Variability in primary productivity determines metapopulation dynamics

Néstor Fernández†, Jacinto Román and Miguel Delibes

Department of Conservation Biology, Estación Biológica de Doñana, Spanish Council for Scientific Research EBD-CSIC, Seville 41092, Spain

Temporal variability in primary productivity can change habitat quality for consumer species by affecting the energy levels available as food resources. However, it remains unclear how habitat-quality fluctuations may determine the dynamics of spatially structured populations, where the effects of habitat size, quality and isolation have been customarily assessed assuming static habitats. We present the first empirical evaluation on the effects of stochastic fluctuations in primary productivity—a major outcome of ecosystem functions—on the metapopulation dynamics of a primary consumer. A unique 13-year dataset from an herbivore rodent was used to test the hypothesis that inter-annual variations in primary productivity determine spatiotemporal habitat occupancy patterns and colonization and extinction processes. Inter-annual variability in productivity and in the growing season phenology significantly influenced habitat colonization patterns and occupancy dynamics. These effects lead to changes in connectivity to other potentially occupied habitat patches, which then feed back into occupancy dynamics. According to the results, the dynamics of primary productivity accounted for more than 50% of the variation in occupancy probability, depending on patch size and landscape configuration. Evidence connecting primary productivity dynamics and spatiotemporal population processes has broad implications for metapopulation persistence in fluctuating and changing environments.

1. Introduction

Ecosystem functioning, understood as the pools and fluxes of matter and energy produced at the ecosystem level, has been claimed to play a key regulatory role in primary consumer populations by determining the net energy flux input into trophic webs [1]. This idea relies on the importance of primary productivity, a major output of ecosystem functioning, in determining the overall quantity and quality of food resources available to herbivores, and ultimately on the role of bottom-up forces in regulating herbivore populations [2]. Furthermore, ecosystem primary productivity has been claimed to be a major link between animal performance and the spatio-temporal variability in the abiotic environment, via trophic interactions [3]. Moreover, herbivore species can develop adaptive physiological and behavioural responses to maximize their fitness according to primary productivity patterns experienced in their habitats; for example, matching their reproduction period to cycles of maximum vegetation activity [4], or adapting their movements to spatio-temporal fluctuations in productivity [5]. Variability in primary productivity may also influence life history and population parameters of animals, such as conception and birth rates, survival and overall population recruitment [6–8]. Thus, primary productivity patterns can play a central role in determining the quality of animal habitats and thereby affect their population dynamics, especially in highly fluctuating environments where animals need to track energy pulses and bottlenecks [9,10].

It remains unclear how temporal fluctuations in primary productivity and, more generally, fluctuations in the habitat quality may determine the dynamics...
and distributions of spatially structured populations. A distinctive characteristic of these populations is that habitat occupancy rates can be highly dynamic depending on the balance between local extinction and recolonization processes in networks of habitat patches [11]. Factors affecting spatially structured populations have motivated extensive research within the framework of the metapopulation paradigm, with a strong focus on how habitat occupancy patterns and colonization–extinction processes respond to the interacting effects of the local habitat characteristics and the structure of the landscape. Yet the influence of spatial and temporal habitat heterogeneity has received uneven consideration in this context [12]. Early observational studies often made simplifying distinctions only between suitable habitats and the non-habitat, which assumes that the size and the spatial distribution of the habitats contained the most significant information for predicting occupancy rates. However, much empirical evidence on real-world metapopulations has later demonstrated that habitat quality is bound to affect all processes determining metapopulation dynamics, from local dynamics to spatial connectivity [13–18]. Differences in habitat quality can have similar or greater influence on occupancy rates than the size and the distribution of the habitats, implying that accounting for the environmental causes of habitat heterogeneity is critical for understanding metapopulation persistence [19]. Beyond spatial habitat heterogeneity, existing theory and experiments also predict that temporal variability in the quality of the habitat is key to the dynamics of many real metapopulations, and that metapopulations are significantly more vulnerable to stochastic extinction risks in fluctuating, rather than constant, environments [20–22]. However, empirical metapopulation studies have largely overlooked habitat-quality fluctuations.

Temporal environmental variability is expected to increase the complexity of habitat effects on the demography of metapopulations in at least two different ways (figure 1). First, environmental variability can generate fluctuations in the quality of habitat patches (e.g. through altering the levels of trophic resources). It is expected that these fluctuations would cause variability in the local colonization and extinction probabilities. Second, changes in habitat quality imply that the spatial pattern of connections between patches may change over time and potentially produce a temporal decoupling between patch connectivity and occupancy probability. For example, the transient time of recovery after new connections are established may cause lower patch occupancy levels in fluctuating environments than what would be expected in a static landscape [23,24]. The key role of habitat dynamics in driving metapopulation dynamic processes has been shown in successional habitats, in which have been observed an overall reduction in patch occupancy levels and a less clear connectivity–occupancy relationship as compared with ‘static’ landscapes [25].

We used a unique long-term dataset on patch occupancy patterns in a metapopulation of Arvicola sapidus, a strictly herbivore rodent, to test the hypothesis that the bottom-up effects from variability in primary productivity regulates the dynamics of spatially structured herbivorous populations. To the best of our knowledge, this is the first time this hypothesis has been tested. Specifically, we predicted that the dynamics of patch occupancy in the metapopulation would be linked to temporal variability in the rates and seasonal course of annual primary production. We analysed the metapopulation–productivity relationship in a highly fluctuating Mediterranean ecosystem, given that we expected that populations would be particularly responsive in highly stochastic environments. Primary productivity patterns in Mediterranean ecosystems are typically characterized by pronounced seasonality and high inter-annual variability [26,27]. Whereas the vegetation growth period mainly occurs between autumn and spring, productivity dramatically decreases as a result of moisture deficits during summer drought periods, which vary considerably in their duration and intensity.

We analysed spectral remote sensing satellite data to characterize inter-annual variability in the course of primary production. These data provide systematic, spatially comprehensive and long-term information on vegetation activity and the energy and matter exchange at the ecosystem level, which ultimately determines the rate of energy input into trophic webs [28–30]. Thus, remote-sensing information is of great value in overcoming some of the practical difficulties that have traditionally challenged the analysis of temporal habitat variability in animals that may result from the changing availability of nutritional resources [9].

We specifically evaluated the following hypotheses and predictions:

(1) Primary productivity regulates spatially structured herbivore populations through classic bottom-up processes, determining the amount of energy available for consumption. At the level of habitat patches, this would manifest as increased habitat quality during years with high vegetation productivity. Thus, we predicted that total annual primary productivity and within-year variability in primary productivity would have a positive and negative effect, respectively, on the species incidence in habitat patches.

(2) Spring productivity determines the amount of energy available prior to a pronounced food shortage period for
herbivores in Mediterranean ecosystems. This period also marks the end of the breeding season in many herbivore species, and therefore population growth may be limited by the timing of the end of the productivity season. We expected temporal dynamics in patch occupancy, colonization and extinction to be affected by the total amount of primary productivity in spring, and by variability in the phenology of productivity as defined by the total duration of the growing season and the timing of its end.

Connectivity plays a key role in metapopulations by determining the probability of patch colonization by migrants from other patches. Thus, fluctuations in patch occupancy may not only depend on local habitat quality but also on the quality of surrounding patches and their capacity to produce emigrants. We studied delayed connectivity effects under the hypothesis that species incidence is affected by primary productivity in surrounding patches during the previous year. Specifically, we tested the prediction that changes in connectivity rates, as determined by the previous year’s primary productivity, would have an additive effect on patch occupancy dynamics.

2. Material and methods

(a) Study metapopulation

The southern water vole is a medium-sized arvicoline rodent ranging throughout France and the Iberian Peninsula. It is a strictly herbivorous species and its habitat has been traditionally described as permanent water courses and ponds with high availability of riverine herbaceous plants that provide feeding and shelter. However, populations in Mediterranean environments may also be found in temporary wetlands subject to drought periods, some of which may even be prolonged [31].

The study metapopulation was located in the Doñana Protected Area in southwestern Spain (37°00' N, 6°30' W). The area is situated at the sea level and has a Mediterranean subhumid climate with well-defined seasonality, having hot and dry summers, and moderately wet and mild winters. Mean annual rainfall is 550 mm, although there is great variability and drought periods, some of which may even be prolonged [31].

The metapopulation was monitored by intensively surveying each habitat patch between the end of June and the end of July each year (i.e. during the drought season, when the species does not reproduce). We assessed species occurrence based on the presence of fresh faeces and latrines, which are highly conspicuous. Preliminary tests based on 279 visits that resulted in occupied patches showed 100% detectability within the first 15 min of survey in patches of less than 0.2 ha, and within the first 25 min in larger patches. Thus, we established a searching time of 20 and 30 min for patches smaller or larger than 0.2 ha, respectively. We identified all colonizations and extinctions at the patch level for 11 of the 13 yearly surveys by examining species occurrence in consecutive years (i.e. for all sampling years except 2001 and 2010).

(b) Variability in primary productivity

Time series of the Enhanced Vegetation Index (EVI) were measured at each study plot as an integrative indicator of aboveground net primary productivity (ANPP). The EVI is a measure of vegetation photosynthetic activity calculated from reflectance in the red, near infrared and blue portions of the electromagnetic band. The normalized infrared/red reflectance ratio is an indicator of the fraction of photosynthetically active radiation intercepted by vegetation, which in turn determines ANPP [33–35]. By using the blue band, the EVI corrects for aerosol effects and is less prone to underlying soil influence and signal saturation [36].

Variability in primary productivity was characterized at each site using the following variables: the annual integral of EVI (iEVI), a proxy for total annual ANPP; the within-year variability in EVI (cvEVI), which captures variations in ANPP (e.g. associated with seasonality); the length of the growing season (LOS) and the date of its end (EOS) as indicators of ecosystem phenology; and the spring EVI (spEVI) as a measure of productivity during the period in which A. sapidus reproduction is at its highest, but prior to drought. These variables were calculated using a 14-year series of composite (16 days) images acquired by the MODIS Terra sensor at a spatial resolution of approximately 240 m (MOD13Q1 Collection 5). Initially, the images were filtered on a per-pixel basis using the accompanying reliability and quality assessment information. Pixels that could have been contaminated by clouds, shadows and high levels of atmospheric aerosols were eliminated. The aggregated EVI time series for each study plot for each date were derived by calculating the median value of all valid pixels intersecting the plots. Time series were finally smoothed using a cubic smoothing spline with quadratic weight in order to remove spikes while compensating for higher EVI values, which are usually less affected by noise in the data.

The iEVI and cvEVI were calculated as the sum and the coefficient of variation, respectively, of all EVI values for the period between summer and spring immediately before each survey, taking 1 June as the start of summer and 31 May as the end of spring. The start of the growing season (SOS) was calculated as the date of the year when the midpoint between the minimum EVI and the next maximum was reached during the annual phase of productivity increase [37]. The EOS was calculated in the same way for the midpoint between the maximum EVI and the next minimum during the decay phase. LOS was the difference (in days) between SOS and EOS. To avoid redundancy,
Table 1. Selected generalized linear mixed models for the effects of the dynamics of primary production and connectivity during the previous year on water vole occurrence, colonization and extinction for 2002–2008 and 2010–2013.

| model       | estimate   | standardized | t     | R^2_GLMN(m) | R^2_GLMN(c) |
|-------------|------------|--------------|-------|-------------|-------------|
| occurrence  |            |              |       |             |             |
| intercept   | -6.77 ± 0.96 | -0.90        | -7.03 | 0.41        | 0.56        |
| area        | 0.46 ± 0.08 | 1.44         | 5.55  | 0.41        | 0.56        |
| spEVI       | 4.76 ± 1.71 | 0.22         | 3.14  | 0.41        | 0.56        |
| EOS         | 0.23 ± 0.05 | 0.33         | 2.78  | 0.41        | 0.56        |
| S_t(t-1)    | 0.19 ± 0.04 | 0.44         | 4.17  | 0.41        | 0.56        |
| colonization|            |              |       |             |             |
| intercept   | -12.17 ± 1.99 | -1.82        | -6.12 | 0.14        | 0.23        |
| area        | 0.31 ± 0.09 | 0.96         | 3.59  | 0.14        | 0.23        |
| iEVI        | 21.50 ± 5.99 | 0.42         | 3.59  | 0.14        | 0.23        |
| cvEVI       | -2.58 ± 1.61 | -0.08        | -1.60 | 0.14        | 0.23        |
| EOS         | 0.23 ± 0.07 | 0.32         | 3.60  | 0.14        | 0.23        |
| LOS         | 0.03 ± 0.03 | 0.14         | 1.02  | 0.14        | 0.23        |
| S_t(t-1)    | 0.15 ± 0.07 | 0.26         | 2.16  | 0.14        | 0.23        |
| extinction  |            |              |       |             |             |
| intercept   | 1.29 ± 0.78 | -0.43        | 1.65  | 0.47        | 0.51        |
| area        | -0.33 ± 0.08 | -0.99        | -4.11 | 0.47        | 0.51        |
| spEVI       | -4.27 ± 2.65 | -0.20        | -1.61 | 0.47        | 0.51        |

only LOS and EOS were analysed. Finally, spEVI was calculated as the sum of all the EVI values between March and May.

(c) Statistical analyses

We evaluated metapopulation responses to ecosystem fluctuations using generalized linear mixed models (GLMM) with binomial distribution and model selection protocols based on the Akaike information criterion (AIC) [38,39]. Three metapopulation parameters measured during summer were modelled under the same scheme: patch occupancy, colonization and extinction.

Two subsets of models were defined a priori. The first subset included two models designed to test the prediction that variability in the annual aboveground primary productivity determines patch occupancy dynamics. The simplest model included iEVI as the only primary productivity effect, and the other model included cvEVI to account for the heterogeneous distribution of productivity within the year (table 1). The second subset was designed to evaluate the prediction that variability in phenology and spring productivity determines occupancy dynamics. This subset consisted of three models: the simplest one included the effect of the spring productivity integral (spEVI), and the more complex models included the effects of EOS and LOS. All tested models included also patch area—often used as a surrogate of potential population size in metapopulation studies [11]. In addition, we specified a saturated and a null model. The saturated model included all variables from the two subsets representing the combined effects of integrated annual productivity and phenology variability, excluding variables highly correlated with others (r > 0.5). The null model only included the area as a reference to determine the mean expected response under the assumption of no effects of temporal variability in primary productivity. All models included the same random component structure with the patch nested within the study plot to model repeated measurements, and an exponential spatial covariance structure to correct for potential random spatial autocorrelation [40]. Finally, fitted GLMMs were compared based on differences in AIC and model probabilities calculated from the Akaike weights (wi) [38].

In a second step, we analysed the lagged effects of ecosystem productivity on occupancy dynamics that may result from changes in connectivity through time. This analysis attempted to capture the effect of the previous year’s habitat quality on patch connectivity and occupancy (i.e. assuming that the more connections to high-quality patches at time t − 1, the higher the probability of finding the species at t). Thus, we calculated a patch connectivity index each year using a modified version of the negative exponential kernel function [11] in which the contribution of surrounding patches was weighted by the previous year’s habitat quality:

\[ S_{(t-1)} = \sum_{i \neq j} \exp(-\alpha d_{ij}) A_i p_{j(t-1)} r^2 \]  

where \( d_{ij} \) is the shortest distance between the outer boundaries of the focal patch i and each surrounding patch j; \( \alpha \) is a scale parameter defined by the mean dispersal distance from the population dispersal kernel (here denoting the distribution of distances between post-dispersal locations and the source location [41]); \( A_i \) is the area of patch i; b defines the power relationship between patch area and species abundance; and \( p_{j(t-1)} \) is the probability of patch occupancy at year t − 1. This probability was calculated using the predictions of the best occupancy model obtained from previous analyses. Therefore, \( p_{j(t-1)} \) reflects the expected effect of primary productivity conditions of the previous year through modifying the habitat quality of surrounding patches. We set \( \alpha = 1/665 \) based on a previous isolation-by-distance genetic study of dispersal distances, which resulted in mean dispersal distances of 668 m for males and 661 m for females. These estimates were obtained using the average squared axial parent–offspring distance estimated on the regression of individual pairwise genetic distances on the geographical distances [32]. In addition, we
calculated $b = 0.27$ based on a power-law relationship between patch size and the mean number of individuals calculated in 44 habitat patches surveyed during 135 capture-recapture campaigns held between 2000 and 2002 ($r = 2662$ captures of 928 different individuals in 7703 trap-nights with a recapture rate greater than 0.98; after [42]). Finally, $S_{\text{m}}(t)$ was estimated by including also all patches within a 665 m radius from each patch coinciding with the 50% accumulated dispersal probability from the dispersal kernel. We restricted the buffer to this radius in order to be able to compare the results with connectivity estimates based on recorded occupancy data in the patch neighbourhood (see below). Ponds outside the study plots were identified using two fine-scale digital maps of the flooding areas in the region [43,44].

We assessed the effect of the connectivity index on patch occupancy dynamics by comparing models with and without $S_{\text{m}}(t)$. Furthermore, in order to test for the specific effect of primary productivity fluctuations on connectivity we also tested competing models where this ‘dynamic-habitat’ connectivity index $S_{\text{p}}(t)$ was replaced by a ‘static-habitat’ index $S_{\text{m}}(t)$, in which $P_{\text{ij}}$ was set constant. The latter represents a situation where the contribution of sources only depended on their size and spatial distribution and not on variations in primary productivity. For these analyses, we only considered models previously supported with probabilities $\psi_i \geq 0.05$. The year 2001 was excluded from these analyses as $P_{\text{ij}}$ could not be estimated due to incomplete MODIS data for the previous year.

Last, we tested the predictive capacity of the dynamic-habitat and the static-habitat connectivity indices against the original incidence–function connectivity $S_{\text{ij}}$ that is, including $P_{\text{ij}}$ (0 for unoccupied and 1 for occupied) instead of $P_{\text{ij}}$. These relationships were tested using linear mixed models with the patch as a random term and specifying an exponential variance structure to account for higher variance at larger connectivity values. This test was performed for a subset of 38 habitat patches and 11 years for which the patch occupancy status by A. sapidus was known for all surrounding patches within a 665 m radius.

Statistical analyses were performed with the R statistical environment v. 3.0.2 [45], except for GLMM with spatial random structures, which were fitted in the SAS statistical package [46]. Pseudo-$R^2$ statistics were estimated as an approximate measure of the model’s goodness of fit, separating the marginal component (i.e. variability explained by the fixed factors; $R^2_{\text{m}}$) and the conditional component (i.e. variability explained by both fixed and random factors; $R^2_{\text{c}}$) [47].

3. Results

(a) Patch occupancy patterns

In total, 145 of the 300 potential habitat patches were occupied by A. sapidus at least once during the 13-year study. Subsequent analyses focused only on patches in which presence was recorded at least once. On average, 32.6% of the 145 patches were occupied each year (range 16–56%). There were 614 recorded occurrences and 1271 recorded absences in patches that had been occupied at least once. We observed 166 colonizations of 1082 possible events, and 186 extinctions of 513. Only three patches were permanently occupied.

(b) Variability in primary productivity

The analysis of the EVI time series confirmed the great variability in annual and seasonal rates of aboveground primary production, as well as in phenology variables; differences in productivity within study sites ranged between 18.3% and 41.1% for iEVI, and between 17.7 and 71.3% for spEVI. Within-site variations in LOS varied between 128 and 288 days, and the difference in EOS ranged between 48 and 96 days. There was a high correlation between iEVI and spEVI (Pearson’s $r = 0.68$, cvEVI and spEVI ($r = 0.83$), and cvEVI and ESVI ($r = 0.77$). All other pairs had $r < 0.5$. The combined effects model thus excluded cvEVI and spEVI.

(c) Patch occupancy, colonization and extinction models

Results of model selection supported the hypothesis that inter-annual variability in seasonal primary productivity determined metapopulation dynamics. We found very high support for a model relating the patch occupancy probability by A. sapidus with higher spring productivity (spEVI) and a later end of the growing season (EOS) ($\omega_i = 0.99$; electronic supplementary material, table S1-A). The colonization model with the highest probability was the combined-effects model ($\omega_i = 0.95$) showing a positive effect of long and late-ending growing seasons (LOS and EOS), as well as positive and negative effects of iEVI and cvEVI, respectively. Last, extinction analyses supported the seasonal hypothesis but were less conclusive. The highest-ranked model included spEVI ($\omega_i = 0.54$), although the probability of the null ‘patch-area’ model was also high ($\omega_i = 0.46$; electronic supplementary material, table S1-A).

(d) Connectivity effects

Static- and dynamic-habitat connectivity were tested through adding $S_{\text{m}}(t)$ and $S_{\text{p}}(t)$, respectively, in models supported with probabilities $\geq 0.05$ in the previous analyses (electronic supplementary material, table S1-B). The additive effect of $S_{\text{p}}(t)$ on the metapopulation dynamics was clearly supported by occupancy analyses ($\omega_i = 0.97$). The predictions from the final selected model (table 1) indicate that the cumulative effects of variability in seasonal productivity in two successive years have a strong impact on patch occupancy probability ($R^2(\omega) = 0.41$), especially in landscapes with a high number of potential connections to other patches (figure 2).

The separate analysis of colonization and extinction supported the effect of the dynamic connectivity on colonization probability ($\omega_i = 0.57$; table 1; electronic supplementary material, table S1-B). The inclusion of $S_{\text{m}}(t)$ instead of $S_{\text{p}}(t)$ always resulted in poorer models, thus confirming the primary role of the course of primary productivity at $t = 1$. On the other side, effects on extinction were highly uncertain; although the highest-ranked extinction model included $S_{\text{p}}(t)$, all the competing models showed a similar degree of support (electronic supplementary material, table S1-B).

Figure 3 shows the results of fitting $S_{\text{ij}}$ against $S_{\text{mi}}$ and $S_{\text{ij}}$, respectively, for the subsample of 38 habitat patches. Linear mixed models confirmed that both relationships were significant ($p < 0.001$) although weighting landscape connectivity by productivity fluctuations captured better the spatial pattern of connections among occupied patches ($\log(\hat{C}) = -596.9$) than the ‘static-habitat’ connectivity index ($\log(\hat{C}) = -624.4$; $\Delta\text{AICc} = 55.0$).

4. Discussion

We found support for the hypothesis that spatio-temporal population dynamics were linked to inter-annual variability in the course of primary productivity, and specifically in the seasonal levels and duration of the productivity pulse preceding the summer energy bottleneck period. This finding was
best captured by the habitat occupancy analyses (table 1): productivity in spring and the date of the end of the growing season explained temporal variations in the incidence of *A. sapidus* within the habitat network.

The results are important because they show that fluctuations in ecosystem functioning can play a major role in regulating the habitat quality of spatially structured populations. Food limitation has been postulated as a key control on the rates and temporal distribution of reproduction and offspring survival in small herbivores, especially in rodents [48–50]. In addition, the course of primary productivity in Mediterranean ecosystems typically displays pronounced seasonality associated with the decoupled distribution of precipitation and high temperatures, the summer water deficit being the critical control of vegetation activity. Thus, a later end of the productivity season extends the favourable habitat conditions for the reproduction of herbivores before the summer bottleneck. This extension would have particularly important effects on the population growth of fast-living species with early sexual maturation like *A. sapidus* [42], resulting in a higher number of newborn individuals reaching sexual maturation within the same breeding season, and thus in a larger reproductive pool. Therefore, our finding that habitat occupancy increases with a later-ending and more productive
This study provides empirical evidence on the effects of habitat dynamics on connectivity in a natural metapopulation. We found that accounting for the course of primary productivity in the previous year significantly increased the capacity of connectivity metrics to predict habitat colonizations and occupancies. Furthermore, the dynamic connectivity index \( S_{i(t-1)} \) fitted better the incidence–function connectivity index—as calculated from observed occupancies \( S_i \)—than an alternative static-landscape index calculated only on the basis of the size and spatial arrangement of the habitats \( S_j \). In other words, the effects of connectivity were best captured by the interactions between habitat-quality fluctuations and the geometry of the network (figure 1). It must be emphasized that the connectivity–occupancy relationship has been scarcely examined for natural metapopulations in fluctuating environments, despite this relationship is the defining driver of the dynamics of metapopulations. However, using simulation modelling, Ellner & Fussman [20] showed that failing to incorporate a ‘patch-dynamics’ perspective had major consequences for predicting metapopulation persistence in the context of successional habitat dynamics. Similarly, Visconti & Elkin [52] advocated for the inclusion of habitat-quality estimates into connectivity metrics in order to determine the contribution of individual patches to metapopulation persistence in fluctuating environments. Hodgson et al. [25] cautioned that metapopulation studies based on time-averaged or snapshot species distribution data may actually underestimate the effect of connectivity on occupancy patterns, because they overlook potentially important changes in the connectivity structure of the network. Our results not only confirm the importance of accounting for temporal habitat heterogeneity for predicting connectivity; they also illustrate a probably common phenomenon in nature in which temporal changes in connectivity may emerge from typical environmental variability affecting the quality of the patches.

The relationship between previous-year primary productivity and occupancy probability also points out a mechanism for carry-over effects on the population dynamics: the rate of patch occupancy was influenced by habitat dynamics operating for at least two consecutive years. This effect entails a dramatic increase in the predicted occupancy rates in a given habitat in time (figure 2). For some landscape configurations, we predicted within-patch differences in the probability of habitat occupancy of up to \( \Delta p > 0.5 \) depending on whether the two previous years were ‘good’ or ‘bad’, respectively, in terms of primary productivity (i.e. area between upper green and lower red lines in figure 2). Hence, cycles of favourable or unfavourable conditions maintained over 2 years would dramatically amplify local population growths and declines. This has important consequences for predicting metapopulation persistence. For example, climate projections indicate that rising temperatures will result in shifts in vegetation phenology in Mediterranean environments, with earlier and longer-lasting summer drought periods [53,54], meaning that populations of primary consumers like A. sapidus would be subject to longer periods of lower habitat-quality conditions, making them more vulnerable to extinction. We argue that a better understanding on the relationships between climate patterns, variability in primary productivity and consumer population regulation is paramount for predicting the propagation of climate change effects through trophic regulation mechanisms.

In this study, we have focused on the bottom-up effects of variability in primary productivity on a small herbivore metapopulation. It is well known that bottom-up processes affecting small mammals can be severely modified by top-down regulation from predators [55]. Indeed, experimental studies in different vole species have shown that introduced predators can suppress population growth in local habitats through interfering with trophic regulation processes. However, the impact of this local suppression on the colonization–extinction dynamics at the metapopulation level was less obvious [56,57]. We found that local extinction events were strongly associated with habitat size, whereas the effect of primary productivity fluctuations was comparatively much smaller. It can be speculated that, with more than 30 potential predator species sporadically consuming A. sapidus [58], predation could have a significant impact on the local probability of extinction depending on the habitat size, as the extirpation of fewer individuals would drive extinction in smaller populations. However, assessing simultaneously the temporal effects of top-down and bottom-up forces on spatially structured populations remains highly challenging, especially in natural systems with different species of coexisting predators.

5. Conclusion

We proposed a novel approach for assessing habitat dynamics and bottom-up regulation processes in the context of spatially structured populations by examining the variability in ecosystem-level indicators related to the rates and phenology of primary productivity. Using long-term metapopulation data, we showed that fluctuations in primary productivity can dramatically increase the variability of habitat occupancy rates in fragmented landscapes, an aspect that a more traditional focus on networks of (presumably) static habitat patches would have not detected. The course of primary productivity preceding the energy bottleneck period also determined annual variations in the degree of connectivity to other suitable patches, suggesting the existence of lagged metapopulation responses to previous year’s conditions. Understanding the effects of primary productivity fluctuations on fragmented
herbivore populations is important because they link potential changes in species habitats with ecosystem degradation processes, such as those resulting from climate change.

Data accessibility. The datasets supporting this article can be accessed in the following digital repository: http://dx.doi.org/10.5061/dryad.vn6esn.

Authors’ contributions. N.F. and M.D. conceived the study. N.F., J.R. and M.D. designed the study. J.R. acquired field data. N.F. analysed remote-sensing data, designed and performed all analyses, and wrote the manuscript. All authors contributed to revisions and gave final approval for publication.

Competing interests. We have no competing interests.

Funding. This study was funded by the Excellence Research Program of Junta de Andalucía, project no. RNM-6685.

Acknowledgements. We thank comments from M. Clavero and two anonymous referees on earlier versions of the manuscript, and the advice and discussions with J. M. Paruelo and E. Revilla during the design of the study. J. Calzada, J.C. Rivilla and G. Ruiz contributed with data collection.

References

1. McNaughton SJ, Oesterheld M, Frank DA, Williams KJ. 1989 Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341, 142 – 144. (doi:10.1038/341142a0)
2. Hopcraft JGC, Olff H, Sinclair ARE. 2010 Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends Ecol. Evol. 25, 119 – 128. (doi:10.1016/j.tree.2009.08.001)
3. Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC. 2008 Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Phil. Trans. R. Soc. B 363, 2359 – 2368. (doi:10.1098/rstb.2007.2206)
4. Sinclair ARE, Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Arcese P. 2000 What determines phenology and synchrony of ungulate breeding in Serengeti? Ecology 81, 2100 – 2111. (doi:10.1890/0012-9658(2000)081[2100:WDPOAV]2.0.CO;2)
5. Mueller T. 2011 Predicting and explaining local patterns of species richness. Oecologia 164, 135 – 149. (doi:10.1007/s00442-010-1733-4)
6. Wittemyer G, Rasmussen HB, Douglas-Hamilton I. 2012 An exploration of habitat-scale plant phenology to alpine reindeer body mass. Biol. Lett. 1, 24 – 26. (doi:10.1098/rsbl.2004.0262)
7. Texeira M, Baldi G, Paruelo J. 2012 An exploration of primary environmental gradients in savannas. J. Anim. Ecol. 81, 151 – 162. (doi:10.1111/j.1365-2664.2011.05591)
8. Mortelliti A, Amori G, Boitani L. 2010 The role of habitat quality in fragmented landscapes: a conceptual overview and prospects for future research. Oecologia 163, 535 – 547. (doi:10.1007/s00442-010-1623-3)
9. Thomas CD, 1994 Extinction, colonization, and metapopulations: environmental tracking by rare species. Conserv. Biol. 8, 373 – 378. (doi:10.1046/j.1523-1739.1994.008020373.x)
10. Van der Hegge B, Van Geeresteijn W, Van Dijk R. 2007 Metapopulation responses to patch connectivity and quality are masked by successional habitat degradation. Landscape Ecol. 22, 35 – 46. (doi:10.1007/s10101-004-0093-z)
11. Thomas CD, 2002 Transient dynamics in metapopulation response to perturbation. Theor. Popul. Biol. 61, 285 – 295. (doi:10.1006/tplb.2002.1586)
12. Hodgson JA, Mollan An, Wintle BA, Thomas CD. 2011 Habitat area, quality and connectivity: striking the balance for efficient conservation. J. Appl. Ecol. 48, 148 – 152. (doi:10.1111/j.1365-2664.2010.01919.x)
13. Fleishman E, Roy C, Sjögren-Gulve P, Boggs CL, Murphy DP. 2002 Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conserv. Biol. 16, 706 – 716. (doi:10.1046/j.1523-1739.2002.00539.x)
14. Schooley RL, Branch LC. 2009 Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. Ecol. Appl. 19, 1708 – 1722. (doi:10.1890/08-2169.1)
15. Jaquiey J, Guelet J, Broquet T, Berset-Breandli L. 2011 The role of habitat quality and connectivity in fragmented landscapes. Oecologia 166, 235 – 248. (doi:10.1007/s00442-011-1835-8)
16. Hodgson JA, Mollan A, Thomas CD. 2009 Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. Ecology 90, 1608 – 1619. (doi:10.1890/08-1227.1)
17. Pereira JS et al. 2007 Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeochemistry 4, 371 – 802. (doi:10.1149/b-4-791-2007)
18. Taylor KA, Smith WK, Zager P, Bonenfant C. 2014 Habitat-quality effects on metapopulation dynamics in northern forest. Phil. Trans. R. Soc. B 369, 683 – 694. (doi:10.1098/rstb.2013.0396)
19. Fedriani J, Delibes M, Ferreras P, Roman J. 2002 Local and landscape habitat determinants of water exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 21, 371 – 402. (doi:10.1149/b-4-791-2007)
20. Muller L et al. 2011 How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Glob. Ecol. Biogeogr. 20, 683 – 694. (doi:10.1111/j.1466-8238.2010.00638.x)
21. Fedriani J, Delibes M, Ferreras P, Roman J. 2002 Local and landscape habitat determinants of water exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 9, 791 – 802. (doi:10.1149/b-4-791-2007)
22. Thomas CD. 1994 Extinction, colonization, and metapopulations: environmental tracking by rare species. Conserv. Biol. 8, 373 – 378. (doi:10.1046/j.1523-1739.1994.008020373.x)
23. Wimberly MC. 2006 Species dynamics in disturbed landscapes: when does a shifting habitat mosaic enhance connectivity? Landsc. Ecol. 21, 35 – 46. (doi:10.1007/s11284-005-0093-2)
24. Ovaskainen O, Hanski I. 2002 Transient dynamics in metapopulation response to perturbation. Theor. Popul. Biol. 61, 285 – 295. (doi:10.1006/tpb.2002.1586)
25. Fedriani J, Delibes M, Ferreras P, Roman J. 2002 Local and landscape habitat determinants of water exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 9, 791 – 802. (doi:10.1149/b-4-791-2007)
26. Fedriani J, Delibes M, Ferreras P, Roman J. 2002 Local and landscape habitat determinants of water exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 9, 791 – 802. (doi:10.1149/b-4-791-2007)
27. Taylor KA, Smith WK, Zager P, Bonenfant C. 2014 Habitat-quality effects on metapopulation dynamics in northern forest. Phil. Trans. R. Soc. B 369, 683 – 694. (doi:10.1098/rstb.2013.0396)
28. Fedriani J, Delibes M, Ferreras P, Roman J. 2002 Local and landscape habitat determinants of water exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 9, 791 – 802. (doi:10.1149/b-4-791-2007)
29. Taylor KA, Smith WK, Zager P, Bonenfant C. 2014 Habitat-quality effects on metapopulation dynamics in northern forest. Phil. Trans. R. Soc. B 369, 683 – 694. (doi:10.1098/rstb.2013.0396)
30. Fedriani J, Delibes M, Ferreras P, Roman J. 2002 Local and landscape habitat determinants of water exchange in three contrasting Mediterranean ecosystems—the effect of drought. Biogeosciences 9, 791 – 802. (doi:10.1149/b-4-791-2007)
vole distribution in a patchy Mediterranean environment. Ecoscience 9, 12 – 19.

32. Centeno-Cuadros A, Román J, Delibes M, Godoy JA. 2011 Prisoners in their habitat? Generalist dispersal by habitat specialists: a case study in southern water vole (Arvicola sapidus). PlaS ONE 6, e24613. (doi:10.1371/journal.pone.0024613)

33. Monteith JL. 1972 Solar-radiation and productivity in tropical ecosystems. J. Appl. Ecol. 9, 747 – 766. (doi:10.2307/2401901)

34. Ruimy A, Saugier B, Dedieu G. 1994 Methodology for the estimation of terrestrial net primary production from remotely sensed data. J. Geophys. Res. Atmos. 99, 5263 – 5283. (doi:10.1029/93JD03221)

35. Paruelo JM, Epstein HE, Lauenroth WK, Burke IC. 1997 ANPP estimates from NDVI for the Central Grassland region of the United States. Ecology 78, 953 – 958. (doi:10.1890/0012-9658(1997)078[0953:AEFFT]2.0.CO;2)

36. Huete A, Didan K, van Leeuwen W, Miura T, Glenn USDA. 2002–2006. New York, NY: Springer Science + Business Media.

37. White MA et al. 2009 Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982 – 2006. Glob. Change Biol. 15, 2335 – 2359. (doi:10.1111/j.1365-2486.2009.01910.x)

38. Anderson DR. 2008 Model based inference in the life sciences: a primer on evidence. New York, NY: Springer Science + Business Media.

39. Zuur AE, Ieno EN, Walker NJ, Saveliev AA, Smith GM, Ebooks Corporation. 2009 Mixed effects models and extensions in ecology with R. New York, NY: Springer Science + Business Media.

40. Dormann CF et al. 2007 Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609 – 628. (doi:10.1111/j.2007.0906-7959.05171.x)

41. Nathan R, Klein E, Robledo-Amorugo JJ, Revilla E. 2012 Dispersal kernels: review. In Dispersal ecology and evolution (eds J Clobert, M Baguette, T Benton, JM Bullock), pp. 187 – 210. Oxford, UK: Oxford University Press.

42. Román J. 2007 Historia natural de la rata de agua (Arvicola sapidus) en Doñana. PhD thesis, University of León, León, Spain.

43. Fernández N. 2005 Spatial patterns in European rabbit abundance after a population collapse. Landsc. Ecol. 20, 897 – 910. (doi:10.1007/s10980-004-3976-7)

44. Gómez-Rodríguez C, Díaz-Paniagua C, Bustamante J. 2011 Cartografía de las lagunas temporales del Parque Nacional de Doñana. Sevilla, Spain: Agencia Andaluza del Agua, Consejería de Medio Ambiente.

45. R Development Core Team. 2015 R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

46. SAS. 2011 The role of the southern water vole Arvicola sapidus in the diet of predators: a review. Mamm. Rev. 45, 30 – 40. (doi:10.1016/j.molint.2015.10.017)