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Spread rates on fragmented landscapes: the interacting roles of demography, dispersal and habitat availability

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ABSTRACT

Aim We still lack a comprehensive understanding of the relative importance of demographic, dispersal and landscape characteristics on species' rates of range expansion (RRE) and on how these factors interact. Here, we provide an analysis of these effects for passive dispersers, by investigating how habitat characteristics, such as habitat quality, availability and fragmentation, interplay with species' dispersal characteristics in determining species' RRE. In addition, we assessed the predictability of RRE in cases where we have the knowledge of a species' demography, dispersal and habitat availability.

Methods Using the newly available individual-based modelling platform, RANGESHIFTER we simulated the range expansion of species with different dispersal abilities, by varying mean dispersal distance and number of emigrants, on various landscapes. Landscapes varied in habitat quality (in terms of carrying capacity and species' growth rates) and in habitat availability (in terms of the proportion of suitable habitat and its degree of fragmentation).

Results Our results show that 55% of the total variation in RRE was explained by our six main effects, being considerably faster in landscapes with more suitable habitat, but only slightly affected by the degree of habitat fragmentation. Also, synergies between the amount of suitable habitat and species dispersal characteristics had significant positive effects on range expansion. Notably, however, 33% of variation in RRE was not explained by any of the tested factors or interactions between them and can be considered inherent and irreducible uncertainty.

Main conclusions Simulation-based approaches provide important insights into the drivers of RRE that are relevant for conservation planning. For instance, our results indicate when it is likely to be better to allocate resources to improve existing habitat rather than creating new habitat, and vice versa. Additionally, our results emphasize that there will often be substantial uncertainty in the RRE, which needs to be taken into account for ecological management.

Keywords
dispersal, habitat fragmentation, habitat quality, individual-based model, range expansion, spatially explicit.

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INTRODUCTION

Understanding and predicting how species will spread across landscapes have become major goals within spatial ecology (Hastings *et al.*, 2005). Substantial effort related to these broad goals focuses both on the range expansion of invasive species (With, 2002; Jongejans *et al.*, 2008; Miller & Tenhumberg, 2010) and on native species shifting their distributions into newly suitable climate space (Dullinger *et al.*, 2012; Pagel & Schurr, 2012; Steenbeek *et al.*, 2016). Classic theory on the rate

of spread of expanding populations has illustrated the importance of reproductive rate and dispersal (Skellam, 1951; see Hastings *et al.*, 2005); indeed, these are the two key processes driving the spread rates predicted by many models, including many that are widely used in a predictive context today (e.g. Jongejans *et al.*, 2011; Leroux *et al.*, 2013; Matlaga & Davis, 2013; Zhou & Kot, 2013). Many of these models make the simplifying assumption of a homogenous landscape. Clearly, for most species this is unrealistic, especially in increasingly anthropogenically modified landscapes. There is a general expectation that species will spread less rapidly over landscapes with less habitat cover (Schwartz, 1993; Collingham & Huntley, 2000; With, 2002; Dewhirst & Lutscher, 2009; but see Bocedi *et al.*, 2014a) and that, when the amount of habitat is above the extinction threshold, higher fragmentation could enhance range expansion, especially for species with good dispersal abilities (McInerny *et al.*, 2007; Hodgson *et al.*, 2012). However, we still lack a robust body of theory that makes clear predictions as to how the amount and spatial arrangement of suitable habitat will influence species' spread rates.

Theory on the spatial spread of populations across homogenous landscapes is well developed, and, in the main, this knowledge has been acquired by analytical modelling approaches. As long ago as the 1950s, Skellam (1951) demonstrated that, assuming indefinite or logistic growth and random displacement, populations would achieve an equilibrium spread rate determined solely by the intrinsic growth rate and the mean square dispersal per generation. Amongst many insights generated by further mathematical modelling of range expansions that have built on Skellam's pioneering work, key ones include the following: the demonstration that fat-tailed dispersal kernels generate faster and potentially ever-accelerating spread rates (Kot *et al.*, 1996); that Allee effects can substantially reduce spread rates (Veit & Lewis, 1996; Keitt *et al.*, 2001; Tobin *et al.*, 2009); that ignoring stage structure, whereby different population stages contribute differently to demographic and dispersal processes, can result in substantial overestimation of spread rates (Neubert & Caswell, 2000; Clark *et al.*, 2001); and, most recently, that intraspecific phenotypic variability, in terms of growth and dispersal rates, can increase spread rates, especially in temporally variable environments (Elliott & Cornell, 2012, 2013; Meeker, 2013).

This theory has provided an improving understanding of how a species' life history characteristics, including dispersal and interindividual variability, and environmental stochasticity, influence spread rates across homogenous landscapes. However, we currently have far less understanding of how rates of population spread will be impacted by habitat loss and fragmentation and how the extent of the impact will depend upon a species' demographic and dispersal attributes. Taking a reaction–diffusion approach, Shigeseda *et al.* (Shigesada *et al.*, 1986; Shigesada & Kawasaki, 1997) explored the spread rate of a species characterized by periodic variation in either diffusivity or growth rate. They established that, at least for this stylized environmental variability, the rate of spread is provided by the geometric mean of the rates of spread in the different environments. Notably, very recent extensions of the integro-difference modelling approach are also showing considerable promise in terms of including spatial heterogeneity (Gilbert *et al.*, 2014a,b; Harsch *et al.*, 2014; Musgrave & Lutscher, 2014), although here again the environmental variability is highly stylized, most often assumed to be periodic. For instance, Gilbert *et al.* (2014a) developed second-order approximations to wave speeds for non-homogeneous landscapes; Gilbert *et al.* (2014b) demonstrated the importance of choosing adequate dispersal kernels to study the relationship between landscape structure and spread rates, and Harsch *et al.* (2014) noted that in a moving habitat model the speed at which patches move can influence population growth rates and survival, as well as influence the importance of fecundity and the effects of long-distance dispersal. As these analytical approaches develop, we can also make complementary use of spatially explicit simulation modelling to gain additional insights into how habitat loss and fragmentation will influence spread rates.

Simulation models, both patch occupancy (With, 2002; e.g. Travis, 2003; McInerny *et al.*, 2007) and individual-based (Hodgson *et al.*, 2012; Bartoń & Hovestadt, 2013; Watkins *et al.*, 2015), have already been used to investigate the spread of populations across fragmented landscapes. Mostly, this has been for tactical applications (e.g. Higgins *et al.*, 1996; Smith *et al.*, 2002), although there is also an increasing number of examples where simulations have been used strategically to develop theory (e.g. With, 2002; McInerny *et al.*, 2007; Dewhirst & Lutscher, 2009; Pachepsky & Levine, 2011; Hodgson *et al.*, 2012). Tactical models have provided valuable information in the context of management strategies for particular invasive species (Smolik *et al.*, 2010; Travis *et al.*, 2011), understanding how well-connected habitat patches are for threatened species (e.g. Kanagaraj *et al.*, 2013; Aben *et al.*, 2014) and for the development of corridors and stepping stones for species of conservation concern (e.g. Landguth *et al.*, 2012; Watkins *et al.*, 2015). In addition, they have provided insights into the spread of species under climate change (e.g. Willis *et al.*, 2009; Cobben *et al.*, 2012). Strategic modelling has helped advance generic understanding of range expansions, showing, for example, that there is likely to be a nonlinear relationship between spread potential and habitat availability (With, 2002); that spread rates may, for a given amount of habitat available, sometimes be faster when habitat is more fragmented and the average gap size between patches is smaller (McInerny *et al.*, 2007); and that, in fragmented landscapes, carrying capacity as well as growth rate can have an important role (e.g. Bocedi *et al.*, 2014a). While we have increasing understanding of how different factors influence range expansions across landscapes, one aspect that remains quite poorly considered is the relative importance of demographic parameters, dispersal parameters and landscape characteristics on the rate of spread and, additionally, on how these factors interact. Some recent work (Pachepsky & Levine, 2011) has already indicated that effects of intraspecific competition can slow the spread of plant populations through patchy

landscapes, by influencing how fast a population produces enough seeds to surpass gaps between habitat patches. This highlights the importance of interactions between demography and landscape heterogeneity in driving spread rates across patchy landscapes, emphasizing the need for greater effort to explore interacting effects.

Here, we use a newly available individual-based modelling platform, RANGESHIFTER (Bocedi *et al.*, 2014b), to examine how the rate of range expansion across patchy landscapes is determined by the amount and spatial pattern of suitable habitat, the reproductive rate and local carrying capacity of the species, and two key characteristics of dispersal, the emigration rate and the mean distance that emigrants travel. We seek general understanding on the relative roles of demographic, dispersal and landscape characteristics on driving the rate of expansion and examine whether there are important interactions between them. Additionally, we seek insight into how predictable are rates of range expansion (RRE), provided that we have good knowledge of a species' demography, dispersal and habitat availability.

METHODS

We used RANGESHIFTER v1.0 (Bocedi *et al.*, 2014b) to conduct a series of individual-based and spatially explicit simulations of a single species spreading across a set of landscapes varying in the amount of available habitat and spatial structure.

Using the landscape generator embedded within RANGESHIFTER v1.0, we created different binary landscapes of 129×257 cells at 100 m resolution, across which we applied five levels of the proportion of suitable habitat (p) and five levels of the degree of spatial autocorrelation (each combination was replicated 20 times, totalling 500 landscapes; Table 1). The first level of spatial autocorrelation was random (i.e. no autocorrelation); the remaining four levels were

fractal landscapes created using the midpoint displacement algorithm (Saupe, 1988), in which the degree of spatial autocorrelation was determined by the Hurst exponent (H).

The population model was an only-females model with non-overlapping generations. At each generation, individuals reproduced, adults then died and offspring dispersed or remained in their natal cell. The number of offspring M produced by a single individual in cell i at time t was drawn from a stochastic, individual-based formulation of Maynard Smith & Slatkin's (1973) population model:

$$M \sim \text{Poisson}\left(\frac{Rmax_{i,t}}{1 + (Rmax_{i,t} - 1) \times \left(\frac{N_{i,t}}{K_{i,t}} \right)^{b_c}} \right) \quad (1)$$

where $Rmax$ is the maximum growth rate, $K_{i,t}$ is the carrying capacity, $N_{i,t}$ is the current population size and b_c is the competition coefficient describing the type of density regulation. We assumed a compensatory density regulation ($b_c = 1$), which leads to the self-regulation of populations around carrying capacity (Münkemüller & Johst, 2007), and varied $Rmax$ and K (Table 1).

Dispersal in RANGESHIFTER v1.0 is explicitly modelled in three phases: emigration (the probability of an individual leaving its natal patch), transfer and settlement. We considered emigration to be passive and density independent, and therefore, the proportion of emigrants, *em,* remained constant throughout each simulation. The transfer of individual emigrants followed a negative exponential dispersal kernel with a mean dispersal distance, d, from which the distance travelled by each individual was sampled. The movement direction was sampled from a uniform distribution between 0 and 2π. The parameter d was also assumed to be constant during each simulation. However, both *em* and d were varied between simulations to simulate species with different dispersal traits. Settlement of the individuals in a new cell was determined by its suitability: if the arrival cell was unsuitable the dispersing individual died.

Simulations

To assess the potentially interacting effects of landscape characteristics and species attributes on species' RRE, we varied habitat availability (p), habitat fragmentation (H), habitat quality (in terms of its impact on the demographic parameters $Rmax$ and K) and dispersal abilities (*em* and d) in a fully factorial experimental design (Table 1, see Fig. S1 in Supporting Information). Preliminary simulations run with fixed $Rmax$ and K (at 3.0 and 40, respectively) for 1000 years indicated that, across combinations of habitat availability and fragmentation, and species dispersal characteristics, RRE reached its maximum and stabilized around 100 years of simulation. It then started decreasing after 250 years, as all available habitats became colonized. Hence, simulations were run for 130 years and each combination of factors was replicated 20 times. Populations were initialized across the entire

Table 1 Values of RANGESHIFTER v1.0 parameters applied in a fully factorial experimental design, comprising the proportion of suitable habitat (p), Hurst exponent (H), maximum growth rate ($Rmax$), carrying capacity (K), the proportion of emigrants (*em*) and mean dispersal distance (d). There were in total 2025 parameter combinations, each of which was run for 150 years and replicated 20 times. Correspondence to variable names used in RANGESHIFTER v1.0 is indicated between square brackets.

Landscape variables		Habitat quality variables		Dispersal ability variables	
p	H	$Rmax$ [R]	K	em [d]	d [δ]
0.05	Random				150
0.10	0.05	2.4	30	0.1	200
0.20 $\times$	0.10 $\times$	3.0 $\times$	40 $\times$	0.2 $\times$	250
0.40	0.15	3.6	50	0.3	300
0.50	0.20				350
					400

width of the landscape (129 cells), but only in the first 25 rows, allowing the species to expand upwards.

To obtain an estimate of the RRE at 100 years (by when expansions had obtained a quasi-equilibrium rate of spread), for each replicate, we calculated the slope of the linear regression between maximum vertical distance (*maximum y*) and time, using the *maximum y* from years 70 to 130, extracted at 10-year intervals. As some replicates suffered extinction before the 130th year, the number of replicates used to calculate the RRE (80,031) differed from the total number of replicates (81,000). Statistical analysis was focused on building linear models that could express the interactive effects of landscape, habitat quality and dispersal variables on species' RRE. We fitted the linear models in R v3.0.2 (R Core Team, 2013), and all explanatory variables were treated as factors. Model construction was accomplished by firstly including only the main effects; we then added within-group pairwise interactions, factor groups being: landscape variables (*p* and *H*), habitat quality variables (*Rmax* and *K*) and dispersal variables (*em* and *d*). Remaining pairwise interactions were then added and, finally, we added all three-way interactions. We also computed a fully factorial, six-way interaction model for comparison. In accordance with White *et al.* (2014), model fitting was primarily focused on accounting for explained variance in RRE.

RESULTS

Only a few populations became extinct before the end of the simulation (0.9% of the total number of replicates) and extinctions were more common in landscapes with low *p* and high *H*, probably due to inherent stochastic effects arising from the populations not being able to compensate demographically for poorly suitable and highly fragmented landscapes. Extinct populations were omitted from further analyses.

The total variance (adjusted R^2) in RRE explained by only the six main effects was 55%, which was slightly increased to 56% by addition of interaction terms within factor groups (landscape, habitat quality, dispersal ability), but substantially more to 66% by further addition of all other between-group two-way interactions (Table 2). However, further addition of all three-way interactions led to a negligible further increase, and even if all possible interaction terms were included, the total variance explained was 67%, that is stochasticity in the replication of randomly generated landscapes together with demographic and dispersal stochasticity accounted for roughly one-third of the variance in RRE. On that basis, interaction terms involving three or more factors were relatively unimportant and are not considered further.

By far, the most important factor in determining RRE was the proportion of suitable habitat in the landscape; in terms of its mean square value, it had almost threefold the effect of the next highest ranked factor (Table 3). The proportion of emigrants, *em*, and the carrying capacity of the landscape, *K*, were the next most important factors. The highest ranked interaction terms were those including the highest ranked

Table 2 Linear models used to explore the effect of the landscape (*p* and *H*), habitat quality (*Rmax* and *K*) and dispersal variables (*em* and *d*) on rate of range expansion (RRE). Model fit is shown as the adjusted R^2 ('adj. R^2'). Star symbols (*) between factors indicate that both the interaction and the main effects of the factors were included in the model (e.g. RRE = *p*H* is actually RRE = *p* + *H* + *p* × *H*), while 'd.f.' stands for the degrees of freedom.

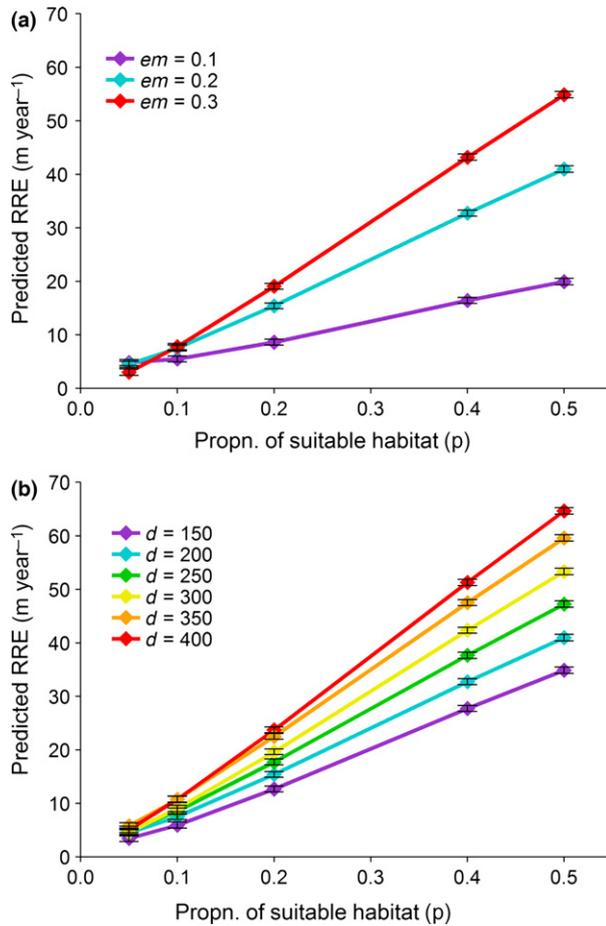| Model	Effects	d.f.	Adj. R^2
Main effects only	*p* + *H* + *Rmax* + *K* + *em* + *d*	19	0.554
Addition of within-group interactions	*p*H* + *Rmax*K* + *em*d*	49	0.560
Addition of all between-group interactions	All two-way interactions	165	0.661
Addition of all three-way interactions	All three-way interactions	765	0.668
Fully factorial	*p*H*Rmax*K*em*d*	4049	0.669

Table 3 General linear model of rate of range expansion including all two-way interaction terms (indicated by '×'). Terms in the model are ranked in order of decreasing mean square.

Term	d.f.	Sum squares	Mean square	F
p	4	20,442,475	5,110,619	23,731.8
em	2	3,649,760	1,824,880	8474.1
K	2	1,275,464	637,732	2961.4
p × *em*	8	2,694,309	336,789	1563.9
Rmax	2	606,184	303,092	1407.4
d	5	1,499,342	299,868	1392.5
H	4	706,535	176,634	820.2
p × *K*	8	640,467	80,058	371.8
p × *d*	20	1,123,100	56,155	260.8
p × *Rmax*	8	316,192	39,524	183.5
em × *Rmax*	4	108,086	27,021	125.5
em × *d*	10	198,645	19,864	92.2
em × *K*	4	79,284	19,821	92.0
K × *d*	10	88,984	8898	41.3
p × *H*	16	114,376	7149	33.2
Rmax × *d*	10	43,814	4381	20.3
K × *Rmax*	4	13,684	3421	15.9
em × *H*	8	20,748	2593	12.0
Rmax × *H*	8	4877	610	2.8
d × *H*	20	9580	479	2.2
K × *H*	8	3361	420	2.0

main effect *p*, that is *p* × *em*, *p* × *K*, *p* × *d* and *p* × *Rmax*, followed by those including the second highest ranked main effect, *em*, that is *em* × Rmax, *em* × *d* and *em* × *K*. Terms incorporating the degree of aggregation in the landscape (*H*) and interactions between dispersal distance (*d*) and the two habitat quality variables (*Rmax* and *K*) were mostly of relatively low importance; indeed, the effect of the degree of

aggregation was essentially limited to slightly higher RRE on the fractal landscapes than on the random landscapes, and H itself had negligible effect (see example in Fig. S2).

Invariably, RRE increased as p increased and the rate at which it did so increased with increasing values of both dispersal parameters, em and d (Fig. 1). When p was low (0.1 or less), RRE was always very low (typically <10 m year^{-1}) and it increased roughly in proportion to the increase in p. Increasing em from 0.1 to 0.2 had a greater effect on the rate of increase of RRE with increasing p than increasing em further from 0.2 to 0.3 (Fig. 1a), whereas constant increases in d resulted in a proportional increase in the response of RRE to p (Fig. 1b). When dispersal capability was at its highest ($em = 0.3$, $d = 400$ m) and the proportion of suitable habitat was high ($P \geq 0.4$), RRE almost invariably exceeded 50 m year^{-1}, and at the highest value of $K = 50$, RRE could range up to 100 m year^{-1} (i.e. one cell per generation) (data not shown).

The effect of habitat quality on the increase in RRE with increasing p was similar whether it was implemented through the demographic parameters $Rmax$ or K (Fig. 2). For the highest value of p, decreasing $Rmax$ by 20% and increasing or decreasing K by 25%, relative to their intermediate values, produced changes in RRE of similar magnitude, whereas increasing $Rmax$ by 20% (relative to its intermediate value) had rather less effect, presumably owing to the effect of density dependence implemented in the fecundity model.

DISCUSSION

Individual-based simulations provide a complementary approach to analytical methods for providing insights into the dynamics of species range expansion. Here, we have taken advantage of a recently released simulation platform
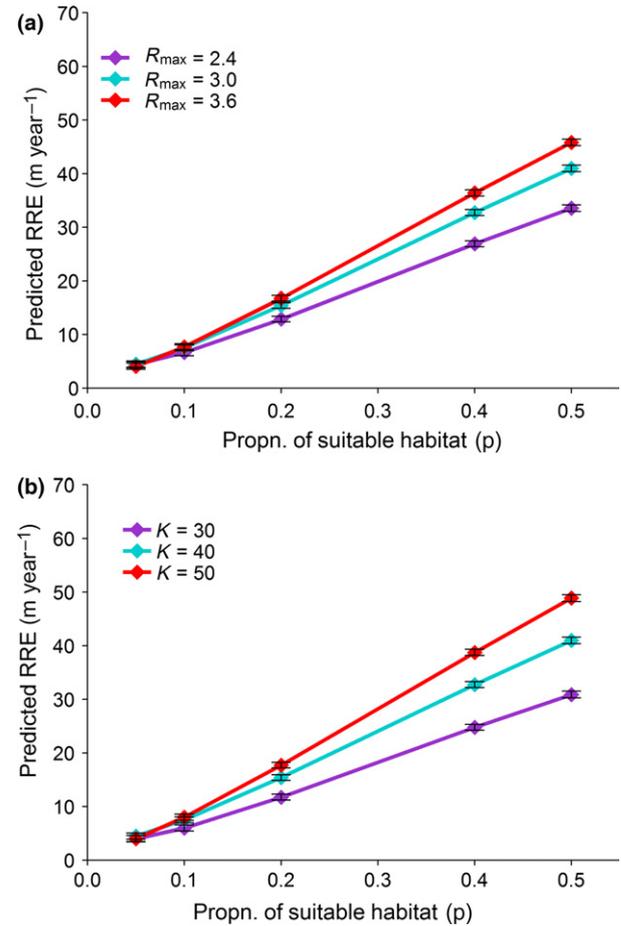

Figure 1 Interaction effects of the proportion of suitable habitat in the landscape p with dispersal parameters, (a) probability of emigration em and (b) mean of the negative exponential dispersal kernel d, on the predicted rate of range expansion (RRE). All other parameters are held constant: Hurst exponent $H = 0.1$, maximum growth rate $Rmax = 3.0$, carrying capacity $K = 40$ and in (a) $d = 200$ m, in (b) $em = 0.2$. Error bars show $\pm$ 1 SE. Colour figure can be viewed at wileyonlinelibrary.com

Figure 2 Interaction effects of the proportion of suitable habitat in the landscape p with habitat quality, (a) acting through maximum growth rate $Rmax$ and (b) acting through carrying capacity K, on the predicted rate of range expansion (RRE). All other parameters are held constant: Hurst exponent $H = 0.1$, emigration probability $em = 0.2$, mean dispersal kernel $d = 200$ m, and in (a) $K = 40$, in (b) $Rmax = 3.0$. Error bars show $\pm$ 1 SE. Colour figure can be viewed at wileyonlinelibrary.com

(RangeShifter; Bocedi *et al.*, 2014b) to explore the potentially interacting roles played by a species' demographic characteristics, its dispersal characteristics and the structure of the landscape in determining the rate of range expansion. Our results highlight important interactions, in particular between the proportion of habitat availability and both the demographic and dispersal characteristics, as well as emphasizing that there are inherent limits to predictability.

Our results confirm past studies that demonstrate the effects of increased dispersal ability, increased growth rate, increased carrying capacity and increased amount of habitat on rates of spread. However, they point out important interactions that may have substantial implications for conservation: notably, the interaction between the proportion of available habitat and the probability of emigration. By distinguishing between two types of dispersal parameters (probability of emigration and mean dispersal distance), we were able to disentangle their different effects on the RRE, especially when low proportions of habitat are available.

For instance, at low proportions of suitable habitat ($P < 0.2$), species range expansion does not seem to be increased with improvement of habitat quality, nor with increased numbers of emigrant individuals. In this case, only increases in the mean dispersal distance produced slightly faster range expansions (considering fairly low fragmentation levels, $H = 0.1$; Fig. 1b). This is in accordance with the study by Musgrave *et al.* (2015), who have shown that the percentage of hostile patches at which populations collapse can depend on individuals' movement behaviour, as introducing hostile patches can increase spread rates if individuals move fast enough.

We also found that for completely passive dispersers, as is the case of wind-dispersed seeds and some mites and spiders, the spatial arrangement of available habitat has a relatively minor effect on the projected rates of spread (at least relative to the amount of suitable habitat, its quality in terms of carrying capacity and growth rates and species' dispersal characteristics). Furthermore, the degree of habitat fragmentation did not show important interaction effects with either habitat quality parameters or species dispersal ability. For example, the interaction between dispersal parameters (such as the probability of emigrating) and landscape configuration is more important regarding proportion of available habitat than the degree of fragmentation. The effects of habitat fragmentation on plants and plant community dynamics are not always generalizable and may be weak in certain cases, and, in general, habitat aggregation may not fully compensate for low habitat quantity and quality (Hodgson *et al.*, 2011). For instance, habitat fragmentation was predicted to have only a slight effect on the expansion of the invasive biomass crop *Miscanthus × giganteus* when compared to the amount of suitable habitat and propagule pressure (Muthukrishnan *et al.*, 2015). However, the importance of habitat fragmentation will certainly be higher for species with active dispersal behaviour, whose dispersal kernels likely result from strong interactions between dispersal behaviour and landscape structure (Baguette & Dyck, 2007; Doerr *et al.*, 2010).

There is a lively current debate related to the relative importance of investing conservation resources in improving habitat quality, increasing the extent of suitable habitat or managing the matrix to improve the dispersal of organisms (Hodgson *et al.*, 2009; Mortelliti *et al.*, 2010; Doerr *et al.*, 2011a; Synes *et al.*, 2015). Results from simulations similar to those presented here can be useful in resolving this debate. For instance, although improving habitat quality is thought to lead to improvements in connectivity (Lawson *et al.*, 2012), being thus an important conservation strategy in terms of climate change (Hodgson *et al.*, 2009), we have not observed this phenomenon in our simulations of passively dispersing organisms. Rather, in situations where habitat quality is already above critical thresholds for species persistence, our results suggest that further improvement of habitat quality may not counterbalance the effect of highly fragmented landscapes, while increasing the proportion of available suitable habitat can (see Fig. S2). We note that this outcome can be quite different for active dispersers (see Bocedi *et al.*, 2014a), where interactions between dispersal behaviour and landscape configuration are likely to affect dispersal cost and effective dispersal distances. In addition, active dispersers are likely to be influenced not only by the degree of habitat aggregation but also by the structural connectivity between patches (Hilty *et al.*, 2006; Doerr *et al.*, 2011a,b). This raises challenges for designing conservation strategies focused on promoting the spread of species responding to climate change that work across species with very different behaviours, as the degree of habitat fragmentation and connectivity between patches will have different consequences depending on the dispersal behaviour of the species.

Importantly, the general approach that we have taken here can provide answers to key questions such as how much would the amount of suitable habitat need to be increased to provide the same benefit (in terms of increased RRE) as increasing the quality of existing habitat (in terms of, for example, species growth rate or habitat carrying capacity). As illustration of this, let us take the example presented in Fig. 2(a) and assume that the starting point is 20% habitat available (p), a habitat quality that results in a carrying capacity (K) of 40 individuals and our hypothetical species having a maximum growth rate ($Rmax$) of 3.0. Here, managing the existing habitat such that it increases $Rmax$ by 20% from 3.0 to 3.6 would yield an increase in RRE from approximately 17–18 m year^{-1}, while managing it to increase K from 40 to 50 would yield an increase to approximately 19 m year^{-1}. To gain an equivalent increase in RRE by increasing the extent of available habitat (assuming the additional habitat provides the same initial $Rmax = 3.0$ and $K = 40$) would require approximately 3% more of similarly suitable habitat. If the sole conservation objective was managing to optimize spread rates, the equation is then related to the relative costs and potential of improving the existing habitat compared to purchasing and managing the additional land. Although here we explored a set of hypothetical species, our approach can be used to investigate similar questions in real-world scenarios and help provide

guidelines for management (Fraser *et al.*, 2015; Sun *et al.*, 2016), provided that species demographic and dispersal parameters are known, or can be approximated. Alternatively, our approach can provide the range of possible outcomes for species range expansion using a set of demographic, dispersal and/or habitat parameters that vary within a plausible range obtained from existing data (Santini *et al.*, 2016; Sun *et al.*, 2016). Given that we may expect different species groups to respond in different ways, a major future challenge will be extending this general approach for assessing the relative merits of alternative interventions to work for multiple species (Synes *et al.*, 2015).

Notably, we find that around one-third of the overall variation in rates of range of expansion is not explained by the landscape characteristics, species demography, dispersal or interactions between them. Uncertainty in our results arises from differences between the generated artificial landscapes for a given set of landscape parameters and from stochasticity in the modelled demographic and dispersal processes. As in any modelling approach, stochastic processes were included to reflect natural unexplained variance that stems from unmeasured or unknown processes. Thus, we consider that the unexplained variance in our results represents irreducible uncertainty that is invariably encountered in empirical studies of RRE. This uncertainty arises from both the inherent stochasticity of species demography and dispersal, which can be particularly pronounced at expanding margins (Clark *et al.*, 2001; Travis *et al.*, 2011), as well as from idiosyncratic, stochastic variation of natural landscapes. In future work, it will be important to recognize that this inherent stochasticity places limits on predictability. Theory can usefully be developed to provide understanding of the conditions under which there will be greater inherent uncertainty in rates of expansion, while methods for effectively illustrating this inherent uncertainty when presenting results to stakeholders require development; moreover, we need a more active consideration of how this uncertainty influences conservation management planning.

Our study presents a first insight into how a species' range expansion dynamics are determined by a combination of demographic and dispersal characteristics together with properties of the landscape. In order to be able to disentangle the effects of the six tested variables, we have made a number of simplifying assumptions, such as assuming no stage structure, passive dispersal, no adaptive or evolutionary mechanisms and a static environment. However, we believe that these factors should be explored in future studies to expand on the theoretical clarifications that we provide here. Extending our approach to actively dispersing species will be important, as the effects of landscape configuration may change for these species and even affect their dispersal behaviour. Previous theoretical work has already shown that species settlement strategies will interact with habitat availability (Bocedi *et al.*, 2014a), and empirical studies have shown that movement speed (Barnes *et al.*, 2015) and movement probability (Vasudev & Fletcher, 2015) depend on habitat

characteristics. Considering the different dispersal capabilities across life stages and sexes is also likely to be relevant for many species. For instance, seed dispersal may lead to faster niche adaptation than pollen dispersal, when habitat heterogeneity and selection are not too strong (Aguilée *et al.*, 2013). Simulating pollen and seed dispersal separately is undoubtedly an interesting expansion to our study, which allows further decomposing dispersal into its different phases. Female-biased dispersal can also change the speed of range expansion by increasing it, especially if there are mating opportunities before females disperse to patches at leading edges (Miller & Inouye, 2013). Adaptation will also play an important role in species expansions, especially if dispersal capabilities are enhanced at leading edges (Fayard *et al.*, 2009; Travis *et al.*, 2010), and may have critical implications in face of environmental change (Dytham *et al.*, 2014). Although here we assumed that the species' rate of expansion is not limited by climate, we highlight the importance of developing theory for how ranges expand when a species is shifting its range due to a shift in an environmental gradient across fragmented landscapes. Both individual-based simulations (e.g. Mustin *et al.*, 2009; Dytham *et al.*, 2014) and recent analytical developments (e.g. Potapov & Lewis, 2004; Harsch *et al.*, 2014) have developed theory in this context. These studies have shown that population dynamics can influence range expansions under moving environmental gradients, with rates of colonization increasing the rate of range expansion (Mustin *et al.*, 2009). They have also shown that the speed at which suitable habitat patches become available can decrease the importance of survival characteristics of the species and increase the importance of fecundity and growth (Harsch *et al.*, 2014), while also increasing the critical patch size for species persistence (Potapov & Lewis, 2004).

However simplified our approach may be, existing theory has not considered the range of effects we have explored here. Future work is required to establish whether the relative importance of different effects and their interactions holds for expansions across environmental gradients and more complex population dynamics. In the context of recent calls for the development of approaches to improve our forecasts for species' distributions under climate change (Urban *et al.*, 2016), it is important that we focus not only on expanding fronts, but also consider the dynamics of range retraction. To date, there has been far less attention paid to the dynamics of retraction both for analytical and individual-based approaches, despite suggestions that negative rates of expansion can occur in populations with Allee effects in fragmented landscapes (Maciel & Lutscher, 2015) and that mismatches between species' local adaptations and climate optimums can also lead to decelerating rates of expansion (Mustin *et al.*, 2009). Future work should apply both approaches to address some key questions related to range retraction, including asking how the spatial lag of a species behind its 'climate envelope' depends upon demographic, dispersal and landscape characteristics. Such work can be very informative in helping to determine species and

landscape characteristics for which we are most likely to see extinction debts (i.e. species persist for some period in time in regions where, even in the absence of further environmental change, they are doomed to extinction); this information can be extremely valuable in guiding the allocation of scarce resources for conservation actions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Snapshots of model runs across landscapes with different degrees of fragmentation and different proportions of suitable habitat.

Figure S2 Effects of the interaction between the degree of habitat fragmentation and the proportion of suitable habitat on the predicted rate of range expansion, acting through different levels of habitat quality.

BIOSKETCH

Ceres Barros is motivated to explore how different species, communities and ecosystems are capable of adapting to and withstand environmental change. Although her work has spanned from using lichens as biomonitors for atmospheric pollution, to theoretical developments of behavioural models and, lately, understanding ecosystem stability under climate and land use changes from different perspectives, she mostly sees herself as an ecological modeller who is drawn to the study of ecosystem stability, resilience and adaptation to disturbances.

Author contributions: J.M.J.T., C.B. and S.C.F.P. conceived the ideas; C.B. conducted simulations and analysis; G.B. and S.C.F.P. developed the RANGESHIFTER software; C.B. led the writing of the manuscript, to which all authors contributed.

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