

# Colonization and extinction dynamics of an annual plant metapopulation in an urban environment

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The metapopulation framework considers that the spatiotemporal distribution of organisms results from a balance between the colonization and extinction of populations in a suitable and discrete habitat network. Recent spatially realistic metapopulation models have allowed patch dynamics to be investigated in natural populations but such models have rarely been applied to plants. Using a simple urban fragmented population system in which favourable habitat can be easily mapped, we studied patch dynamics in the annual plant *Crepis sancta* (Asteraceae). Using stochastic patch occupancy models (SPOMs) and multi-year occupancy data we dissected extinction and colonization patterns in our system. Overall, our data were consistent with two distinct metapopulation scenarios. A metapopulation (*sensu stricto*) dynamic in which colonization occurs over a short distance and extinction is lowered by nearby occupied patches (rescue effect) was found in a set of patches close to the city centre, while a propagule rain model in which colonization occurs from a large external population was most consistent with data from other networks. Overall, the study highlights the importance of external seed sources in urban patch dynamics. Our analysis emphasizes the fact that plant distributions are governed not only by habitat properties but also by the intrinsic properties of colonization and dispersal of species. The metapopulation approach provides a valuable tool for understanding how colonization and extinction shape occupancy patterns in highly fragmented plant populations. Finally, this study points to the potential utility of more complex plant metapopulation models than traditionally used for analysing ecological and evolutionary processes in natural metapopulations.

Since first defined by Levins (1969), the metapopulation concept has been widely accepted and developed in both theoretical and empirical ecology (Hanski 1998). The metapopulation framework provides a quantitative basis for analysing and predicting species distribution at the regional scale by evaluating the colonization and extinction of local populations (Hanski 1998). Initially based on Levins' model assumptions (Levins 1969), the generalization of colonization and extinction processes integrating for instance the rescue effect on extinction – the decrease in the extinction rate with increasing metapopulation occupancy (Hanski 1982) – or the propagule rain model, in which colonizing propagules come from large and often unknown populations (Gotelli 1991), now provides a general framework within which to analyse various metapopulation scenarios. Moreover, the development of spatially realistic models (Ovaskainen and Hanski 2004a) coupled with extensive statistical tools (Etienne et al. 2004) allows the analysis of empirical data. Thus, stochastic patch occupancy models (hereafter 'SPOMs') allow the modelling of population turnover and assessments of how population dynamics occur at large scales. These models provide estimates of colonization and extinction probabilities for each patch as well as an estimation of the dispersal kernel based on the colonization pattern (Ovaskainen and Hanski

2004a). These models consider a patch as occupied or empty and do not consider local demographic status in accordance with the initial assumptions of Levins' model (Levins 1969). Thus, from easy-to-collect data (presence/absence) and the cartography of the favourable habitat, different metapopulation models (e.g. classical Levins' metapopulation vs propagule rain models) can be compared as in the pioneering studies on *Melitaea cinxia* (Hanski 1994) to understand species' persistence in a highly fragmented landscape.

Over the last decade, SPOMs have been applied in empirical studies of insects and small mammals (Hanski 1994, Moilanen et al. 1998, Ozgul et al. 2006), which have documented the importance of colonization/extinction processes in spatial occupancy patterns within fragmented landscapes. In recent years, the metapopulation concept has become a robust framework in animal ecology and evolutionary biology, providing a link between ecology, genetics and evolution (Hanski and Gaggiotti 2004). On the contrary, SPOMs have rarely been applied to plants (see however Verheyen et al. 2004, Snäll et al. 2005) and the accuracy of the plant metapopulation concept was recently debated (Freckleton and Watkinson 2002, Ehrlén and Eriksson 2003) although every naturalist would agree that most plant populations exhibit a patchy structure (Husband

and Barrett 1996). The scarcity of plant metapopulation studies can be explained first by practical problems such as the a priori determination of a favourable habitat, which limits the use of the metapopulation approach (Ouborg and Eriksson 2004, Schurr et al. 2007). Second, aspects of plant biology such as seed dormancy and low population turnover or resilience (Eriksson 1996, Ouborg and Eriksson 2004) may obscure the signature of dispersal limitation in plant regional dynamics. In particular, the seed bank, if present, can lead to pseudo-colonization via the germination of seeds already present in a patch, which may be wrongly considered as a colonization event (discussed by Dostal 2005, Kalamees and Zobel 2002). In addition, extinction can be overestimated when a patch is considered as empty although it is actually occupied but by a dormant stage (Eriksson 1996). However, the importance of the seed bank in comparison to seed dispersal has rarely been investigated and the actual impact of the seed bank on patch dynamics remains unclear. Thus, although the roll of colonization/extinction processes in the pattern of spatial occupancy is poorly understood, given all these plant-specific limitations the metapopulation approach has rarely been applied to plants.

As a case study, we studied the colonization/extinction dynamics of the annual plant *Crepis sancta* (Asteraceae) in urban fragmented populations. Urban environments typically represent a matrix of several square kilometres that are mostly unsuitable for plants due to the presence of asphalt and buildings, interspersed with a few isolated favourable habitats. We specifically focused on the highly fragmented habitat composed of the widely distributed small patches around pavement trees in Montpellier (southern France), which *C. sancta* has successfully colonized. Within these patches, *C. sancta* forms small populations that are subject to frequent disturbance. The metapopulation approach should be applicable to providing information on how this species can survive within this fragmented landscape. Interestingly, suitable habitats in the urban environment are clearly defined, allowing us to discriminate a priori favourable habitats (patches) from unfavourable habitats (the asphalt). In addition, because of the high frequency of disturbance and the small size of patches, a high population turnover is expected, which should allow us to reveal the importance of colonization and extinction processes in the maintenance of *C. sancta* within the fragmented landscape.

In this study, we used SPOMs to infer the most parsimonious metapopulation models for *C. sancta* in an urban environment by comparing the fit of various metapopulation models to data. In order to test for a seed bank in *C. sancta*, we performed a complementary analysis that aimed to evaluate seed germination from soil cores. We found that patch dynamics in different patch networks were best explained by two contrasting metapopulation models: the propagule rain model and the classical Levins model with a rescue effect, despite their similar spatial patch conformation. No *C. sancta* seedlings grew from any of the analysed soil cores, which suggests that the extinction/colonization dynamics provide a satisfactory picture of the spatiotemporal dynamic in the urban landscape. Thus, this study shows that SPOMs provide informative results on plant population dynamics, demonstrating that plant distribution is governed not only by habitat properties but also by the intrinsic properties

(e.g. dispersal) of species. Finally, we highlight the fact that the metapopulation approach can provide relevant information for conservation biology (in particular for invasive species) and also for evolutionary biology.

## Material and methods

### Study species

The allogamous species *Crepis sancta* (Asteraceae) is an annual plant that is widespread in southern France, in particular in vineyards, where it forms very large populations. In urban environments (Montpellier, France), both large (e.g. in parks and gardens) and small reproducing populations can be found. Urban populations growing in patches on the sidewalk (generally less than 40 plants, Supplementary material Appendix 1) are subjected to frequent disturbance and more than 100 common weed species occur in these patches within Montpellier. *Crepis sancta* is heterocarpic and produces two types of achenes: light achenes with a pappus that disperse by wind and heavy achenes without a pappus that do not disperse (Imbert 1999). Using controlled germination tests, Imbert (1999) revealed the absence of seed dormancy for both types of achenes. The germination rate is about 95% in optimal conditions for seeds produced in the last season, dropping to 10–20% after four years of conservation in lab conditions (Imbert 1999).

### Sampling design

We monitored 289 patches over four consecutive years (2005–2008) within two independent networks separated by 4 km within Montpellier. These are designated the ‘HM network’ (Henri Marès street: 96 patches forming a single line and spaced 5–7 m apart) at the periphery of the city and the ‘JC network’ (Jacques Cartier street: 193 patches spread in several lines spaced 5 or 10 m apart within or between different lines; Supplementary material Appendix 2) within the city centre. For each network, all patches were localized with GPS and sampled annually over four consecutive years, and the state of each patch (empty or occupied) was noted to allow population turnover estimates. In order to limit the risk of false detection, population monitoring was carried out at least twice per year during each reproductive period. As the networks revealed different amounts of heterogeneity based on field observations (e.g. spatial occupancy pattern), we decided to divide them into sub-networks, which were considered more homogeneous. For the JC network, a ‘western’ sub-network of 81 patches was isolated (Supplementary material Appendix 2) due to the higher temporal homogeneity of patch occupancy (Supplementary material Appendix 3), a requisite for a good SPOM application (Etienne et al. 2004). The HM network was split into two sub-networks (36 patches [HMpharma] and 60 patches [HMInra]) due to slight differences in the patch areas; these two sub-networks were separated by about 100 m, a much greater distance than the inter-patch distance. We statistically tested the relevance of such heterogeneity by comparing the metapopulation dynamics of the whole networks with those of their respective sub-networks.

## Seed bank analysis

In order to check whether the absence of dormancy translates into the absence of a seed bank in the soil, we collected soil cores (3 to 5 cm depth) in 50 patches chosen at random (either occupied or empty patches in 2008) in the JC network. Sampling was performed at the beginning of the 2009 flowering season i.e. before seed production, in order to capture seeds that had not germinated in autumn 2008. Within each patch, the sample was obtained by mixing three soil samples randomly chosen from the patch surface. The soil samples were dried out and stored in laboratory conditions in paper bags over the summer. In the autumn, the soil samples were watered and placed in optimal germination conditions in a greenhouse at CEFÉ-CNRS (Montpellier). Due to limited space, only 25 samples were tested, corresponding to 13 patches occupied by *C. sancta* in 2008 and 12 patches that were not occupied by *C. sancta*. Various species germinated several days after watering, and germination was checked weekly. The species were identified at the seedling stage by VP and the presence of species within each patch was recorded.

## Model structure

We used the SPOM formalization (Moilanen 1999) in order to estimate the transition probability of patch state year by year and to compare different metapopulation models based on colonization and extinction functions (Ovaskainen and Hanski 2004a). SPOMs follow Markov chains and estimate the probability of occupation of a patch at time  $t$  according to both the state of the patch and the mean state of the metapopulation in the previous year (Moilanen 1999). Thus, let  $X_i(t)$  represent the state of a patch  $i$  at time  $t$  with  $X_i(t) = 1$  if the patch is occupied and  $X_i(t) = 0$  if the patch is empty.  $\bar{X}(t)$  represents the vector of the total state of the metapopulation at time  $t$ . Each year an unoccupied patch  $i$  is colonized with the probability  $C_i$  or stays empty with the probability  $1 - C_i$ . An occupied patch goes extinct with the probability  $E_i$  or remains occupied with the complementary probability  $1 - E_i$ . Following Moilanen (1999), the probability of observing a metapopulation state change from  $\bar{X}(t)$  to  $\bar{X}(t+1)$  is:

$$P[\bar{X}(t+1) | \bar{X}(t)] = \prod \begin{cases} E_i & \text{if } X_i(t) = 1 \text{ and } X_i(t+1) = 0 \\ 1 - E_i & \text{if } X_i(t) = 1 \text{ and } X_i(t+1) = 1 \\ C_i & \text{if } X_i(t) = 0 \text{ and } X_i(t+1) = 1 \\ 1 - C_i & \text{if } X_i(t) = 0 \text{ and } X_i(t+1) = 0 \end{cases}$$

In metapopulation models, patch area is used as an estimate of the local population carrying capacity (Ovaskainen and Hanski 2004a). Since all patches were of the same size within each network or sub-network, patches were considered as identical within each network. We constructed five contrasting metapopulation scenarios that are based on whether or not extinction or colonization depends on occupancy patterns (Table 1). The simplest model assumes that colonization and extinction are constant. More specifically, this means that the number of occupied patches does not affect the number of colonization events in the metapopulation, which is the signature of external colonization. We hereafter refer to this as the propagule rain model (PRM, Table 1, Gotelli 1991).

The four other models assume that the colonization probabilities and/or extinction probabilities depend on the metapopulation state (Gotelli 1991) and assume a negative exponential dispersal kernel. The contribution of neighbouring patches is synthesized by the connectivity measure (Moilanen and Nieminen 2002),  $S_i(t)$ , defined as:

$$S_i(t) = \sum_{j \neq i} \exp(-\alpha d_{ij}) X_j(t)$$

where  $d_{ij}$  is the Euclidian distance between patch  $i$  and patch  $j$ , and  $\alpha$  is the parameter of the dispersal kernel following a negative exponential, which represents the inverse of the mean dispersal distance (Hanski 1994). The 'Levins model' (spatially realistic Levins model, SRLM, Hanski and Ovaskainen 2000, Table 1) considers in a spatially realistic way that colonization increases with connectivity as a consequence of limited dispersal. The incidence function model (IFM, Hanski 1994, Table 1) considers an Allee-like effect; that is, the colonization rate increases with occupancy. The extinction function is considered constant in these two models. Where a rescue effect was considered i.e. when extinction decreased with connectivity, we defined two other models: IFM + rescue effect and SRLM + rescue effect (Table 1).

## Model selection

For each of the five models, we estimated parameters using the method developed by Moilanen (1999) implemented in SPOMSIM software (Moilanen 2004) and we checked the convergence of Markov chains with different sets of initial values. The 95% confidence intervals of parameter estimates were obtained using likelihood profiles (Moilanen 2004). The best models were chosen using the AIC informative criterion corrected for small samples (AICc; Moilanen 2004) and a model was considered better than another if the change in AIC was higher than 2 (Burnham and Anderson 2002).

## Results

During the study, many populations went extinct while many empty patches were colonized, leading to a constant occupancy rate except for the last year, during which

Table 1. Colonization and extinction functions used in the metapopulation models. Different metapopulation models were obtained with colonization and extinction functions: [C1] and [E2]: PRM; [C2] and [E1]: SRLM; [C3] and [E1]: IFM; [C3] and [E2]: IFM + rescue effect; [C2] and [E2]: SRLM + rescue effect. The rescue effect parameter ( $R$ ) can be either fixed at 1 or estimated. As models in which  $R$  was estimated were never found to be better than models in which  $R$  was fixed at 1, only models with  $R$  fixed at 1 are shown in this study.

Colonization function	Extinction function
[C1] $C_i = y$	[E1] $E_i = \min(1, e)$
[C2] $C_i(t) = 1 - \exp(-yS_i(t))$	[E2] $E_i(t) = E_i(1 - C_i(t))^R$ (Rescue effect)
[C3] $C_i(t) = \frac{S_i(t)^2}{S_i(t)^2 + y^2}$ (Allee-like effect)	

colonizations were higher than extinctions (Supplementary material Appendix 3). The occupancy rate fluctuated around 0.6 for HM, 0.3 for JC, and 0.45 for the JC ‘western’ sub-network (Supplementary material Appendix 3).

### Seed banks

Over the 25 patches, 32 species were identified. The most common species were *Conyza sumatrensis*, *Poa annua*, *Sonchus oleraceus* and *Lactuca scariola* (see Supplementary material Appendix 4 for the complete species list). All these species are frequently observed in patches. A small fraction of seedlings was only identified at the genus level and five seedlings of a tree species remain unidentified. The fact that many seedlings germinated allowed us to consider that our sampling design was powerful enough to detect viable seeds in the soil, especially for weeds such as *C. sancta* that are common in urban patches. The most important finding was that no *C. sancta* seedlings were found, indicating that no viable seeds were conserved in the soil after germination in the autumn.

### Metapopulation dynamic

Across all the models considered for the HM network, the propagule rain model provided the best fit (Table 2). Independent analysis of each of the sub-networks (HMpharma and HMinra) showed no significant variation in metapopulation scenarios, which means that the HM network can be considered a single metapopulation (Table 2). In this network, the estimated colonization probability was 0.37 and

the estimated extinction probability was 0.20 (Table 3). The occupancy rate at equilibrium in the propagule rain model is given by  $p^* = c / (c+e)$  i.e. 0.64 (0.60–0.66) for HM, which is congruent with the mean observed occupancy rate (0.59). For the JC network, the results for the ‘western’ sub-network were incongruent with those for the entire network. For the entire network, the propagule rain model again provided the best fit (Table 2) with a colonization probability of 0.15 and an extinction probability of 0.19 (Table 3). Comparison between the predicted occupancy rate at equilibrium (0.44 (0.42–0.45)) and the observed occupancy rate (0.29), suggests that the entire JC network may be far from equilibrium or heterogeneous. However, the SRLM with a rescue effect was the best fit for the ‘western’ sub-network effect (Table 2). Here, the presence of a rescue effect could not be discriminated from SRLM ( $\Delta AIC = 1.57$ ) but for our purpose we emphasize that the SRLM (with or without a rescue effect) was better than the propagule rain model ( $\Delta AIC \gg 2$ ). From these sub-network results, we estimated that the mean dispersal distance is about 2 m ( $\alpha = 0.45$  (0.43–0.50); Fig. 1, Table 3), suggesting that patch colonization mainly occurs between immediately neighbouring patches (Fig. 1). The colonization probability greatly increased with connectivity, such that highly connected patches had a 25% probability (close to 0.4 at the upper bound of the confidence interval) of being colonized whereas patches with low connectivity values were being colonized with less than 10% probability (Fig. 1). In addition, the presence of a significant rescue effect revealed that well-connected patches were less driven to extinction than isolated patches (Fig. 1).

Table 2. Fit of metapopulation models for *C. sancta* urban populations. The model was fitted to data maximizing the likelihood. The maximum likelihood was log-transformed and the best model was the minimum negative log-transformed likelihood [-ln(likelihood)]. Parameters estimated: extinction (e) and colonization (y) parameters (PRM) added to the dispersal kernel parameter ( $\alpha$ ) in the four other models.  $\Delta AICc$  represents the AICc difference from the best model.

	Model	No. of parameters	-ln(likelihood)	$\Delta AICc$
HM entire	PRM	2	<b>241.48</b>	–
	SRLM	3	253.39	25.85
	SRLM + rescue	3	255.69	30.45
	IFM	3	254.69	28.45
	IFM + rescue	3	248	15.07
HM Pharma	PRM	2	<b>74.77</b>	–
	SRLM	3	76.8	6.16
	SRLM + rescue	3	76.44	5.44
	IFM	3	77.57	7.7
	IFM + rescue	3	77.63	7.82
HM INRA	PRM	2	<b>177.19</b>	–
	SRLM	3	177.1	1.89
	SRLM + rescue	3	178.3	4.27
	IFM	3	177.50	2.67
	IFM + rescue	3	180.1	7.87
JC entire	PRM	2	<b>377.79</b>	–
	SRLM	3	383.1	12.64
	SRLM + rescue	3	381.5	9.44
	IFM	3	387.79	22.02
	IFM + rescue	3	386	18.44
JC ‘western’ sub-network	PRM	2	160.30	13.015
	SRLM	3	153.6	1.575
	SRLM + rescue	3	<b>152.8</b>	–
	IFM	3	156	6.4
	IFM + rescue	3	153.89	2.18

Table 3. Estimates of parameters for the best model and 95% CI for: (a) HM and (b) JC entire network and the ‘western’ sub-network. NA represents the absence of the parameter in the model. Model names are the same as in Table 2.

	Model	$\alpha$	Y	E	R
(a)					
HM entire	PRM	NA	0.37 (0.36–0.39)	0.20 (0.20–0.24)	NA
(b)					
JC entire	PRM	NA	0.15 (0.14–0.15)	0.19 (0.18–0.19)	NA
JC ‘western’ sub-network	SRLM + Res	0.45 (0.43–0.50)	0.65 (0.62–1.03)	0.15 (0.15–0.21)	1

In Supplementary material Appendix 5, we show the computed observed colonization and extinction rates for different classes of connectivity. Consistent with the model, observed colonization increased with connectivity while

extinction decreased with connectivity for the JC ‘western’ sub-network. Colonization and extinction did not exhibit a clear trend with connectivity in the HM network, consistent with the PRM. For the entire JC network colonization was not related to connectivity whereas extinction decreased with connectivity.

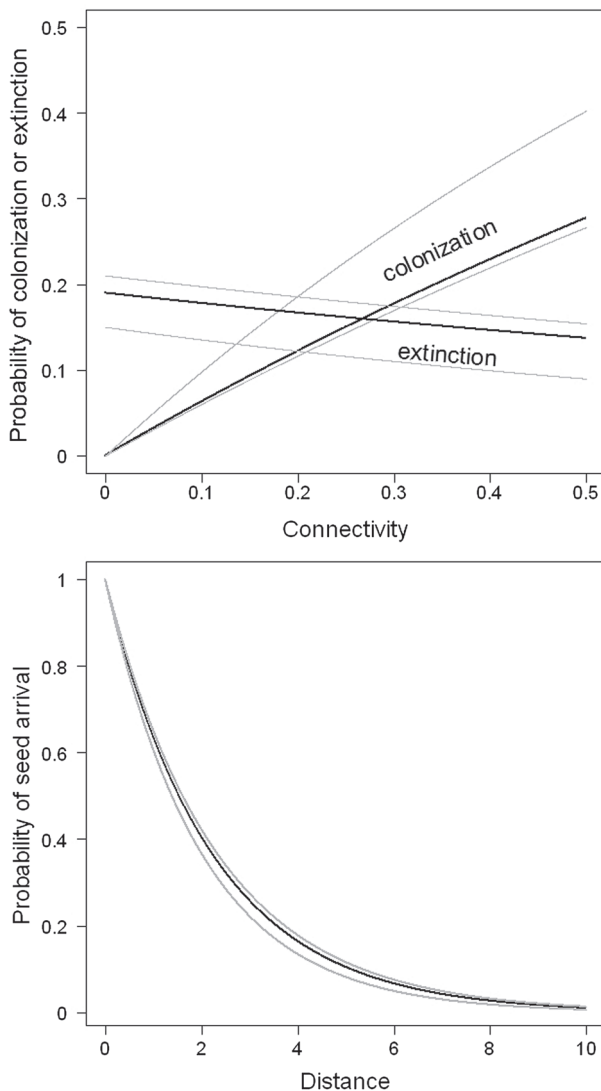


Figure 1. Estimated extinction and colonization probabilities as a function of connectivity for the JC sub-network (up) and seed dispersal kernel as a function of distance (down). Fitted values were obtained with the SRLM + rescue effect metapopulation model. Connectivity values were computed with the  $\alpha$ -estimate ( $\alpha = 0.45$ ) and the observed inter-patch distance of the ‘western’ sub-network. Black lines represent the estimate and grey lines represent the upper and lower bounds of the 95% CI. The dispersal kernel ( $f(d) = \exp(-\alpha d)$ ) is represented below with a black line for the  $\alpha$ -estimate ( $\alpha = 0.45$ ), and the upper and lower bounds [ $\alpha = (0.43–0.50)$ ] are represented in grey.

## Discussion

In this study, we used an urban environment in which favourable habitat was easily distinguishable from unsuitable habitat for the strict application of SPOMs in plants. We parameterized and compared different metapopulation models with simple presence/absence data-snapshots of the annual plant *Crepis sancta* within patches around pavement trees. Our results provide quantitative estimates of metapopulation processes in urban fragmented populations of *C. sancta*, illustrating how natural processes can be revealed in urban environments. Interestingly, contrasting patch dynamics were found for the studied networks despite the similar patch conformation. While the HM network was best described by the propagule rain model, we showed that the western JC sub-network was best described by the Levins metapopulation dynamic (the model with the rescue effect was marginally better). Overall, our study reveals that urban metapopulations cannot be considered as a closed system, but that they probably interact with external seed sources. This study provides an example of the utility of SPOMs in plants and should encourage the development and application of more complex models of plant metapopulation dynamics.

The simplicity of our study model, such as the constant patch area and constant distance between patches, allowed us to detect metapopulation signals that may be more difficult to detect in complex natural habitats. The SPOM analysis suggested variation in colonization and extinction processes among the two metapopulations, despite their very similar habitats, from simple presence/absence data obtained over four consecutive years. Where the propagule rain model provided the best fit, this suggests that colonization was independent of patch occupancy and connectivity. Since the seed dispersal traits of the two urban networks have been shown to be similar (Cheptou et al. 2008), the fact that colonization was independent of connectivity in HM (but not in western JC) suggests external colonization from a source population (Gotelli 1991). A potential source population has subsequently been found in a private garden not far from the HM metapopulation, but its impact on HM patch dynamic remains to be demonstrated. The contrast in the metapopulation dynamics between the two

networks emphasizes the ability of SPOMs to detect the role of a potential source even if it is not identified a priori in the study system. The propagule rain scenario provided the best fit for the entire JC network but this result may be an artefact of the patch occupancy heterogeneity of the two sub-networks, which is known to affect parameter estimation (Etienne et al. 2004). However, we detected a signal that local colonization and extinction were the drivers of patch occupancy in the homogeneous 'western' JC sub-network. Interestingly, extinction was reduced by the presence of occupied neighbouring patches (rescue effect). The presence of the rescue effect may be due to better pollinator activity favouring reproduction, a process that has previously been demonstrated in our metapopulation (Cheptou and Avendano 2006). Based on the absence of seed dormancy and the absence of viable seeds in the soil, the possibility of dormant but non-extinct patches is unlikely, which emphasizes that the inferred colonization/extinction dynamic shapes occupancy patterns. The contrasting patch dynamics that we estimated in the HM network and JC sub-network suggest that urban metapopulations cannot be considered as closed systems but rather that the dynamics of *C. sancta* are likely to be dependent on external populations. In addition, it is interesting to note that the signature of patch dynamics that are independent from external sources was detected in the western JC sub-network (located close to the city) while the more peripheral HM network was dependent on an external source. These results are consistent with the fact that source populations are expected to be more common at the periphery of the city than in the inner city.

The importance of dispersal limitation as a major process structuring plant spatiotemporal dynamics versus the availability of favourable habitat is still an open question, notably due to the scarcity of empirical data (Freckleton and Watkinson 2002). When a favourable habitat is a priori unknown, methodological problems limit the capacity to disentangle the effects of seed dispersal and establishment limitations in natural populations (Clark et al. 2007, Ehrlén and Eriksson 2000, see however Munoz et al. 2007). In contrast, because the favourable habitat was known, our system allowed us to evaluate the role of dispersal limitation in *C. sancta* in an urban environment. For the JC 'western' sub-network, our data suggest that dispersal occurs over a short distance (the mean colonization distance was estimated to be 2 metres) and that dispersal limitation may be an important factor in *C. sancta* dynamics. Interestingly, the experimental measurement of dispersal distance in dispersing achenes (Imbert 1999) showed very a similar dispersal distance with few achenes exceeding 5 m, suggesting that our estimate is congruent with direct dispersal measures (Imbert 1999). The fact that the colonization distance was of the same order as the inter-patch distance may indicate that colonization is frequent in our system. The fact that the occupancy rate was about 50% implies high extinction, which justifies analysing occupancy patterns as a result of the balance between colonization and extinction. However, the fact that colonization was local and frequent may suggest that patch dynamics are governed by local processes rather than regional processes. Thus, our system may be closer to patchy populations than a 'true' metapopulation system (Harrison and Taylor 1997, Freckleton

and Watkinson 2002). By assumption, metapopulation models consider that local patches are at carrying capacity and not affected by dispersal, which we know to be false in our system and probably in most natural systems. Indeed a complementary study (Dornier and Cheptou unpubl) showed that local population sizes vary in our system. While the role of local demography in metapopulation systems remains unknown, we showed that metapopulation modelling provides a simple description of the spatiotemporal dynamics of *C. sancta* in an urban environment. Individual-based models provide an alternative way to describe patch dynamics. On the one hand, they have the advantage of integrating local demographic processes but on the other hand, these are complex and parameter-heavy models. It is not clear how adding demographic details to metapopulation models will result in a better understanding of the ecological dynamics of the species (Hanski and Gaggiotti 2004), and recent theoretical studies (Keeling 2002, Ovaskainen and Hanski 2004b) have suggested that ignoring local demography may not alter the results of metapopulation inferences (see however Ozgul et al. 2009). The development of individual-based models remains in its infancy and SPOMs constitute a well-established and general framework for describing plant dynamics.

In our study, we used the metapopulation approach to understand how colonization and extinction shape the occupancy pattern of a *C. sancta* population in an urban landscape. While seed dispersal is commonly difficult to estimate in plants (Bullock et al. 2006), we showed that SPOMs provide easy tractable models with which to investigate the effect of colonization limitation in natural plant populations. Admittedly, our study system is much simpler than most natural systems (*sensu stricto*) because we can easily discriminate between favourable unoccupied and unfavourable habitat, providing the ideal conditions for metapopulation application. However, ecological systems with binary habitats such as forest gaps (Valverde and Silvertown 1997, Verheyen et al. 2004), small ponds, or trees for epiphytic plants (Snäll et al. 2005) are frequent and the metapopulation approach is relevant in such systems for analysing colonization/extinction processes. Thus, although SPOMs are not the only way to investigate spatiotemporal dynamics, we suggest that they can provide reliable information on colonization/extinction dynamics in a fragmented landscape from simple and easy-to-collect data (presence/absence).

To conclude, our study showed that SPOMs, requiring only simple presence/absence data, can provide important insights into plant regional dynamics and possess the advantage of being highly flexible. In particular, we were able to detect the dependence of patch dynamics on external sources without knowing the explicit sources. These results have practical implications for the management of weeds in a city. For a set of patches functioning as a propagule rain model, the eradication of weeds by preventing seed production in patches will not be efficient because of the constant external colonization. On the contrary, preventing seed production in a 'true' metapopulation system can be a good strategy for managing weeds. Such advice may also be useful in conservation biology for the understanding and the control of the colonization of invasive species. Finally, the metapopulation approach also provides an interesting

framework for the understanding of evolutionary processes such as dispersal ability (Riba et al. 2009) or plant mating systems (Pannell and Dorken 2006).

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Supplementary material (available online as Appendix O18959 at <[www.oikosoffice.lu.se/appendix](http://www.oikosoffice.lu.se/appendix)>). Appendix 1–5.