The University of Chicago

Metapopulation Dynamics of Species with Cryptic Life Stages

Thomas Lamy,[1],* Olivier Gimenez,[1] Jean-Pierre Pointier,[2] Philippe Jarne,[1] and Patrice David[1]

1. Unité Mixte de Recherche 5175–Centre d'Ecologie Fonctionnelle et Evolutive, campus Centre National de la Recherche Scientifique (CNRS), 1919 route de Mende, 34293 Montpellier cedex 5, France;   2. Unité de Service et de Recherche 3278 CNRS–Ecole Pratique des Hautes Etudes, 52 avenue Paul Alduy, 66860 Perpignan cedex, France

ABSTRACT: Quantifying metapopulation dynamics is a challenging task. Difficulties particularly arise in species that possess unobservable resistance forms that bias the estimation of colonization and persistence rates. Here, we develop a general multistate occupancy model that allows estimation of species persistence for both normal and resistant forms, even when the latter are not detectable. We apply this model to an 11-year data set on the tropical freshwater snail *Drepanotrema depressissimum* in a network of 229 ponds. These ponds frequently dry out, and the snails can persist by aestivating in the ground, where they are not detected. Our model adequately captures this feature because it infers a high persistence rate for the resistant form, while models ignoring aestivation tend to overestimate extinction and colonization. In addition, we find that, surprisingly, colonization and persistence are even higher in sites prone to desiccation and during years with low rainfall than in more humid sites and years, suggesting that *D. depressissimum* favors unstable sites where competitors are rare and where it can rely on aestivation to persist. Our model has the potential to provide valuable insights into the metapopulation dynamics of many species that otherwise could hardly be studied because of the existence of undetectable life forms.

Keywords: detection, extinction-colonization, metapopulation, multistate occupancy model, resting form, seed bank.

Introduction

Many species live in highly fragmented landscapes composed of discrete habitat patches. For such species, a large body of theoretical work has been dedicated to metapopulation dynamics, with a special emphasis on the estimation of extinction and colonization rates (Hanski 1999; MacKenzie et al. 2003). Extinction and colonization can affect several important processes, such as trait evolution, species coexistence, and persistence (Harrison and Hastings 1996; Leibold et al. 2004). Moreover, extinction and colonization rates have become critical parameters informing management and conservation decisions in a con-

text of increasing habitat fragmentation (Fahrig 2002). Empirical estimates of these rates generally rely on time series of presence/absence data in sets of sites. Extinction and colonization rates are viewed as transition probabilities between two states (site occupied or not) of a Markov process (i.e., independent of the past history of occupancy; Hanski and Ovaskainen 2003).

However, reliably inferring colonization and extinction rates from field data is difficult, and empirical estimates remain scarce. The main issue is that species are not always detected when present in a patch, which can bias the estimation of parameters of interest, such as occupancy, colonization, and extinction rates (MacKenzie et al. 2003; Wintle et al. 2005; Mazerolle et al. 2007). This issue of imperfect detectability can be addressed by resorting to spatial replication of visits within a season to estimate detectability and its potential dependence on covariates such as geographic location or environmental variables (MacKenzie et al. 2003; Royle 2006). When sites are visited over multiple seasons, these models can be extended to explicitly take into consideration patch dynamics in terms of extinction and colonization probabilities (MacKenzie et al. 2003).

Besides the issue of imperfect detection, specificities of the species biology might hamper the investigation of metapopulation dynamics. Of particular importance, many species display different forms throughout their life cycle, some of which are not amenable to observation. These cryptic life stages may persist locally while the main life stage has disappeared, hence mimicking extinction. For example, annual plants can disappear from a habitat patch, leaving only a seed bank in the soil. In this situation, extinction does not occur, but standard patch occupancy models will suggest extinction with high certainty because the presence/absence record of the conspicuous form (i.e., the plant) is highly repeatable. In the same vein, insect species may persist as larvae or resistant eggs in the soil, and aquatic crustaceans (*Artemia*, *Daphnia*) produce long-lived cysts or ephippia that persist in the sediment when swimming adults disappear. These situations are encoun-

* Corresponding author; e-mail: thomas.lamy27@gmail.com.

tered often, because cryptic forms occur in several major taxonomic groups (Brendonck and De Meester 2003; Brönmark and Hansson 2005; Fenner and Thompson 2005). Whenever the presence of cryptic forms is suspected, one could simply discard the observation and record a "missing observation." However, using patch occupancy in that context requires making the strong assumption that transition rates are similar for all life stages, which is highly unlikely to be true.

Recently, patch occupancy models have been extended to deal with more than the two usual states (occupied, not occupied). So-called multistate occupancy models (MacKenzie et al. 2009) allow the estimation of transition probabilities between occupancy states, such as reproductive states (site not occupied, occupied with successful reproduction, and occupied with unsuccessful reproduction; e.g., Martin et al. 2009; Green et al. 2011) or relative abundance states (site not occupied, occupied with low abundance, and occupied with high abundance; e.g., Martin et al. 2010). To our knowledge, multistate occupancy models have never been used to model cryptic stages. However, as cryptic life stages are by definition unobservable, transition probabilities cannot be obtained between the cryptic life stage and other states. In this context, additional information is needed to parameterize multistate occupancy models. Cryptic life stages are frequently associated with a particular status of the habitat (e.g., dry sites for resistant eggs or cysts), and this environmental feature can be easily recorded in the field. Here, we propose to estimate colonization and extinction rates while conditioning on this information. By doing so, we highlight how multistate occupancy models can be extended to address the long-standing problem of cryptic life stages that has hindered the analysis of metapopulation dynamics from field surveys. To illustrate our approach, we consider the metapopulation of a tropical freshwater snail, *Drepanotrema depressissimum*, that inhabits a network of highly unstable and temporary ponds. These habitats often dry out completely during the dry season, and the snails can then persist as a resting stage in the ground (aestivation), as attested by both direct observation (Pointier and Combes 1976) and indirect genetic evidence (Lamy et al. 2012). This state cannot be detected in large-scale surveys unless huge amounts of time are spent digging and sieving. However, information as to whether a site is completely dry can easily be recorded during a survey. In this study, we compare results obtained from an analysis explicitly incorporating cryptic stages to those obtained from models that treat dry sites either as wet sites where the species is never detected or as sites where the species cannot persist. This allows us to draw novel and insightful conclusions about the population dynamics of the species under investigation. Cryptic stages are often life forms that allow a species to persist locally in spite of a perturbation (such as pond desiccation in our system). Along with the ability to colonize and persist in stable sites, the ability to resist perturbation is a key component of species regional persistence as well as of its coexistence with other species (storage effect; Chesson 1994) Consequently, we think that our approach, which allows for more realistic predictions, has the potential to unravel important new features of population dynamics of species with cryptic life stages.

Material and Methods

Multistate Occupancy Model

We introduce our model in general terms, referring to the snail case study to fix ideas. The approach remains generic and applicable to other systems, pending adjustments. We describe our model by using a state-space modeling approach in which a distinction is made between two processes: a state process capturing the transitions between states (occupied/not occupied) and an observation process linking the data (detection/nondetection) to the underlying states, hence allowing the accommodation of imperfect species detection (e.g., Royle and Kéry 2007).

We consider occupancy data from M sites over T occasions (e.g., yearly surveys). On each occasion, a subsample of sites is surveyed twice (or more). The observation status of site i for survey j at occasion t is denoted $y_j(i, t)$ and takes the value 1 if the species is detected and 0 otherwise. The true occupancy status of site i at occasion t is denoted $x(i, t)$ and takes the value 1 if the site is occupied and 0 if it is not occupied. To model occupancy dynamics, we used a two-step cycle between two surveys, with extinction occurring before colonization. This assumption is likely to be valid in the snail case study because sampling occurred at the beginning of the dry season. The extinction risk is higher during this season, because water availability decreases and, consequently, both competition and abiotic stress (e.g., pH, temperature) increase. Ponds may dry out completely during this season. On the other hand, colonization is more likely to occur during the rainy season, when water level is high, environmental conditions improve, and overflows often allow water connections between neighboring sites. The order of colonization and extinction can be reversed to accommodate the specificities of other biological systems. Note that by assuming that colonization follows extinction, our model automatically incorporates rescue effects (i.e., when extinction is immediately followed by recolonization within a seasonal cycle; Hanski 1994).

Multiseason patch occupancy models (MacKenzie et al. 2003; Royle and Kéry 2007) consider two occupancy states (occupied/not occupied) in which dynamics is driven by

two parameters: persistence Φ—or its complement local extinction $(1 - \Phi)$—and colonization γ. Here we assume that the species exhibits two different life forms: a resistance form with null detectability and a normal form with nonnull detectability. We assume that these forms are associated with different habitat states, referred to as D (for dry) and W (for wet). When a site is in state D, only the resistance form can be present, while in state W, the species, if present, produces the normal life form. The colonization and extinction rates therefore vary between D and W sites as they harbor different life forms. In the snail case study, the resistance form consists of snails aestivating in the dry ground, while the normal form is the active aquatic form. At the beginning of the dry season, each site can be characterized as either dry (D) or wet (W). In *D* sites, snails can only aestivate and must usually remain in this form for a long time, until the next rainy season. In W sites, there will be no, or a shorter, desiccation period during the dry season, so snail populations will spend the dry season mostly in the active form (fig. 1). The persistence probability between t and $t + 1$ in a site observed to be in state D (W) at time t is denoted Φ_{D} (Φ_{W}) and corresponds to the aestivating (active) form. We can similarly define colonization rates between t and $t + 1$ conditional on whether the site is W or D at time t. However, we believe that conditioning on site status at $t + 1$, rather than t, is a better option, given the biology of our system. In our case, colonization cannot occur through the resistance form (buried in the ground), and the opportunities for colonization mostly arise during the rainy season. Long and intense rainy seasons are assumed to offer more opportunities for colonization. The intensity of the rainy season is better described by the state of the site at $t + 1$ than by its state at time t. Indeed, sites found to be dry at $t + 1$ have, on average, been in water for a shorter time during the preceding rainy season. Thus, we defined γ_{D}, the colonization rate between t and $t + 1$, as conditional on the site being in state D at $t + 1$, and likewise for γ_{W} and state W.

The dynamics described above can be represented by transition probability matrices (TPMs) that give the probabilities of occurrence of the species at time $t + 1$ as a function of its occurrence at t (MacKenzie et al. 2009), conditional on sites' features. In our case, we consider four matrices (for DD sites, i.e., found dry at both times t and $t + 1$, as well as for DW, WD, and WW sites). The four matrices $\mathbf{P}_{\mathrm{DD}}$, $\mathbf{P}_{\mathrm{DW}}$, $\mathbf{P}_{\mathrm{WD}}$, and $\mathbf{P}_{\mathrm{WW}}$ can be combined into a single TPM (see fig. 1):

$$\mathbf{P} = q_{i,t}q_{i,t+1}\mathbf{P}_{\mathrm{DD}} + q_{i,t}(1 - q_{i,t+1})\mathbf{P}_{\mathrm{DW}} \qquad (1)$$
$$+ (1 - q_{i,t})q_{i,t+1}\mathbf{P}_{\mathrm{WD}} + (1 - q_{i,t})(1 - q_{i,t+1})\mathbf{P}_{\mathrm{WW}},$$

where $q_{i,t}$ is a binary indicator of the status of site i at time t, taking the value 1 if dry and 0 otherwise.

Our approach can be seen as an extension of MacKenzie et al.'s (2003, 2009) in the following sense: we are interested in three states (not occupied, occupied wet sites, and occupied dry sites), but because the latter state is not accessible to observation, we compute the TPM on the basis of only two states (occupied/not occupied), conditional on the sites' characteristics. Note that in a different system, in which the state of the site at $t + 1$ would not matter, equation (1) would have only two terms (one for D and one for W sites).

Effect of Covariates on Extinction and Colonization Rates. Depending on the system under investigation, one would like to test the effect of a set of covariates on extinction and colonization rates. These covariates usually are environmental variables specific to site, year, or both and are suspected of having an effect on extinction and colonization rates on the basis of knowledge of the system and the species under investigation. In this case, transition probabilities (TPs; $\Phi_{\mathrm{W}_{i,t}}$, $\Phi_{\mathrm{D}_{i,t}}$, $\gamma_{\mathrm{W}_{i,t}}$ or $\gamma_{\mathrm{D}_{i,t}}$) can be modeled as linear-logistic functions of the environmental variables of interest,

$$\mathrm{logit}(\mathrm{TP}) = \mu + \sum \beta_p X_p, \qquad (2)$$

where μ is the intercept, βs are regression coefficients to be estimated, and X_p represents the pth covariate.

Observation Model. Because in every system detection of the species is imperfect, observations may not always reflect the true state of a site. The observation model allows the taking of this ambiguity into account by connecting the true states to observations. One of our model specificities is that the detectability of the cryptic form (in D sites), p_{D}, is 0, because we assume that it would require too much effort to investigate for cryptic individuals in D sites. The matrix $\mathbf{p}_{\mathrm{O}}$ of state-dependent detection probabilities is therefore

$$\mathbf{p}_{\mathrm{O}} = q_{i,t}\mathbf{P}_{\mathrm{OD}} + (1 - q_{i,t})\mathbf{P}_{\mathrm{OW}}, \qquad (3)$$
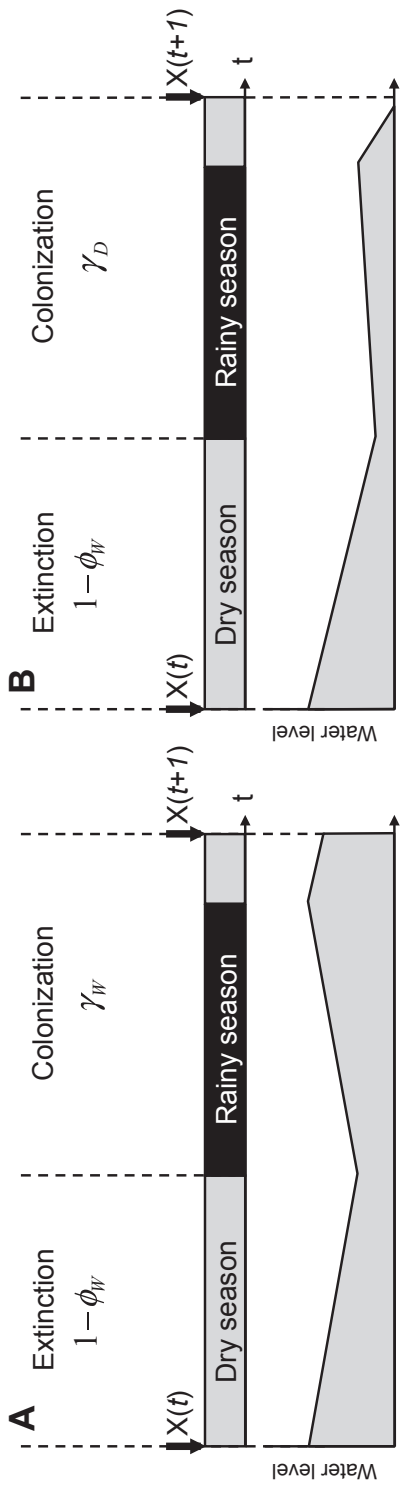
where

$$\mathbf{P}_{\mathrm{OD}} = \begin{bmatrix} 0 & 1 \\ 0 & 1 \end{bmatrix}$$

is the detection matrix in D sites and

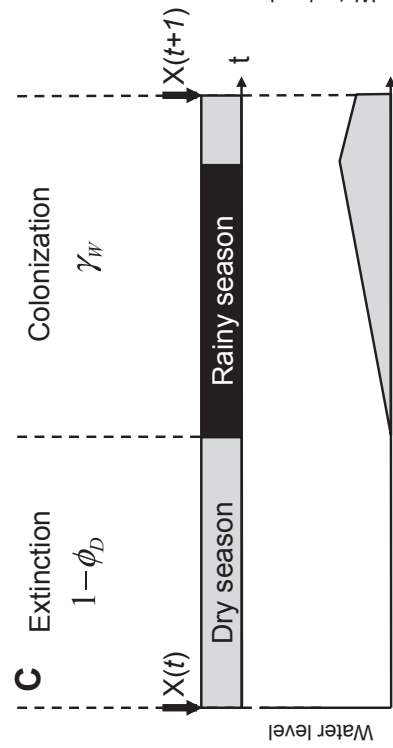$$\mathbf{P}_{\mathrm{OW}} = \begin{bmatrix} p_{\mathrm{W}} & 1 - p_{\mathrm{W}} \\ 0 & 1 \end{bmatrix}$$

is the detection matrix in W sites (p_{W} being the detectability of the species in W sites). In these matrices, rows
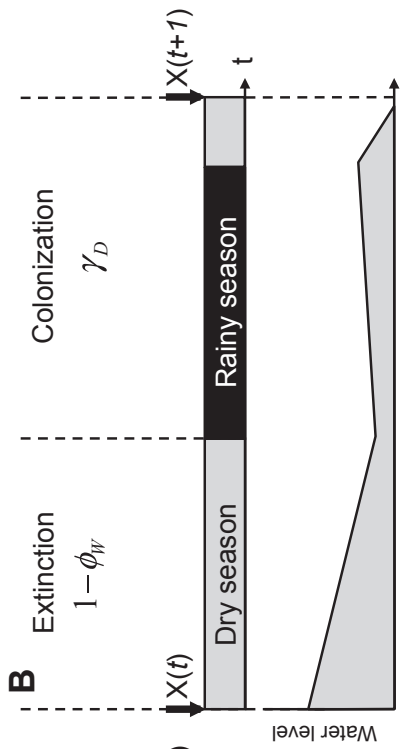
A

Extinction
$1 - \phi_W$

Colonization
γ_W

Water level

X(t)　　　Dry season　Rainy season　　X(t+1)　t

$$P_{WW} = \begin{array}{c} 0 \\ 1 \end{array} \begin{bmatrix} 0 & 1 \\ (1-\Phi_W)*(1-\gamma_W) & \Phi_W + (1-\Phi_W)*\gamma_W \\ 1-\gamma_W & \gamma_W \end{bmatrix}$$

B

Extinction
$1 - \phi_W$

Colonization
γ_D

Water level

X(t)　　　Dry season　Rainy season　　X(t+1)　t

$$P_{WD} = \begin{array}{c} 0 \\ 1 \end{array} \begin{bmatrix} 0 & 1 \\ (1-\Phi_W)*(1-\gamma_D) & \Phi_W + (1-\Phi_W)*\gamma_D \\ 1-\gamma_D & \gamma_D \end{bmatrix}$$

C

Extinction
$1 - \phi_D$

Colonization
γ_W

Water level

X(t)　　　Dry season　Rainy season　　X(t+1)　t

$$P_{DW} = \begin{array}{c} 0 \\ 1 \end{array} \begin{bmatrix} 0 & 1 \\ (1-\Phi_D)*(1-\gamma_W) & \Phi_D + (1-\Phi_D)*\gamma_W \\ 1-\gamma_W & \gamma_W \end{bmatrix}$$

D

Extinction
$1 - \phi_D$

Colonization
γ_D

Water level

X(t)　　　Dry season　Rainy season　　X(t+1)　t
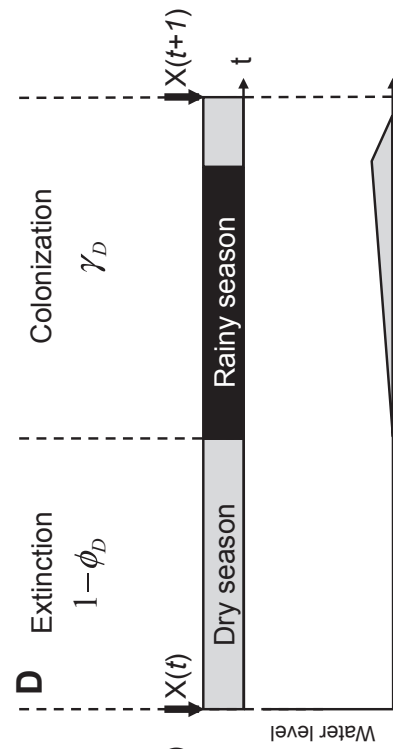
$$P_{DD} = \begin{array}{c} 0 \\ 1 \end{array} \begin{bmatrix} 0 & 1 \\ (1-\Phi_D)*(1-\gamma_D) & \Phi_D + (1-\Phi_D)*\gamma_D \\ 1-\gamma_D & \gamma_D \end{bmatrix}$$

correspond to true states (occupied and not occupied) and columns to observations (species observed or not observed).

Model Implementation in a Bayesian Framework. In line with recent work (e.g., Royle and Kéry 2007), this model was fitted to data in a Bayesian framework with Markov chain Monte Carlo (MCMC). The Bayesian framework has the advantage of being very flexible. The analyses were performed with WinBUGS 1.4.3 (Lunn et al. 2000) called by the R package R2WinBUGS (Sturtz et al. 2005).

Application

Species and Study System. Our study was carried out in Grande-Terre (Guadeloupe), a 570-km^2 island in the Lesser Antilles. This island harbors several types of freshwater habitats, including many ponds (∼2,000), a few small rivers, and swamp grasslands connected to mangroves. Some sites are permanent, but many ponds dry out completely either yearly or more irregularly during the dry season (December to March). Sites can be dry for up to several months, especially in the driest parts of Grande-Terre (the north and east). These sites may then refill either during the so-called little rainy season (from March to May) or during the rainy season (July to January). Freshwater snails make up the major part of the invertebrate communities in these environments (Pointier and David 2004; Pointier 2008). We focus on *Drepanotrema depressissimum* (Gastropoda: Basommatophora: Planorbidae), one of the most common species in the freshwater snail community. It is found in predominantly stagnant water bodies with abundant aquatic vegetation. Previous studies indicated that it is able to aestivate under rocks or vegetation in dry sites (Pointier and Combes 1976). At the metapopulation level, the persistence of *D. depressissimum* thus depends on two processes: recolonization of truly extinct sites and avoidance of extinction through aestivation. Genetic data (Lamy et al. 2012) suggest that snails reappearing after long droughts are more often related to the local gene pool than from external gene pools, suggesting that aestivation is more important than recolonization for persistence in temporary habitats.

We use data on the occupancy of *D. depressissimum* collected in 229 sites in Guadeloupe that were surveyed annually from 2001 to 2011 (see the appendix, available online). Surveys were conducted at the beginning of the dry season, when the density of mollusk populations was the highest and water levels started to decrease. Each site was explored by at least three persons for 10–15 min. We searched for *D. depressissimum* in wet sites but not in dry sites, as it would have required too much time to dig into the ground to look for aestivating snails. Snails were caught with a scoop (0.5 m) that allowed foraging in both the sediment and plant strata. We also visually surveyed rock surfaces or floating debris when present. Each year, we selected a random subset of these sites (∼30), for which surveys were repeated within a few days. This "robust design" protocol (Pollock 1982; Kendall et al. 1995) is a conventional way to obtain presence/absence data and estimate detectability (MacKenzie and Royle 2005).

A set of environmental variables was also characterized for each site, including size (pond diameter or river width) and vegetation cover (in percent). Sites were also classified with respect to two permanent characteristics: overall hydrological regime (five levels, from fully permanent to frequently dry during the dry season) and water connectivity to neighboring freshwater habitats (four levels, from always completely isolated to always connected). Connectivity characterizes the overall probability that the focal population will be connected to surrounding freshwater habitats during the rainy season when flood occurs. These were estimated on the basis of field experience, the visual aspect of water margins, and topographical considerations (outlets, slopes, etc.).

Effect of Covariates on Extinction and Colonization Rates. We incorporated information on factors that may affect transition parameters (table 1). We considered four site-specific environmental variables, namely, site size (S_i), vegetation cover (V_i), water connectivity (C_i), and site stability (Stab$_i$). The first three variables were averaged over the 11 survey years, and S_i and V_i were log transformed to approximate a normal distribution. The fourth, Stab$_i$, was computed as the first axis (56% of total variance) of a principal component analysis including average hydrological regime, the proportion of visits during which the site was dry over the 2001–2011 period, the temporal variances

Figure 1: Schematic representation of the model. Each diagram represents one of the four possible transitions between years t and $t + 1$ according to the dry or wet status of the site (*A*, wet at t and $t + 1$; *B*, wet at t and dry at $t + 1$; *C*, dry at t and wet at $t + 1$; *D*, dry at t and $t + 1$). The representative dynamics of water levels is pictured for each situation. The four corresponding transition probability matrices ($\mathbf{P}_{WW}$, $\mathbf{P}_{WD}$, $\mathbf{P}_{DW}$, and $\mathbf{P}_{DD}$) are given below each diagram, where the rows and columns represent states (nonoccupied and occupied, in that order) at years t and $t + 1$, respectively. For example, in a WW site, the probability that an empty site will remain empty (0–0) is ($1 - \gamma_W$) because colonization must not have taken place; the probability that an occupied site will remain occupied (1–1) is $\Phi_W + (1 - \Phi_W) \times \gamma_W$ because the population either has persisted (Φ_W) or has become extinct and later been recolonized (($1 - \Phi_W) \times \gamma_W$). All other elements of the four matrices can be deduced from similar reasoning.

Table 1: Description of the seven environmental variables used in this study and their putative influence on transition parameters

Variable	Description	Persis-tence rate		Coloniza-tion rate	
		Φ_W	Φ_D	γ_W	γ_D
Site specific:					
S_i	Site size	+	+	+	+
V_i	Fraction of site covered by aquatic vegetation	+	+	+	+
C_i	Water connectivity to surrounding freshwater habitats during the rainy season	NA	NA	+	+
$Stab_i$	Temporal water stability	+	+	+	+
Year specific:					
LRS_t	Cumulated rainfall during the little rainy season (March–May)	+	+	NA	NA
RS_t	Cumulated rainfall during the rainy season (July to the survey date)	NA	NA	+	+
Site and year specific:					
$D_{i,t}$	Propagule pressure	NA	NA	+	+

Note: See text for more details. A plus sign indicates that the variable is expected to have a positive effect on the transition parameter; NA indicates that no effect is expected.

in size of the water body and in vegetation cover during the same period. We also considered two year-specific (i.e., identical for all sites within a year) environmental variables, LRS_t and RS_t, representing the cumulated rainfall during, respectively, the little rainy season (March–May, a short episode that is on average slightly more humid than the rest of the dry season but irregular over years) and the rainy season (from July to the survey date), before each survey. We also constructed an index of potential propagule pressure per site i and year t, by estimating the number of *D. depressissimum* populations in the vicinity of site i as $D_{i,t} = N_i P_{i,t}$, where N_i is the number of freshwater habitats occurring within a 4-km-radius circle around site i on the basis of detailed maps of freshwater ponds in Grande-Terre (including surveyed and nonsurveyed sites; Bruyère and Questel 2001) and $P_{i,t}$ is the proportion of occupied sites at time t among the surveyed sites within that circle. We assumed that the proportion of occupied sites in a circle was the same for surveyed and nonsurveyed sites. Consequently, $P_{i,t}$ is the mean probability of occupancy of all sites, surveyed and nonsurveyed, within the 4-km-radius circle around site i during visit t. Note that the results were unchanged when we used different radial distances instead of 4 km (i.e., 8, 12, or 16 km).

Size, vegetation cover, stability, and the little rainy season are suspected to increase both persistence and colonization rates (table 1) because they tend to increase the duration of favorable periods for snails; the colonization process can also be positively influenced by connectivity and potential propagule pressure. Thus, transition probabilities were modeled as linear-logistic functions of the seven environmental variables:

$$\mathrm{logit}(\Phi_{W_{i,t}}) = \mu_1 + \beta_1 S_i + \beta_2 V_i + \beta_3 Stab_i + \beta_4 LRS_t, \quad (4)$$

$$\mathrm{logit}(\Phi_{D_{i,t}}) = \mu_2 + \beta_5 S_i + \beta_6 V_i + \beta_7 Stab_i + \beta_8 LRS_t, \quad (5)$$

$$\mathrm{logit}(\gamma_{W_{i,t}}) = \mu_3 + \beta_9 S_i + \beta_{10} V_i + \beta_{11} Stab_i$$
$$+ \beta_{12} C_i + \beta_{13} D_{i,t} + \beta_{14} RS_t, \quad (6)$$

$$\mathrm{logit}(\gamma_{D_{i,t}}) = \mu_4 + \beta_{15} S_i + \beta_{16} V_i + \beta_{17} Stab_i$$
$$+ \beta_{18} C_i + \beta_{19} D_{i,t} + \beta_{20} RS_t, \quad (7)$$

where the μ's are intercepts and β's are regression coefficients to be estimated. All environmental variables were standardized to have identical (0) mean and (unity) variance so that the regression coefficients were expressed in comparable and nondimensional scales.

Model and Covariate Selection. Different models can be derived from the above parameterization (table 2). We decided to compare five models. First, if the autocovariate $q_{i,t}$, which takes into account the site state, is not included (i.e., is set to 0), then the model reduces to a standard patch occupancy model (hereafter model 0) in which no distinction is made between dry and wet sites. This means equating Φ_D and γ_D to, respectively, Φ_W and γ_W and assuming a single detectability p_W in all sites, irrespective of their D or W state. This model ignores all the different aspects that arise when different life stages are present, and it was considered only to quantify the bias that usually arises when this issue is ignored.

Because we have strong evidence that *D. depressissimum* often persists in dry sites (Pointier and Combes 1976; Lamy et al. 2012), we included the autocovariate $q_{i,t}$ to generate a family of four alternative candidate models (models 1–4) that were explored and compared via sto-

Table 2: Description of the five models compared in this study

Model	Detectability		Persistence rate		Colonization rate		Model description
	p_W	p_D	Φ_W	Φ_D	γ_W	γ_D	
Model 0	+	p_W	+	Φ_W	+	γ_W	Standard patch occupancy model; assumes no differences between wet and dry sites
Model 1	+	0	+	0	+	0	Assumes that the species cannot persist in dry sites and has not colonized them during the preceding rainy season
Model 2	+	0	+	0	+	+	Assumes that the species cannot persist in dry sites but can have colonized them in the preceding rainy season
Model 3	+	0	+	+	+	0	Assumes that the species can persist in dry sites but cannot have colonized them in the preceding rainy season
Model 4	+	0	+	+	+	+	Assumes that the species both can persist in dry sites and can have colonized them in the preceding rainy season

Note: A plus sign means that the corresponding parameter is estimated by the model, 0 that it is set to a constant (0), and another parameter that it is constrained to equal that parameter. Models 1–4 are compared by means of stochastic search variable selection (see "Model and Covariate Selection").

chastic search variable selection (SSVS; George and McCulloch 1993; O'Hara and Sillanpää 2009). In these models, Φ_D and γ_D were either estimated or set to 0 (table 2). Setting Φ_D to 0 amounts to denying the possibility that snails might persist in dry periods (i.e., ignoring the possibility of aestivation), while setting γ_D to 0 amounts to denying the possibility that a site found to be dry has been recently colonized. Hence, model 0 make no distinction between dry and wet sites, while model 1 assumes that snails are always absent in dry sites. The principle of SSVS is to build a "metamodel" that includes all models in the series as special cases; this is done by including additional parameters in the form of binary indicator variables, $\alpha_k = 1$ or 0, that act by either allowing the estimation of a given parameter or excluding it by setting it to a constant. In a Bayesian framework, a way to constrain a parameter to a certain value (0, in our case) is to specify an extremely informative prior concentrated on this value; conversely, a flat prior, such as $U(0, 1)$, is used for parameters to be estimated. We also tested other priors, such as Beta(0.1, 0.1), which gave similar posterior results (Zhu and Lu 2004; Miconnet et al. 2005). The prior distribution of Φ_D and γ_D over the whole model space is

$$\Phi_D \sim (1 - \alpha_1)0 + \alpha_1 U(0, 1), \tag{8}$$

$$\gamma_D \sim (1 - \alpha_2)0 + \alpha_2 U(0, 1), \tag{9}$$

where α_1 and α_2 are Bernoulli variables whose probabilities are themselves hyperparameters that are estimated. The prior probabilities (or means) for α_1 and α_2 were set to 0.5 (giving equal weight to all parts of the model space). Their posterior means indicate the weight of evidence for including a nonzero estimate of Φ_D or γ_D.

In a second step, we selected model 4, which includes both Φ_D and γ_D, and explored the model space generated

by including or excluding covariates (β_p), using SSVS as above. The priors for regression parameters were

$$B_p \sim (1 - \alpha_p)N(0, 0.0001) + \alpha_p N(0, 1) \tag{10}$$

(prior mean of α_p is 0.5, and N means a normal distribution). A final model was run that included only covariates with posterior means of $\alpha_p > 0.6$.

We performed all our analyses in the Bayesian framework described above. We used three chains and based our inferences on 100,000 samples from the posterior distribution of parameters, after 10,000 iterations as burn-in. Chain mixing was visually assessed, while convergence was checked with the Brooks-Gelman-Rubin diagnostic (Brooks and Gelman 1998). The source codes to run these models in R are provided as supplementary material, available online (note that WinBUGS runs only on Windows).

Results

During our visits, at the beginning of the dry season, the proportion of sites that were found to be dry was 4.3%, on average, and varied between 0.4% and 18.8%. We detected *Drepanotrema depressissimum*, on average, in 47.5% of the sites (minimum 28.4%, maximum 72.9%); in 11.3% of the sites, the snail was never observed during the whole period (2000–2011). Finally, *D. depressissimum* was observed at each occasion in only a single site. Therefore, in most sites the species was detected on some occasions and not detected on others.

Specific extinction and colonization rates for dry sites (Φ_D and γ_D) were not included in two models (tables 2, 3). Both models are necessarily invalid, because we know that our protocol does not detect aestivating snails (contradicting an assumption of model 0) and, from previous data, that such snails are often present in dry sites (con-

Table 3: Summary on the five different models compared in the study with their parameter estimates and posterior probability

Model	$q_{i,t}$	Parameter	Estimates in wet sites (CI)			Estimates in dry sites (CI)		P
			p_W	Φ_W	γ_W	Φ_D	γ_D	
Model 0	−	$\Phi_W + \gamma_W$	.72 (.68, .76)	.87 (.81, .91)	.22 (.17, .27)	...	...	...
Model 1	+	$\Phi_W + \gamma_W$	.79 (.75, .82)	.76 (.69, .82)	.32 (.28, .36)	...	...	0
Model 2	+	$\Phi_W + \gamma_W + \gamma_D$	.79 (.75, .82)	.76 (.69, .82)	.32 (.28, .36)	...	.50 (.03, .98)	0
Model 3	+	$\Phi_W + \gamma_W + \Phi_D$	.74 (.71, .78)	.86 (.81, .90)	.22 (.17, .27)	.97 (.90, 1)	...	.01
Model 4	+	$\Phi_W + \gamma_W + \Phi_D + \gamma_D$	.74 (.71, .78)	.86 (.81, .90)	.21 (.16, .26)	.96 (.88, 1)	.64 (.23, .95)	.99

Note: The five models differ in (1) distinguishing between dry and wet sites (plus or minus, respectively, for $q_{i,t}$) and (2) including or not the probability of persistence in/colonization of dry sites (Φ_D and γ_D). When they were not included, parameters were not identifiable (model 0) or were set to 0 (other models). Estimates are mean posterior probabilities, together with their 95% credible intervals (CIs). P refers to the posterior probability (models 1–4), that is, the number of times the model was explored during the stochastic search variable selection (using α_1 and α_2; see "Material and Methods") on Φ_D and γ_D.

tradicting an assumption of model 1). Thus, rather than testing the validity of these models, we are interested in how these invalid assumptions may affect the estimates. Model 0 exhibited, relative to model 1, a lower detectability estimate (posterior mean [95% credible interval] = 0.72 [0.68–0.76] vs. 0.79 [0.75–0.82]), a lower colonization rate (0.22 [0.17–0.27] vs. 0.32 [0.28–0.36]), and a higher persistence (0.87 [0.81–0.91] vs. 0.76 [0.69–0.82]). The metapopulation dynamics of *D. depressissimum* was better explained when aestivation was taken into account. Indeed, among models 1–4 (tables 2, 3), model 4, which included separate estimates of Φ_D and γ_D, had by far the highest posterior probability (P = .99; this posterior probability corresponds to the proportion of iterations that the SSVS spent exploring this model). Surprisingly, the persistence rate in dry sites, Φ_D, from model 4 was close to 1 (0.96 [0.88–1.00]), higher than that in wet sites ($\Phi_W = 0.86$ [0.81–0.90]; fig. 2). The colonization rate also seemed

higher in dry sites ($\gamma_D = 0.64$ [0.23–0.95]; $\gamma_W = 0.21$ [0.16–0.26]; fig. 2), although the estimation was rather imprecise in those sites. The probability of detecting *D. depressissimum* in wet sites was estimated to be 0.78 [0.74–0.81].

We tested for the effect of 20 regression coefficients on persistence and colonization rates. Seven of them were conserved in the final model, and a summary of their effects is given in table 4 and figure 3. Persistence in wet sites, Φ_W, was negatively affected by rain during the little rainy season and positively affected by vegetation cover (table 4; fig. 3). Persistence in dry sites, Φ_D, increased in more unstable sites and decreased in years with abundant rain during the little rainy season. Colonization in wet sites, γ_W, increased in large and connective sites but decreased in relatively stable sites. None of the variables had a detectable effect on colonization in dry sites, γ_D.
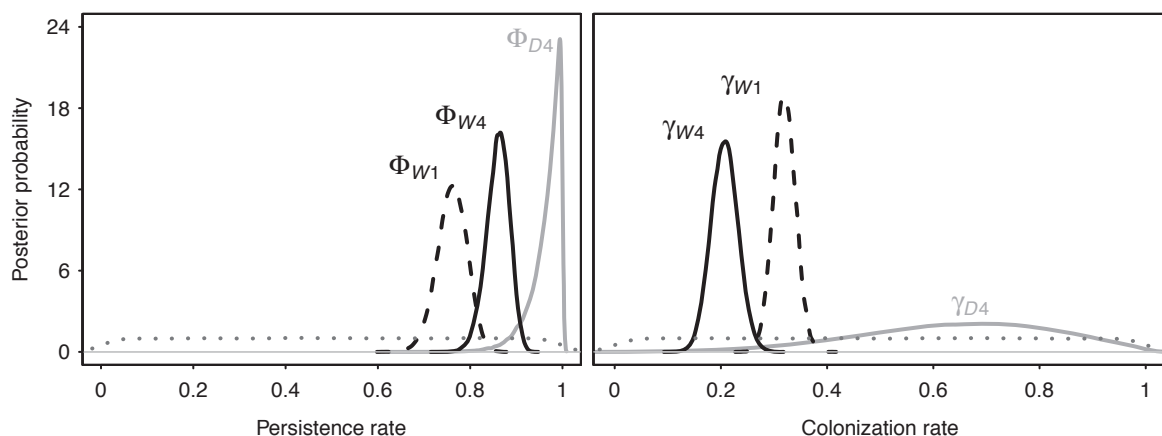

Figure 2: Posterior distributions of persistence and colonization rates. The solid black line represents the posterior distribution of Φ_{W4} (γ_{W4}), the persistence (colonization) rate in wet sites (model 4), and the gray line represents the posterior probability of Φ_{D4} (γ_{D4}), the persistence (colonization) rate in dry sites (model 4). The dashed black line represents the posterior probability of Φ_{W1} (γ_{W1}), the persistence (colonization) rate when Φ_D and γ_D are set to 0 (model 1). Uniform prior distributions are also pictured as dotted gray lines.

Table 4: Posterior means of intercept and covariate effects in the final model and their 95% credible intervals (CIs)

Parameter	Coefficient	Mean (95% CI)	Predicted mean
$\Phi_{W_{i,t}}$			.787
Intercept	a_1	1.31 (.883, 1.758)	
Vegetation	β_2	.961 (.650, 1.297)	
Little rainy season	β_4	−.631 (−.998, −.298)	
$\Phi_{D_{i,t}}$			.967
Intercept	a_2	1.285 (−.288, 2.902)	
Stability	β_7	−.831 (−2.336, .621)	
Little rainy season	β_8	−.895 (−2.318, .460)	
$\gamma_{W_{i,t}}$			.288
Intercept	a_3	−.843 (−1.100, −.599)	
Size	β_9	.382 (.166, .604)	
Stability	β_{11}	−.839 (−1.180, −.538)	
Connectivity	β_{12}	.353 (.142, .575)	
$\gamma_{D_{i,t}}$			.502
Intercept	a_4	.007 (−1.670, 1.621)	
p_W:			
Detectability		.777 (.742, .811)	

Note: Each coefficient is given in logit scale. Consequently, for each parameter (Φ_W, Φ_D, γ_W, and γ_D), we computed the predicted mean by setting all covariates to their conditional means in wet sites (for Φ_W and γ_W) or dry sites (for Φ_D and γ_D) in the prediction formula (eqq. [4]–[7]) and using the inverse-logit function to back-transform into the natural scale.

Discussion

The different models explored in this study unvaryingly yielded positive estimates of colonization and extinction rates, suggesting that detectability of *Drepanotrema depressissimum* could not account for the totality of the turnover observed on the field. As a consequence, the dynamics of *D. depressissimum* in the network of ponds from Guadeloupe seems to correspond to the metapopulation model (Hanski 1999). However the extent of extinction-colonization dynamics was not correctly assessed when cryptic life stages were not taken into account. Here, we developed a multistate occupancy model (MacKenzie et al. 2009) to explicitly incorporate this component of the life cycle that was not accessible to observation. Given the complexity of the model likelihood, the Bayesian approach, in conjunction with the MCMC machinery, turned out to be an efficient way to estimate parameters and to retain relevant covariates in the final model using SSVS.

In a metapopulation, the production of resistance forms tends to buffer local populations against demographic stochasticity and extinction (MacDonald and Watkinson 1981; Kalisz and McPeek 1992; Jarry et al. 1995). Ignoring resistance forms in patch occupancy models biases extinction and colonization rates upward, because the local persistence of the species in its cryptic form during a time interval mimics an extinction followed by a recolonization. The magnitude of this bias depends on the frequency of populations represented exclusively by resistance forms

(here, dry sites). In our biological model, if the species is assumed to be totally absent in dry sites (i.e., when ignoring aestivation; model 1), extinction and colonization rates are increased by more than 50% compared to those in the full model (i.e., model 4; extinction: 24% vs. 14%; colonization: 32% vs. 21%). This bias is substantial, given the low frequency of dry sites (on average, 4.3% of visited sites were found to be dry each year). An even larger bias would be expected with higher frequencies of such sites, which could have occurred if, for example, sampling was done later on in the dry season. On the other hand, a different type of bias arises when one simply ignores the difference between dry and wet sites (model 0). As the species is never recorded in dry sites, this model considers that it is either absent or present but not detected and therefore tends to underestimate detectability in wet sites and as a consequence to underestimate extinction and colonization rates. This bias was moderate in our case study (detectability was 72% in model 0 vs. 74% in model 4, extinction 13% vs. 14%, and colonization 22% vs. 21%). This relatively weak effect of ignoring the dry/wet state of the site and therefore the specificity of aestivation forms is simply due to the fact that persistence in the active state (in wet sites) and persistence in the resistance form (in dry sites) do not happen to be very different in this species. In a general case, we expect that model 0 will provide highly biased estimates if resistance forms behave very differently from active ones, while model 1 estimates will
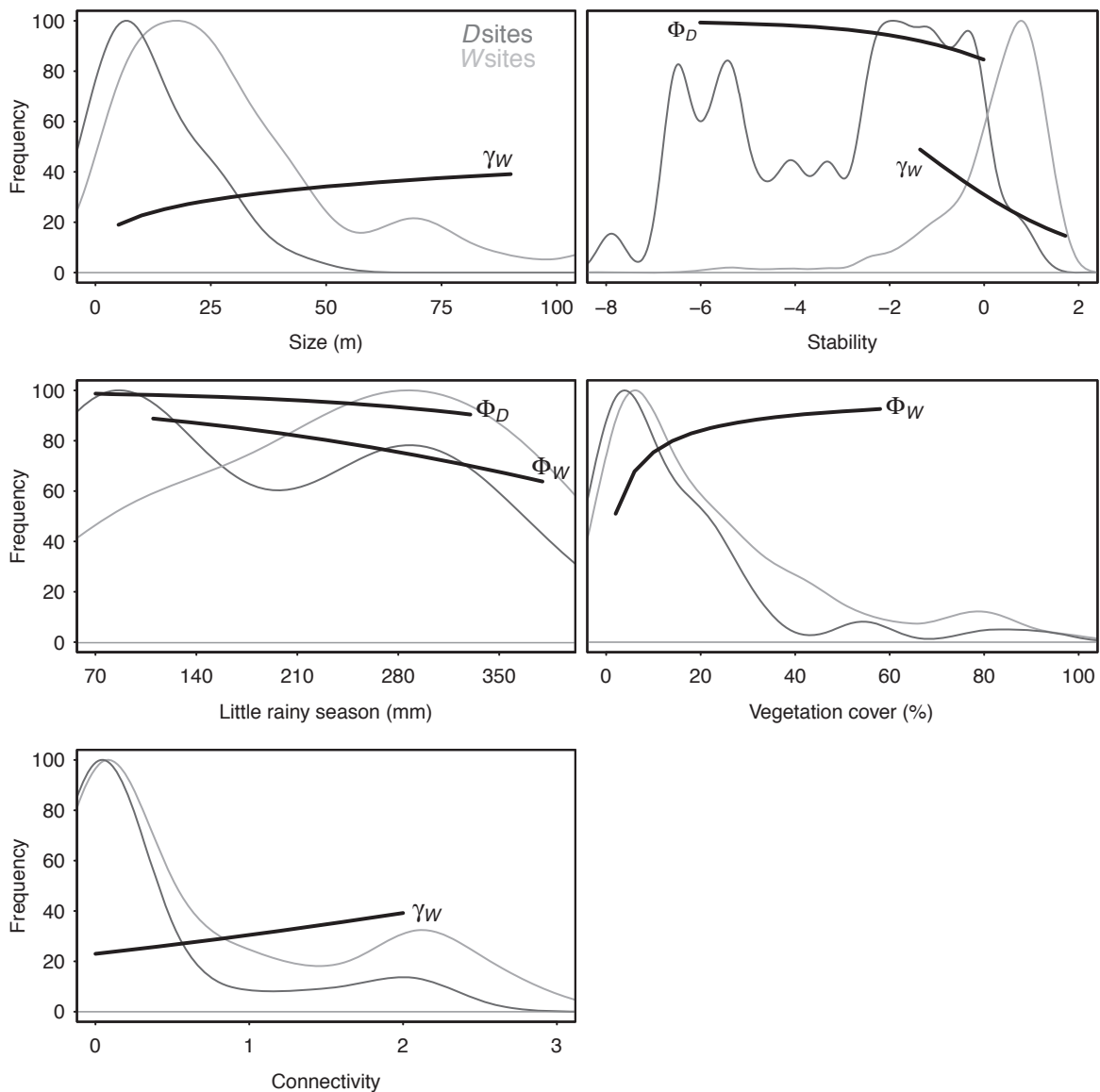
Figure 3: Effects of environmental variables on persistence rates in dry (Φ_D) and wet sites (Φ_W) and on colonization rate in wet sites (γ_W; thick lines). No environmental variable acting on colonization rate in dry sites (γ_D) was retained in the model. Environmental variables do not have the same distribution in dry and wet sites. Distributions of each selected environmental variable (vegetation cover, size, stability, connectivity, and the little rainy season) conditional on sites being dry (thin black lines) or wet (thin gray lines) are represented as smoothed histograms (frequencies are scaled to a maximum height of 100 to increase visibility, although the total number of occurrences in dry sites is much lower than that in wet sites). To avoid extrapolation, effects are represented only in the relevant conditional distribution (10%–90% interval) of each environmental variable as thick dark lines. In each plot, all nonfocal environmental variables were set to their conditional means (for dry or wet sites, as needed).

be highly biased if the two forms behave relatively similarly (as in our study system). However, these conditions cannot be known a priori, and estimates obtained from models 0 or 1, ignoring the specificity of resistant forms when they are present, should not be trusted in the general case.

Importantly, incorporating resistance forms uncovers important and original aspects of metapopulation dynamics that could not previously be documented. Indeed, our most novel and surprising result is the extremely high persistence (near 100%, with a narrow credible interval) of *D. depressissimum* in dry sites. Note that the upper bound of this estimate is equal to 1, probably because we

do not have enough information in our data: given that the detectability is imperfect, it is difficult to exclude the possibility that persistence was complete in the (relatively few) dry sites we sampled. Although the aestivation ability of freshwater snails had already been recognized (review in Brown 1994; Dillon 2000), its importance with regard to metapopulation dynamics had never been assessed. It comes as a surprise that a species can exhibit a higher persistence rate resting in the dry ground than through its active adult form in the water.

Quantifying the role of resistance forms in overcoming perturbation (in our case, pond desiccation) is particularly interesting in a community context, where the various reactions of different species to perturbation may be the key to understanding how they persist in the long term and can coexist in spite of competition (Chesson 1994; Sears and Chesson 2007). In our snail example, *D. depressissimum* is observed to undergo frequent extinctions in large, stable sites that remain wet year-round. This behavior is at odds with that of most freshwater species, which tend to prefer such sites, where species diversity is therefore usually higher (Brown 1994; Dillon 2000). This is also true in the snail metacommunity of Grande-Terre (Pointier 2008), where site stability is associated with higher species diversity (the regression coefficient of mean species diversity over the 2001–2011 period on stability is 0.24 ± 0.05; $t = 4.71$, $P < .001$). We hypothesize that *D. depressissimum* is a weak competitor that is locally driven to extinction in stable sites by the abundance of competing species while it has developed a strategy to persist in very unstable sites. This hypothesis awaits further confirmation but is consistent with one of the prevailing paradigms in metacommunity theory, which assumes that diversity is maintained because inferior competitors have more access to patches recently affected by perturbation, either because they are better colonists or because they have lower extinction rates during perturbation (Leibold et al. 2004). Evidence from experimental ponds suggests that assemblages of drought-resistant species can persist in temporary habitats, protected from more competitive species that invade permanent sites (Chase 2007). Our approach is a way to obtain realistic parameterizations of metapopulation models while accounting for species' ability to overcome perturbation through resistant life forms. Applied to several species in a metacommunity, this could be a step toward testing metacommunity theory in natural rather than experimental systems.

The ability to persist in dry sites is confirmed by our study of the effects of environmental covariates. Indeed, colonization and persistence tend to be higher in unstable sites (i.e., prone to frequent desiccation) and in years with very low rainfall during the little rainy season. Although the dry or wet state of sites during surveys at the beginning

of the dry season is a robust binary indicator, more sites may dry out later, and covariates seem to capture more of this quantitative variation in the effect of drought on freshwater habitats. It is therefore not surprising to observe several effects that all point in the same direction. The other covariate effects, such as the positive effects of vegetation on persistence and of both site size and connectivity on colonization rate, have simple interpretations not related to the effect of drought. Indeed, vegetation provides a shelter, a microhabitat, and a food source to these snails, and immigrants are probably more likely to reach large sites as well as sites more often connected to their neighbors through temporary floods. These results are fully consistent with conclusions from a recent population genetic analysis (Lamy et al. 2012) that no genetic signatures of extinctions were detected in comparisons of populations in sites sampled before and after complete desiccation (suggesting persistence by aestivation) and that connectivity positively affected genetic diversity (suggesting a positive effect of connectivity on immigration).

The issue of resistance forms in metapopulation dynamics has been raised for many years, especially for plants that exhibit seed banks (Husband and Barrett 1996; Kalamees and Zobel 2002; Dostál 2005; Dornier et al. 2011), although it is relevant as well to the many animal species exhibiting resting stages (Brendonck and De Meester 2003). As far as we know, our study is the first one to address this issue. The methodology we propose is of wide applicability. In our model, the nonobservable life stage was associated with a specific, unambiguously observable state of sites, dryness. This allowed parameterization of the metapopulation dynamics conditionally on this feature. The existence of nonobservable life stages associated with a special feature of sites is a characteristic shared by many other invertebrate freshwater species living in temporary environments, such as zooplankton communities for which resting eggs are a way to survive long periods of time without water (Brönmark and Hansson 2005). In other species, such as plants, using multistate occupancy modeling with low or null detection rates for some life stages remains valid, but cryptic stages are not necessarily associated with a specific, observable site feature and/or may coexist with adult stages. Future extensions will have to take this difference into account to broaden the applicability of our method. Besides, large data collections, both in space (to collect large array of ecologically different sites) and through time (to capture the specific dynamics), are needed to obtain precise parameter estimates of the models. This may involve years of collection, as in our case, but could be limited to a smaller number of years if sites associated with cryptic life stages were more prevalent during each visit. This also outlines the importance of long-term monitoring.

Acknowledgments

Literature Cited

Brendonck, L., and L. De Meester. 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia 491:65–84.

Brönmark, C., and L.-A. Hansson. 2005. The biology of lakes and ponds. 2nd ed. Oxford University Press, Oxford.

Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Brown, D. 1994. Freshwater snails of Africa and their medical importance. Taylor & Francis, London.

Bruyère, F., and Y. Questel. 2001. Etude de recensement des mares et des canaux en Guadeloupe. DIREN Guadeloupe, Basse-Terre.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences of the USA 104:17430–17434.

Chesson, P. 1994. Multispecies competition in variable environments. Theoretical Population Biology 45:227–276.

Dillon, R. 2000. The ecology of freshwater molluscs. Cambridge University Press, Cambridge.

Dornier, A., V. Pons, and P.-O. Cheptou. 2011. Colonization and extinction dynamics of an annual plant metapopulation in an urban environment. Oikos 120:1240–1246.

Dostál, P. 2005. Is the population turnover of patchy-distributed annuals determined by dormancy dynamics or dispersal processes? Ecography 28:745–756.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12:346–353.

Fenner, M., and K. Thompson. 2005. The ecology of seeds. Cambridge University Press, Cambridge.

George, E., and R. E. McCulloch. 1993. Variable selection via Gibbs sampling. Journal of the American Statistical Association 88:881–889.

Green, A. W., L. L. Bailey, and J. D. Nichols. 2011. Exploring sensitivity of a multistate occupancy model to inform management decisions. Journal of Applied Ecology 48:1007–1016.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

———. 1999. Metapopulation ecology. Oxford University Press, Oxford.

Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical Population Biology, 64:119–127.

Harrison, S., and A. Hastings. 1996. Genetic and evolutionary consequences of metapopulation structure. Trends in Ecology and Evolution 11:180–183.

Husband, B. C., and S. C. H. Barrett. 1996. A metapopulation perspective in plant population biology. Journal of Ecology 84:461–469.

Jarry, M., M. Khaladi, M. Hossaert-McKey, and D. McKey. 1995. Modeling the population dynamics of annual plants with seed bank and density dependent effects. Acta Biotheoretica 43:53–65.

Kalamees, R., and M. Zobel. 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. Ecology 83:1017–1025.

Kalisz, S., and M. A. McPeek. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. Ecology 73:1082–1093.

Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308.

Lamy, T., J.-P. Pointier, P. Jarne, and P. David. 2012. Testing metapopulation dynamics using genetic, demographic and ecological data. Molecular Ecology 21:1394–1410.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS, a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325–337.

MacDonald, N., and A. R. Watkinson. 1981. Models of an annual plant population with a seedbank. Journal of Theoretical Biology 93:643–653.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

Martin, J., S. Chamaillé-Jammes, J. D. Nichols, H. Fritz, J. E. Hines, C. J. Fonnesbeck, D. I. MacKenzie, and L. L. Bailey. 2010. Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. Ecological Applications 20:1173–1182.

Martin, J., C. L. McIntyre, J. E. Hines, J. D. Nichols, J. A. Schmutz, and M. C. MacCluskie. 2009. Dynamic multistate site occupancy models to evaluate hypotheses relevant to conservation of golden eagles in Denali National Park, Alaska. Biological Conservation 142:2726–2731.

Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology 41:672–689.

Miconnet, N., M. Cornu, A. Beaufort, L. Rosso, and J. B. Denis. 2005. Uncertainty distribution associated with estimating a proportion in microbial risk assessment. Risk Analysis 25:39–48.

O'Hara, R. B., and M. J. Sillanpää. 2009. A review of Bayesian variable selection methods: what, how and which. Bayesian Analysis 4:85–118.

Pointier, J.-P. 2008. Guide to the freshwater molluscs of the Lesser Antilles. ConchBooks, Hackenheim, Germany.

Pointier, J.-P., and C. Combes. 1976. La saison sèche en Guadeloupe et ses conséquences sur la démographie des mollusques dans les biotopes à *Biomphalaria glabrata* (Say, 1818), vecteur de la bilharziose intestinale. La Terre et la Vie 30:121–147.

Pointier, J.-P., and P. David. 2004. Biological control of *Biomphalaria glabrata*, the intermediate host of schistosomes, by *Marisa cornuarietis* in ponds of Guadeloupe: long-term impact on the local snail fauna and aquatic flora. Biological Control 29:81–89.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Royle, J. A. 2006. Site occupancy models with heterogeneous detection probabilities. Biometrics 62:97–102.

Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813–1823.

Sears, A. L. W., and P. Chesson. 2007. New methods for quantifying the spatial storage effect: an illustration with desert annuals. Ecology 88:2240–2247.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software 12:1–16.

Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, and M. A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. Journal of Wildlife Management 69:905–917.

Zhu, M., and A. Y. Lu. 2004. The counter-intuitive non-informative prior for the Bernoulli family. Journal of Statistics Education 12, http://www.amstat.org/publications/jse/v12n2/zhu.pdf.

Associate Editor: Volker Grimm
Editor: Mark A. McPeek

Top, *Drepanotrema depressissimum*, a freshwater snail that relies on aestivation to persist in the ground of dried-out ponds. *Bottom*, one of the surveyed ponds located on the island of Grande-Terre (Guadeloupe, Lesser Antilles). Photographs by Jean-Pierre Pointier.