by connectivity, and are extinctions explained by local population processes or patch dynamics? We also investigate the relative importance of local dispersal between patches in the study area and long-distance dispersal from the surrounding landscape. Finally, we investigate whether the colonization rates are explained by niche breadth or propagule size. We hypothesize that the colonization rates are highest in generalists (colonizing younger trees) with small propagules, and lowest in specialists (colonizing older trees) with large propagules (Fig. 1).

METHODS

The field work was conducted June–August 2008 at "Tinnerö Eklandskap" (58°22′ N, 15°36′ E), an oak-rich nature reserve situated in southeastern Sweden. The area was an important hay producer from the beginning of the 17th century until about 1960, with a high proportion of oak-rich wooded meadows (Anonymous 2006; see Plate 1). We choose this study area because of the known high current and historical oak density (Anonymous 2006). Another reason was that the current age distribution of potentially suitable trees suggests that the system is in regeneration and mortality equilibrium (Appendix A: Fig. A1). Thereby, we also expect an equilibrium in lichen colonization–extinction dynamics, where the extinction rate is determined by the sum of stochastic extinctions from intact trees and deterministic extinctions as trees die and their bark falls off.

We studied five oak-associated crustose lichen species, with varying propagule size and niche breadth (Fig. 1; Appendix A: Table A1). All species except *Chaenotheca phaeocephala* are mainly found on old oaks (Ranius et al. 2008). This species occurs also on old deciduous trees of other species. All species except one are red-listed (Gärdenfors 2010).

Within an area of 2.1 km², all potentially suitable oaks were mapped using GPS (Appendix A: Fig. A2). For each tree (in total 2083), we also measured tree and environmental variables that were hypothesized to affect lichen metapopulation dynamics or tree age (Appendix A: Table A2). On all trees within the area and within a buffer zone around the area (Appendix A: Fig. A2) we recorded the occurrence of each study species. The ages of all trees were either measured using increment cores or estimated based on tree and environmental characteristics (Appendix A).

The metapopulation model

We applied the IFM that has been extended to be applicable on dynamic landscapes (Verheyen et al. 2004). To incorporate patch dynamics, Verheyen et al. (2004) added a temporal dimension to the IFM (Hanski

TABLE 1. Deviance information criterion (DIC) values for metapopulation models for five epiphytic lichen species, with the final model in boldface type.

Model	*Chaenotheca phaeocephala* ($N = 994$)	*Cliostomum corrugatum* ($N = 196$)	*Lecanographa amylacea* ($N = 25$)	*Buellia violaceofusca* ($N = 95$)	*Schismatomma decolorans* ($N = 18$)
Null model, background deposition (Ξ), $\Psi = 0$	1927	1062	217.4	677.2	172.7
Age threshold, Ψ	1619	892.9	174.2	609.3	**139.8**
Kernel, $E = 0$	1296	866.7		596.3	
Kernel $+ \Xi$, $E = 0$	1371	**851.8**	**144.3**	**577.0**	
Kernel, $E > 0$	**1233**	865.4		596.3	
Kernel $+ \Xi$, $E > 0$	1317	852.9		577.5	

Notes: From top to bottom, parameters are successively included, starting with the null model, which only includes a background deposition of dispersal propagules (Ξ), and assumes that trees are suitable from age = 0. The model with the age threshold estimates the age at which the trees become suitable (Ψ). The remaining models include a dispersal kernel, a background deposition of dispersal propagules (Ξ), or an extinction rate (E) larger than 0. For *L. amylacea* and *S. decolorans*, an empty cell means that the model could not be fitted. N is the number of occupied trees.

1994) by using an equation from Feller (1967) to solve for the conditional probability that a patch is occupied at an arbitrary age:

$$J_i(\text{age}) = \frac{C_i - C_i(1 - C_i - E_i)^{\text{age}-\psi}}{C_i + E_i}. \qquad (1)$$

This extension also facilitates the solving for colonization (C_i) and extinction (E_i) rates, which may otherwise be difficult as very different rates can lead to similar patterns of species occupancy. We further extended the model by adding the parameter Ψ, which defines the age at which a patch (here, a tree) becomes suitable for colonization. This parameter estimates the breadth of the niche: a species colonizing young trees also (i.e., a generalist) has a wider niche than a species colonizing only old trees (i.e., a specialist). In the code for fitting the model, age-Ψ was set to 0 if age $< \Psi$. Thus, $J_i(\text{age}) = 0$ if age $< \Psi$.

We modeled the colonization probability (C_i) as a function of connectivity (S_i) as

$$C_i = 1 - \exp\left(\frac{-\left(\Xi + \Phi \sum_{j \neq i} p_j \left(\frac{\alpha^2}{2\pi} \exp(-\alpha \times r_{ij})\right)\right)}{S_i}\right). \qquad (2)$$

This relationship assumes independent colonization success among propagules, which is biologically reasonable for our study species. The original IFM used a sigmoid relationship, which is a way to model Allee effects (Hanski 1994). Our connectivity measure (S_i) assumes that propagules are dispersed from unknown background sources at long distance with the rate Ξ, or from local (within the area) occupied patches according to a dispersal kernel, where α regulates the dispersal range and r_{ij} is the distance in meters between tree i and j (see Appendix B). The variable $p_j = 1$ if tree j is occupied by the species; otherwise $p_j = 0$. The colonization parameter Φ includes the rate of emigration of dispersal propagules from occupied patches, and the propagule

establishment ability ("the force of infection" using epidemiological terminology). We calculated the relative contribution of the background deposition (Ξ) in the connectivity measure as $\Xi/\bar{S}$, where $\bar{S}$ is the mean of the connectivity for all patches. For testing the relative importance of local stochastic extinctions on metapopulation dynamics, we compared metapopulation models where we estimated the extinction rate, E, with models where the extinction rate was fixed at 0.

We built the Bayesian models based on the deviance information criterion (DIC; Appendix C; Spiegelhalter et al. 2002), which is an information-theoretic approach with properties similar to Akaike's information criterion (Burnham and Anderson 2002). For model code, also including a sub-model for patch occurrence, see the Supplement.

RESULTS

For all species, the model was improved by including the age at which a tree becomes suitable for lichen colonization, i.e., the parameter Ψ (Table 1), which defines niche breadth. This threshold differed among species (Fig. 2a), and agreed with our hypothesis (Fig. 1), giving species-specific niche breadths and number of suitable trees in the study area (Fig. 2b).

The mean colonization rate of suitable trees differed among species (Fig. 2c). Generalists (having wide niches) with small dispersal propagules (Appendix A: Table A1), *Chaenotheca phaeocephala* and *Cliostomum corrugatum*, had the highest rates (Figs. 1 and 2c). The two specialists (with narrow niches), *Lecanographa amylacea* and *Schismatomma decolorans* (Appendix A: Table A1), had the lowest mean colonization rates (Figs. 1 and 2c). A similarly low colonization rate was found for *Buellia violaceofusca*, which has a wider niche but is dispersed by large propagules.

For four species (all except the one with the fewest occurrences), the models were substantially improved by including spatially explicit connectivity to occupied patches (Table 1). Adding the background deposition parameter (Ξ), which essentially models long-distance
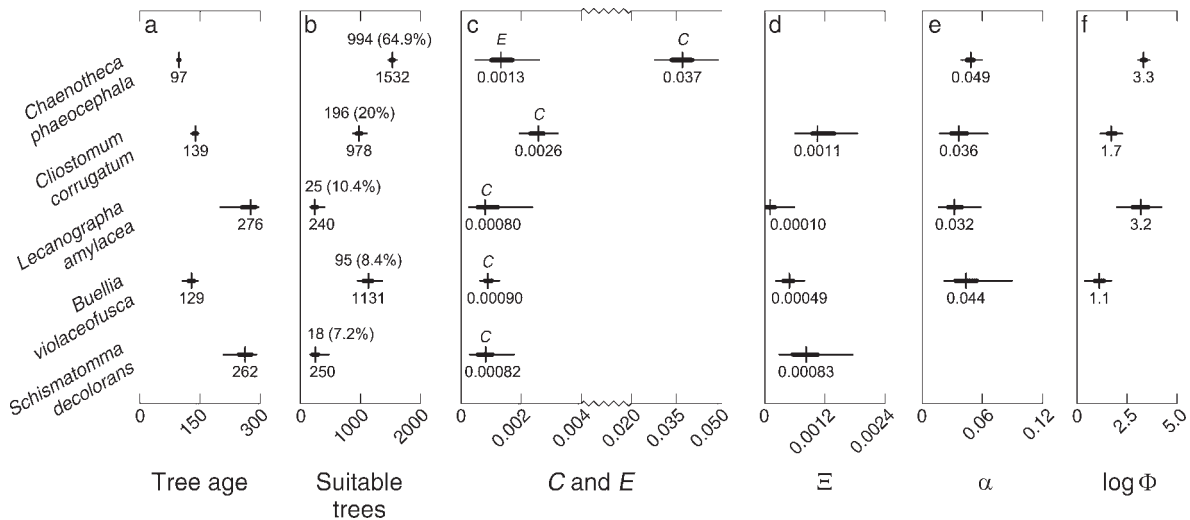
FIG. 2. (a) The age at which the trees become suitable for lichen colonization, (b) the number of suitable trees (niche breadth) for each lichen species, (c) the mean lichen colonization (C) and extinction rate (E) per year among suitable trees, (d) the background deposition of lichen dispersal propagules from unknown sources Ξ, (e) the dispersal range parameter α, and (f) the colonization parameter Φ. Modes (short vertical lines) and 50% (thick horizontal lines) and 95% (thin horizontal lines) highest posterior density intervals (Bayesian confidence intervals) of the parameters in the best model for each species are shown. Numbers underneath are the modes. In panel (b), the number of the occupied trees and occupancy (in parenthesis) are shown for each lichen species.

dispersal, improved model fit for all species but *Chaenotheca phaeocephala*. Among species with the background deposition parameter in the best model (Fig. 2d), it constituted 46% of the connectivity term for *B. violaceofusca*, and 52% and 10% for *Cliostomum corrugatum* and *L. amylacea*, respectively. *B. violaceofusca* is dispersed by large propagules and the others are dispersed by small ones. The estimate of the dispersal range parameter (α) was relatively similar among species (Fig. 2e). However, the colonization probability on different distances from a source tree, which depends on the combination of α, Φ, and Ξ (Eq. 2), varied considerably between species (Fig. 3). The colonization parameter (Φ) was highest for *Chaenotheca phaeocephala* and *L. amylacea* (Fig. 2f), both dispersed by small propagules.

Stochastic extinctions from suitable trees were rare; the models were generally not improved by estimating a stochastic extinction rate (E) compared to fixing $E = 0$ (Table 1). When estimating E for these species, the posterior distribution was close to 0. Using the mode of this posterior distribution as a fixed value also resulted in worse models. Only for *Chaenotheca phaeocephala*, the model was improved by estimating E, suggesting that stochastic extinctions may occur from standing trees. However, its extinction rate was also close to zero (Fig. 2c).

DISCUSSION

Using data from only a single snapshot of sessile species confined to dynamic habitat patches, we have shown (1) that colonization rates in epiphytes are

strongly affected by connectivity to occupied patches, (2) that colonization rates are related to niche breadth and propagule size, (3) that local extinctions may be negligible in epiphytic lichens, and (4) that the age at which patches become suitable for colonization can be estimated based on snapshot data. Moreover, the Bayesian modeling approach applied allowed us to (5) investigate the relative importance of local and long-distance dispersal, (6) to provide credible intervals for all model parameters, reflecting natural variability and uncertainty, and (7) to make full use of the dataset on species occupancy although age had not been measured for all trees.

Our study shows a clear effect of connectivity on the colonization rate of all species except the one with fewest occurrences. This agrees with metapopulation theory (e.g., Hanski 1999) and earlier findings for many sessile species (Verheyen et al. 2004, Snäll et al. 2005, Jönsson et al. 2008). Moreover, we present what is to our knowledge the first study of epiphyte colonization rates in relation to species traits.

We found the highest mean colonization rates and occupancy for the two generalists with small dispersal propagules, *Chaenotheca phaeocephala* and *Cliostomum corrugatum*, in accordance with our hypothesis (Fig. 1). This implies that generalists occur more frequently than specialists (Brown 1984), which result in higher connectivities and, thus, higher colonization rates, in accordance with theory (Hanski 1999). Moreover, the colonization rate is determined by propagule size, and is higher for species with small propagules, which agrees with results from forest plant metapopulations (Verhey-

en et al. 2004). Our models suggest that species with a high colonization rate have a long dispersal range, high propagule production, or high establishment capacity. For *Cliostomum corrugatum*, the dispersal range parameter (α) suggested rather short local dispersal, but the best model also included the parameter for background deposition constituting half of the connectivity term, and this results in a relatively high colonization rate over long distances (Fig. 3). This suggests frequent long-distance dispersal, as expected for species dispersed by small propagules (Okubo and Levin 1989, Kimmerer 1991, Löbel et al. 2009). The finding also agrees with its random spatial genetic structuring among areas in the region (Lättman et al. 2009). *Chaenotheca phaeocephala* had the highest mean colonization rate, probably resulting from its wide niche (the widest) and small propagules. The high colonization parameter value (Φ) suggests that this species has large spore production or high establishment capacity, rather than long dispersal range (Fig. 3). The most likely explanation is high spore production, as the species forms numerous apothecia (V. Johansson, *personal observation*), and as the establishment capacity of small propagules is low (Löbel and Rydin 2010). Its high occupancy leads to high spore production within the study area, and it may mask the background deposition, which may be extensive.

We found the lowest mean colonization rates and occupancies for specialists or species with large propagules, i.e., for *L. amylacea*, *S. decolorans*, and *B. violaceofusca* in accordance with our hypothesis (Fig. 1). *Lecanographa amylacea* has a narrow niche, and thereby low occupancy and colonization rate, in spite of its small propagules and background deposition, suggesting a long dispersal range. The low colonization rate of *S. decolorans* can be a result of both the narrow niche and the large propagules. We could not fit the full spatial model, but its clumped occurrence pattern suggests a restricted dispersal range, as expected for a species dispersed by large propagules (Okubo and Levin 1989, Kimmerer 1991, Löbel et al. 2009). *Buellia violaceofusca* had a wide niche, and the low mean colonization rate is thereby probably a result of the large propagules. However, it surprisingly seems to disperse over long distances as the background deposition constituted half of the connectivity term. This suggests that a vector other than wind transports its propagules (Will and Tackenberg 2008). The low colonization parameter (Φ) value is most likely a result of low propagule production in accordance with Jakobsson and Eriksson (2000), which means few potential dispersers and colonization events. This explanation is also supported by the finding that species with large asexually produced propagules, such as this, should have a high establishment capacity once they arrive at a patch, because large asexual propagules are less sensitive to variation in pH or drought (Löbel and Rydin 2010).

Our results suggest that when an epiphyte has established on a tree it is unlikely to go extinct until
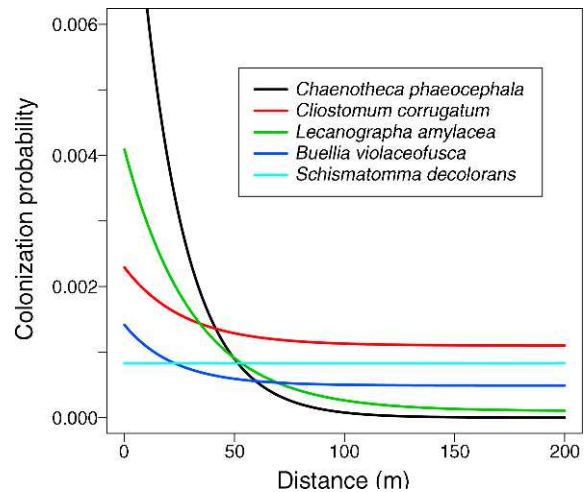

FIG. 3. The yearly colonization probability of a tree for five lichen species as a function of the distance to one single occupied tree and species-specific estimates of the parameters Φ, Ξ, and α (Eq. 2).

the tree dies; extinctions are deterministic, caused by tree fall (Snäll et al. 2003). In four out of five species, the model was not improved by including stochastic extinctions (E). The same was found in an epiphytic moss (Snäll et al. 2005) and in wood-decaying fungi (Jönsson et al. 2008). In contrast, significant stochastic extinction rates have been reported for other sessile species confined to dynamic patches. We believe that one explanation can be the stability of the patches or the species' life form. In systems where the substrate is stable and when the species grows closely attached or even inside the substrate (the current study, Snäll et al. 2005, Jönsson et al. 2008), the local extinction risk can be assumed to be low. In contrast, when the species grows on the surface of a substrate that is unstable, for example growing, decomposing, or even moving, the local stochastic extinction risk can be assumed to be higher. Examples are leaves (Zartman and Shaw 2006), branches (Laube and Zotz 2007), and decomposing stumps (Caruso et al. 2010). One exception is Öckinger and Nilsson (2010) who reported significant stochastic extinctions in the epiphytic lichen *Lobaria pulmonaria* growing on the bark of old trees. Its extinction rate increased with increasing tree size, and the mechanism behind this finding is difficult to explain. We too found support for a non-zero extinction rate for *C. phaeocephala*, suggesting that stochastic extinctions from viable trees indeed occur. However, the low extinction rate, 0.0013, gives a mean local population lifespan of 770 years. As the oaks in the study region rarely become older than 500 years (Ranius et al. 2009), they are available as habitat for this species for roughly 400 years (500 minus 100). This means that tree fall is the main cause of local (deterministic) population extinctions also in this species. It should be noted, though, that local

PLATE 1. A group of old oaks in the study area in southeastern Sweden. Photo credit: V. Johansson.

extinctions may increase if the management of these wooded pastures is abandoned (Paltto et al. 2011).

The modeling approach applied in this study is applicable on also other organisms with equilibrium metapopulation dynamics that are much affected by the dynamics of their patches. However, if the focal species influences the dynamics of the patches, such as in host–parasite systems, the model needs further extension. Fitted models for joint metapopulation and patch dynamics can be used to project the dynamics into the future, and are useful tools in metapopulation viability analysis for comparing species persistence in scenarios of land use or climate change (e.g., Snäll et al. 2009, Roberge et al. 2011).

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SUPPLEMENTAL MATERIAL

Appendix A

Patch characteristics, tree age model, and the lichen survey (*Ecological Archives* E093-022-A1).

Appendix B

Modeling colonization probability and connectivity (*Ecological Archives* E093-022-A2).

Appendix C

Model building and prior and posterior distributions of model parameters (*Ecological Archives* E093-022-A3).

Supplement

Model code and data structure for fitting the general model using OpenBUGS (*Ecological Archives* E093-022-S1).

Reports