

APPLICATION

RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes

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Summary

1. Rapid environmental changes are threatening biodiversity and exposing species to novel ecological and evolutionary pressures. The scientific community increasingly recognizes the need for dynamic models integrating sufficient complexity both to improve our understanding of species' responses to environmental changes and to inform effective management strategies.
2. Using three illustrative examples, we introduce a novel modelling platform, RangeShifter, which integrates complex population dynamics and dispersal behaviour, includes plastic and evolutionary processes and simulates scenarios on spatially explicit landscapes. The software provides functionality for a wide variety of modelling applications ranging from applied questions, where it can be parameterized for real landscapes and species to compare alternative potential management interventions, to purely theoretical studies of species' eco-evolutionary dynamics and responses to different environmental pressures.
3. RangeShifter provides an important tool for facilitating the advancement of ecological theory on species' spatial dynamics in response to environmental changes, and linking it directly to application in biodiversity conservation.

Key-words: dynamic modelling, individual-based modelling, environmental change, dispersal, population dynamics, connectivity, population viability

Introduction

Habitat loss, habitat fragmentation and climate change constitute major threats to species persistence, exposing species to novel ecological and evolutionary pressures and challenging conservation biologists to develop mitigation strategies (Loarie *et al.* 2009; Dawson *et al.* 2011). A concerted effort by the ecological and evolutionary communities aims to understand how we should expect species to respond to rapid environmental changes and where and how we should intervene. Clearly, understanding how complex eco-evolutionary systems will respond to environmental drivers requires modelling species' spatial dynamics by integrating demography, dispersal and eco-evolutionary processes. The correlative species distribution models, which have dominated the recent literature, are, by themselves, insufficient, and there is a major demand for integrated dynamic models (Guisan & Thuiller 2005; Franklin 2010; Huntley *et al.* 2010; Schurr *et al.* 2012; Thuiller *et al.* 2013).

A dynamic model of species' responses to climate change should incorporate demography and dispersal at its core. A growing body of theoretical and empirical studies has highlighted these as two key processes for determining how species will respond to rapid changes through range shifting or through adaptation enabling local persistence. Dispersal and demography are vital for determining survival in fragmented landscapes, where the capability of individuals to disperse between small subpopulations allows the system to function as a viable metapopulation. Moreover, they are the main drivers of the speed of a species' range expansion into newly suitable areas (Neubert & Caswell 2000; Clark, Lewis & Horvath 2001). Demographic and dispersal traits often vary between individuals, and according to local population density and environmental conditions. They are also likely to be influenced by environmental changes and evidence for both plastic and evolutionary responses is accumulating (Travis *et al.* 2013).

Substantial progress in understanding the causes and consequences of dispersal has occurred over recent decades (Clobert *et al.* 2012). Dispersal is now recognized to comprise three dis-

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tinct phases, emigration, transfer and settlement (Clobert *et al.* 2009, 2012). Theory clearly demonstrates that the details of these phases may strongly influence the potential spread rate of a species and also highlights that behavioural rules associated with them can come under strong selection during range shifts (Bartoń *et al.* 2012). However, while a framework for modelling eco-evolutionary dispersal dynamics accounting for these distinct phases has been developed (Travis *et al.* 2012), there are no existing modelling platforms for simulating this degree of complexity, either to predict species responses to climate change, or generally for tackling spatial ecological and evolutionary questions.

In parallel with the progress in understanding dispersal has been a substantial advance in movement ecology (Nathan *et al.* 2008; Morales *et al.* 2010; Jeltsch *et al.* 2013). We now have much greater ability to obtain and analyse movement data and to model how organisms move in complex environments (Cagnacci *et al.* 2010; Morales *et al.* 2010). Movement is key to the transfer phase of dispersal and a natural way to meet the major outstanding challenge of integrating movement modelling with population dynamics (Morales *et al.* 2010) is through the dispersal modelling framework recently proposed (Travis *et al.* 2012).

A major division has existed between the approaches employed for modelling local-scale population responses to landscape changes, such as habitat fragmentation, and those for modelling large-scale distributional responses to climate change. Population viability analyses (Pe'er *et al.* 2013) and metapopulation modelling (Hanski & Ovaskainen 2000, 2003) approaches for determining the persistence of species in fragmented landscapes have incorporated, to differing degrees, both population dynamics and dispersal. In contrast, broad-scale projections of species' responses to climate change are largely based on static species distribution models (SDMs), which regress current distributions on climate, and then project future distributions from future climate scenarios (Elith & Leathwick 2009). However, there is now substantial interest in integrating these two approaches to provide a more mechanistic understanding and predictive capability of how species will respond to potentially interacting environmental drivers (Huntley *et al.* 2010; Schurr *et al.* 2012; Conlisk *et al.* 2013; Thuiller *et al.* 2013). Integrating SDMs with process-based models for species' range dynamics will undoubtedly open new opportunities to improve our understanding of how species are likely to respond to combined pressures (Dormann *et al.* 2012).

An individual-based modelling (IBM) approach (Grimm & Railsback 2005) holds much appeal for dynamic modelling of species' responses to environmental changes for two important reasons. First, individuals may vary in their key demographic and dispersal traits. This variability, which may be due to heritable differences, environmental heterogeneity or both, may play an important role in determining eco-evolutionary population-level responses. Secondly, local populations in fragmented landscapes or at range margins are frequently small. Here, demographic stochasticity is significant; for example, modelling stochastic processes at the individual level is crucial to avoid overestimation of spread rate (Clark, Lewis &

Horvath 2001). An IBM approach accounts for the role of demographic and dispersal stochasticity and facilitates the incorporation of individual variation in life-history traits, behaviours and genetics. While IBMs have been used successfully for theory development [e.g. on causes and consequences of dispersal (Clobert *et al.* 2012)] and for (typically localized) species-specific tactical models (Grimm & Railsback 2005), their application in multi-purpose, multi-scale simulation modelling for investigating species' responses to environmental changes is still in its infancy.

In response to recent calls for moving towards integrated dynamic modelling approaches (Franklin 2010; Huntley *et al.* 2010; Schurr *et al.* 2012; Thuiller *et al.* 2013), we developed RangeShifter, a novel dynamic modelling platform for investigating species' spatial dynamics, which provides flexibility in terms of its spatial extent and resolution, and in the degree of complexity incorporated in representing different processes. The RangeShifter software is unique in at least two key respects: it includes the capability for much greater realism in modelling the dispersal process and, as an IBM, allows for inter-individual variability and accounts for potentially key stochasticities in demographic, dispersal and evolutionary processes. RangeShifter offers possibilities for a broad range of simulation-based modelling experiments, from fundamental theoretical investigations of eco-evolutionary dynamics, to strategic modelling of management options and real species' range dynamics. The software is coded in C++ and packaged as a freely available, standalone application for Microsoft Windows (Appendix S1). A graphical user interface facilitates initial model exploration and is suitable also for demonstrations and teaching purposes. However, RangeShifter can also be run in batch mode for complex and computationally demanding simulations. Here, we describe the general structure of the model and demonstrate its capabilities with three examples. For a detailed description of the model, we refer to the RangeShifter v1.0 user manual (Appendix S2) and to Appendix S3.

Model description

RangeShifter is an individual-based, spatially explicit and stochastic dynamic model (Fig. 1a). At its core is the integration of population dynamics and dispersal. The model runs over grid-based landscapes, which can be land-cover maps, habitat suitability maps or artificial maps produced by an embedded landscape generator. Initial species' distribution data can be imported. An environmental gradient impacting population dynamics can be superimposed on the landscape and the gradient can be shifted through time to simulate climate change. Temporal environmental stochasticity in population growth rate or in carrying capacity can be included, allowing for different degrees of temporal autocorrelation at either global or local scale.

The population dynamics module provides options for different levels of complexity, details and rationale (Fig. 1b). The population can have discrete generations or it can be stage-structured (overlapping generations). For stage-structured

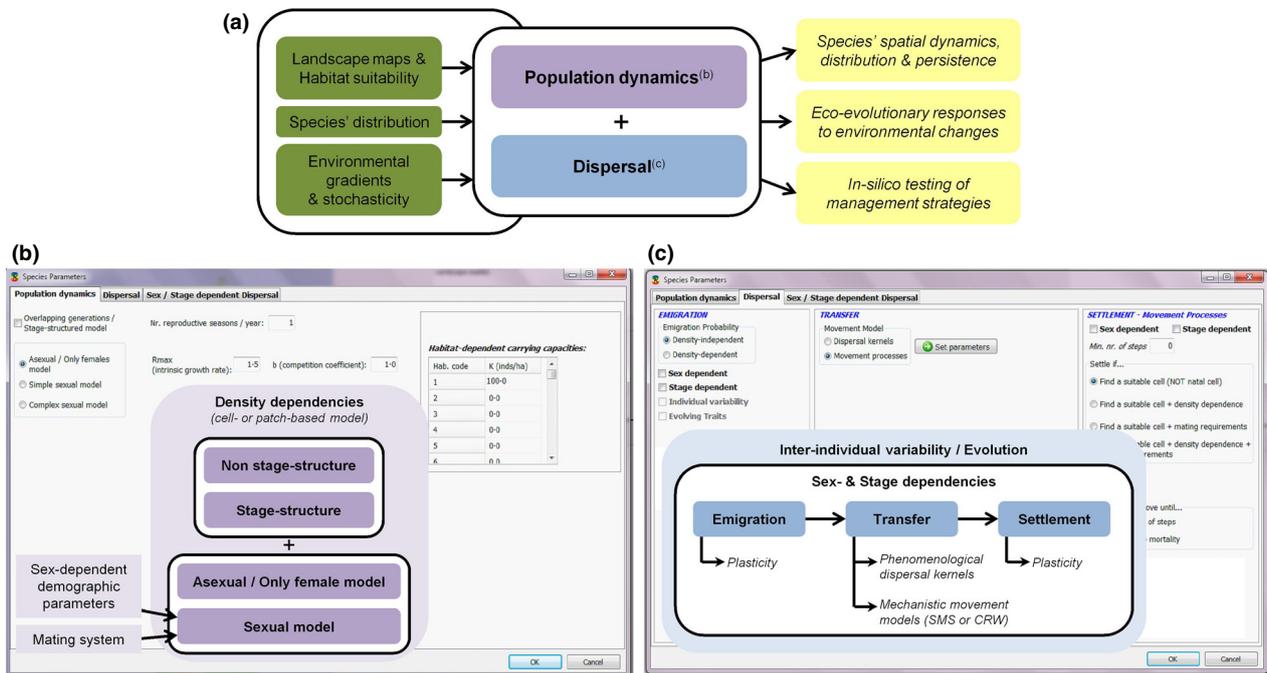


Fig. 1. The RangeShifter platform. (a) General framework of RangeShifter. Inputs and features related to the abiotic environment are illustrated in green, while in yellow are examples of possible types of output. (b) Schematic of the main components of the population dynamics module and (c) the dispersal module, over a screenshot of the relevant windows in the graphical user interface.

models, transition matrices [as in classic stage-based matrix models (Caswell 2001)] are converted into equivalent probabilities for the IBM, which yields three particular advantages. First, matrix models are widely applied, a large community is familiar with them and they have been constructed and parameterized for many species. This makes parameterization easier and bridges between analytical models and IBMs, the joint use of which can benefit applied ecology and conservation (Travis *et al.* 2011). Secondly, it minimizes the number of parameters. Thirdly, it allows for cross-validation between the two approaches.

The population model in RangeShifter can be asexual (female-only) or sexual. Different mating systems can be simulated and demographic parameters can be sex-dependent. Density dependencies can be incorporated, acting independently on fecundity, survival and development and can be stage-dependent. Importantly, the model can be either cell- or patch-based, where either the cell or the patch (an assemblage of neighbouring cells) defines the population unit and hence the scale at which density dependencies act.

Dispersal is modelled as successive emigration, transfer and settlement phases (Clobert *et al.* 2009; Fig. 1c), following recent work highlighting the importance of modelling dispersal as a complex three-phase process, with associated mechanisms, context dependencies and costs (Bonte *et al.* 2012; Travis *et al.* 2012; Altwegg *et al.* 2013). Emigration can be density-independent or density-dependent. The transfer phase either utilizes a phenomenological dispersal kernel or, addressing the demands for integration of movement behaviours and population dynamics (Morales *et al.* 2010), one of two mechanistic movement models [Stochastic Movement Simulator, SMS (Palmer,

Coulon & Travis 2011) or correlated random walk]. Importantly, through using these movement models, the dispersal kernel becomes an emergent property of the interaction between individual behaviour and landscape characteristics (Hovestadt *et al.* 2012). In the last phase, the settlement decision can be a function of habitat suitability, a plastic response to density or availability of mates or a combination of these. All three phases of dispersal can be sex- and/or stage-dependent.

RangeShifter allows for inter-individual variability in dispersal traits. Individuals possess loci (assumed to be unlinked) that carry trait-coding alleles, which are inherited from parents assuming full heritability. Dispersal traits can also evolve following specified mutation probabilities and mutation sizes.

Example applications

RANGE EXPANSION, LONG-DISTANCE DISPERSAL AND ENVIRONMENTAL STOCHASTICITY

We use a hypothetical grassland species to illustrate RangeShifter's capability for modelling range expansion at national scales and to show how accounting for rare long-distance dispersal events and environmental stochasticity can considerably change the final projected species' distribution (Fig. 2; for methods see Appendix S4). Initially, the species occurred only inside a set of 10 km × 10 km squares, which we assumed represented its recorded range. Population dynamics were run at a 1 km × 1 km resolution. The species was allowed to expand its range for 100 years, mimicking situations where constraints to expansion are removed. Assuming all emigrants draw their

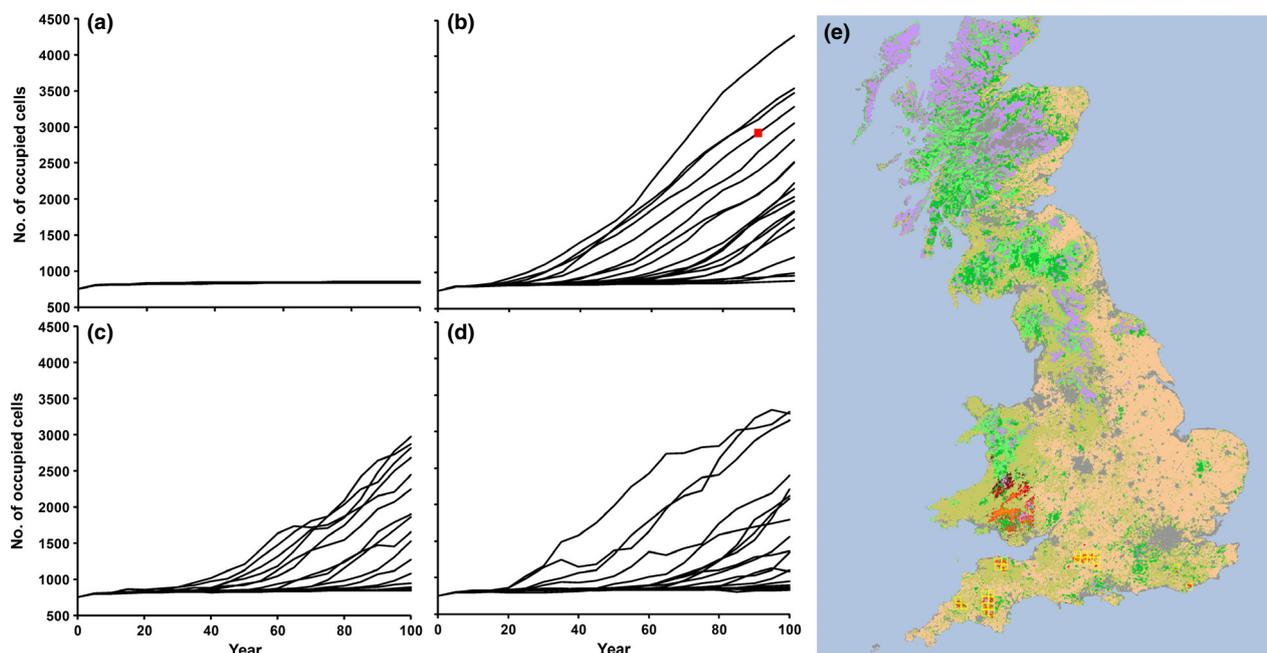


Fig. 2. Species' range expansions and environmental stochasticity. The rate of range expansion (no. of occupied 1 km cells dominated by semi-natural grassland) over a period of 100 years of a hypothetical grassland species located initially in the 10 km × 10 km cells in southern England marked in yellow in (e). (a) The dispersal distance of each individual is drawn from a negative exponential kernel of mean 2 km; (b) same as (a) except that 1% of individuals exhibit long-distance dispersal drawn from a negative exponential kernel of mean 10 km; (c) same as (b) but the species is subjected to temporally uncorrelated environmental variation in maximum growth rate; (d) same as (b) but with temporally correlated variation (autocorrelation coefficient $\kappa = 0.7$) in maximum growth rate. (a–d) Each line depicts one of the 20 replicate runs. (e) Example output map produced by RangeShifter showing the species' distribution for a single replicate in (b), 90 years after the start of range expansion as marked by the red square. Population density within each occupied 1 km cell is depicted from dark red (low) to orange (high). Note the recently established outlying subpopulation resulting from long-distance dispersal near the coastline in west Wales. Cells dominated by semi-natural grassland are shown in light green, woodland in dark green, improved grassland in light brown, arable in pale pink, heath/bog in mauve and other habitats (urban, montane, coastal) in grey. Dominant habitat types are derived from the U.K. Land Cover Map 2007 © and data base rights NERC (CEH) 2011. All rights reserved.

displacement distances from a dispersal kernel of mean 2 km resulted in negligible range expansion (Fig. 2a; mean rate \pm SD = 0.93 ± 0.041 cells year⁻¹). However, when 1% dispersers adopted a kernel of mean 10 km, a substantial increase in the rate of range expansion and in the variability between runs was observed (Fig. 2b; mean rate = 15.1 ± 9.44 cells year⁻¹). Moreover, the expansion front became discontinuous, proceeding from stochastic long-distance disjointed colonization foci (Fig. 2e). Introducing temporal environmental stochasticity also had an important effect, almost halving the mean rate of expansion (Mustin *et al.* 2013; temporally uncorrelated: mean rate = 8.7 ± 7.96 cells year⁻¹, Fig. 2c; temporally autocorrelated: mean rate = 8.9 ± 8.52 cells year⁻¹, Fig. 2d).

LANDSCAPE-SCALE CONNECTIVITY, MATRIX PERMEABILITY AND DISPERSAL BEHAVIOUR

RangeShifter enables different landscape-scale applications for issues related to connectivity, species persistence and conservation management. We illustrate this potential and demonstrate some of the complexity that can be modelled, by simulating a hypothetical species inhabiting a woodland network within a highly anthropogenic landscape (Fig. 3). We show how the assumptions made regarding demographics, dispersal behaviour and habitat-dependent movement mortality can

substantially alter projected outcomes. We simulated for 100 years a patch-based, stage-structured population exhibiting density-dependent emigration and initialized in a single patch (for methods see Appendix S4). The measures chosen for illustrating the connectivity between the initial patch and the rest of the woodland network (i.e. final probability of occupancy and mean time to first colonization) highlight the dependency of outcomes on the landscape characteristics and movement abilities of the species and, importantly, also on the population dynamics. Notably, these measures both represent multi-generation connectivity.

Connectivity depended upon how dynamics and dispersal were modelled. A sexual species, whose individuals had to find a mate to colonize new patches, had occupied only $17 \pm 3.0\%$ of suitable patches after 100 years (Fig. 3b). When females settled as soon as they found a patch of suitable habitat and males settled only in patches with female(s) present, the overall patch occupancy increased to $27 \pm 7.5\%$ (Fig. 3c). In a female-only model, where mate-finding no longer limited colonization, patch occupancy increased to $64 \pm 6.5\%$ (Fig. 3d). These results were obtained assuming that dispersing individuals responded to the landscape in terms of movement choices, but that per-step mortality was constant across different landscape types. Introducing potentially more realistic habitat-specific movement mortalities, specifically higher across roads, urban

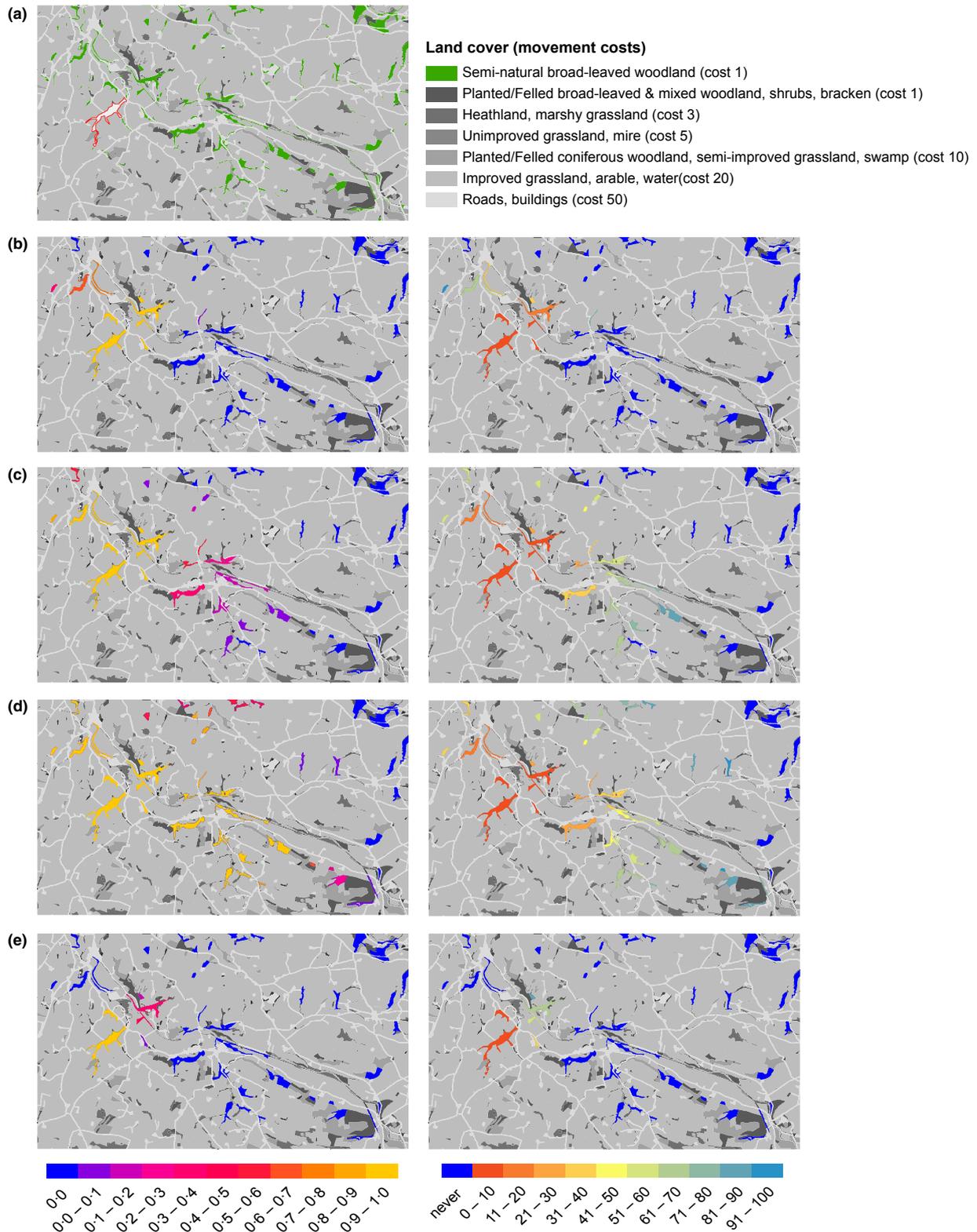


Fig. 3. Dependence of landscape connectivity on the settlement behaviour and movement model assumed for dispersal. (a) Land-cover types and relative costs to movement (map derived from Watts *et al.* (2010); 10 m \times 10 m resolution). The green patches represent patches of semi-natural broad-leaved woodland, those with area ≥ 1 ha were considered as breeding habitat for the simulated species. In all cases, individuals were initially introduced in the red-bordered patch. (b–e) Left panels: occupancy probability for each patch after 100 years calculated over 20 replicates for the four experiments (see Appendix S4). Right panels: mean time to first colonization for each patch that had occupancy probability > 0 at year 100. (b) Sexual model with both sexes settling only in the presence of a mate. (c) Sexual model where female dispersers settle in suitable patches regardless of males, while males settle only when finding a mate. (d) Female-only model. (e) Same model as in (b) but with habitat-specific per-step mortality. All maps were produced with ArcGIS10[®].

and arable (Fig. 3e; see Appendix S4), substantially reduced network connectivity, both in terms of overall patch occupancy ($6 \pm 2.4\%$) and waiting time to colonization (Fig. 3b,e, right-hand panels).

EVOLUTION OF DISPERSAL DURING RANGE SHIFTING

As an illustrative example of the broad range of theoretical applications of RangeShifter, we modelled dispersal evolving across a species' range during climate change. We illustrated how the evolution of emigration probabilities and dispersal distances can be modelled jointly and how a response to environmental change may differ when accounting for evolution of only one or both traits (Fig. 4; for methods see Appendix S4). In agreement with existing theory (Dytham 2009), across a stationary gradient (before year 500) dispersal strategies became spatially structured, having higher emigration probabilities and/or dispersal distances at the range margins (Table 1). When the gradient started shifting northwards, the species started falling behind its suitable space, and the range contracted. Simultaneously, increasing dispersal evolved, start-

ing from the leading edge and gradually surfing backwards, enabling the species eventually to keep track of its suitable climate space. At the end of the shifting period (year 800), dispersal distances and emigration probabilities had increased across the whole range. Interestingly, after 400 years of the post-shifting period, emigration probabilities had evolved back to pre-change values, whereas dispersal distances remained at the level reached at the end of the shifting phase.

When emigration probabilities and dispersal distances evolved simultaneously (third experiment, Appendix S4), the same pattern occurred (Fig. 4). While emigration probability changed in a comparable way to when evolving alone, dispersal distance increased to a lesser extent than when evolving independently. Note also that there was high variability among replicates, suggesting that stochastic founder effects at the range front and genotypes surfing backwards from the leading edge are important processes influencing the evolutionary and ecological dynamics of range shifting. Notably, whether emigration, dispersal distance or both evolved, had substantial consequences on total population abundance and number of cells occupied, changing the range dynamics during the shifting

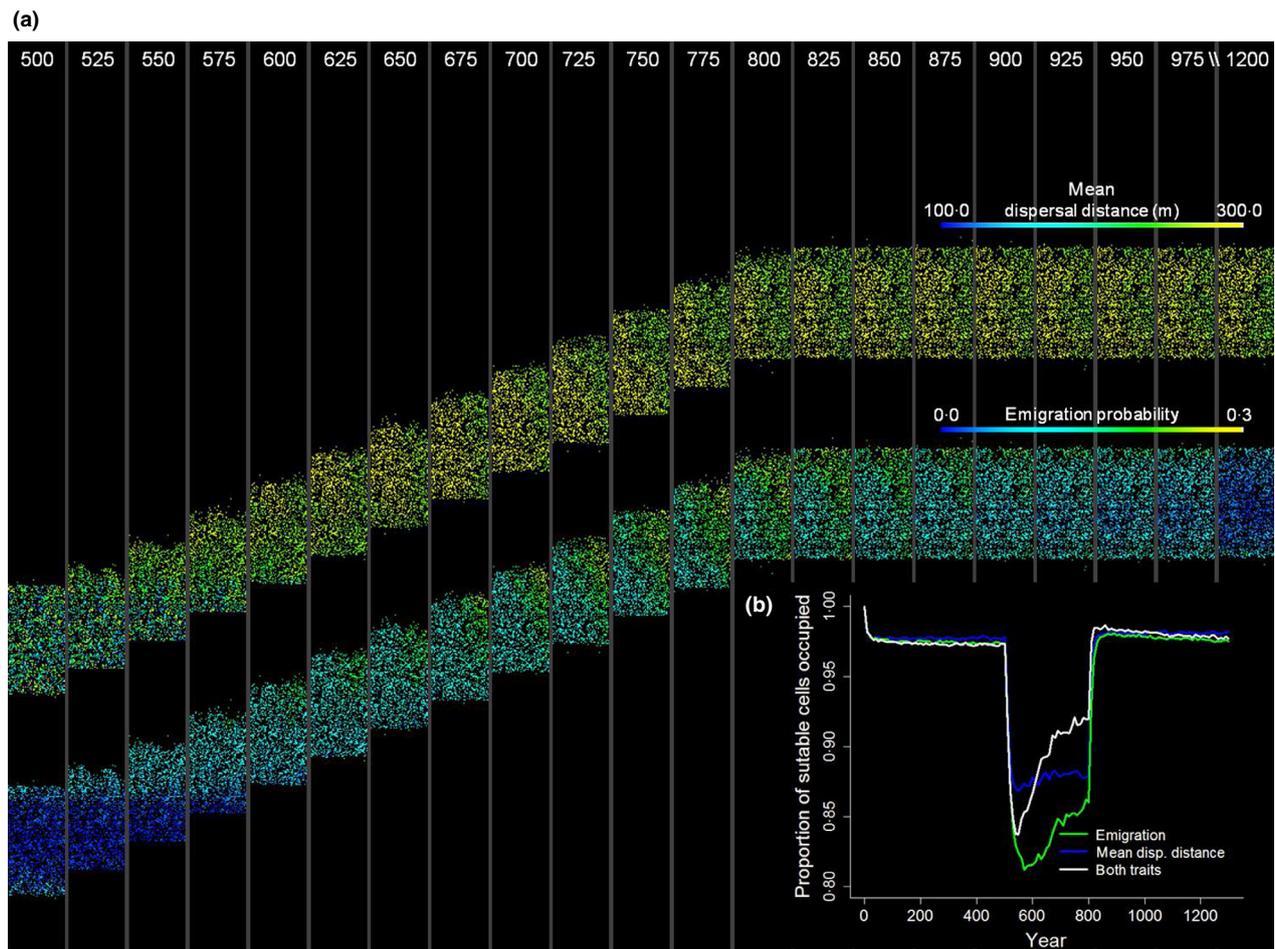


Fig. 4. Evolution of dispersal during range shifting. (a) The vertical panels represent the changes through time of emigration probability (lower strips) and mean dispersal distance (upper strips) over a single simulation where both traits are evolving. The numbers at the top indicate time (years). Each pixel represents a population, and the colours depict the mean trait value for the population. The range is shifting northwards (from bottom to the top) from years 500 to 800. (b) Changes in the cell occupancy (proportion of suitable occupied cells) through time when only emigration probability evolves (green), only dispersal distance evolve (blue) or both traits evolve (white). The lines represent the mean of 20 replicates (see Appendix S4).

Table 1. Evolution of dispersal during range shifting: example of high-resolution spatio-temporal, individual-based outputs from RangeShifter. The mean and the standard deviation of the dispersal distance and emigration probability are calculated over the 100 north-most (front), middle and south-most (back) individuals in each replicate. Means and standard deviations were then averaged across 20 replicates. Values are reported for three different scenarios (blue): only mean dispersal distance, only emigration probability and both traits evolving. The yellow cells highlight how RangeShifter provides spatially explicit individual-level output data at high temporal resolution (minimum one reproductive season). Note the difference between the two traits when they are evolving alone (green cells): both traits are structured along the gradient at the starting of climate change (year 500) and dispersiveness increases as the shifting progresses. However, after 400 years following the cessation of climate change, while emigration probability has evolved back close to the initial values, the mean dispersal distance has not. In this example, when the two traits evolve concurrently, emigration probability shows patterns that are comparable to when it evolves independently, while the mean dispersal distance increases less that it does when evolving alone (purple cells)

Year	Part of the range	Mean dispersal distance alone		Emigration probability alone		Both traits			
		Mean	SD	Mean	SD	Mean dispersal distance (m)	SD	Mean	SD
500	Front	227	51.1	0.08	0.032	211	53.3	0.08	0.034
	Middle	198	60.4	0.01	0.009	192	47.7	0.01	0.012
	Back	222	49.4	0.07	0.031	220	49.6	0.07	0.031
650	Front	289	77.2	0.16	0.007	267	3.7	0.16	0.017
	Middle	293	11.4	0.09	0.019	251	20.0	0.09	0.023
	Back	279	15.5	0.11	0.031	264	15.6	0.10	0.030
800	Front	297	6.4	0.19	0.009	269	6.4	0.21	0.017
	Middle	290	7.7	0.13	0.033	242	8.6	0.10	0.010
	Back	292	8.9	0.15	0.027	270	7.5	0.15	0.032
1200	Front	296	12.9	0.11	0.031	272	13.5	0.10	0.031
	Middle	292	14.2	0.02	0.016	239	13.4	0.02	0.013
	Back	293	12.5	0.10	0.032	271	13.1	0.09	0.028

phase. In fact, when both traits evolved, the rescue of the species was much quicker than when only one trait evolved (Fig. 4b). Clearly, more work is needed to understand the role that multiple trait evolution plays in driving spatial population dynamic processes including species responses to climate change.

Discussion

The novel dynamic modelling platform, RangeShifter, introduced here responds to the ecological and evolutionary communities' demands for integrated dynamic models (Huntley *et al.* 2010; Morales *et al.* 2010; Schurr *et al.* 2012; Thuiller *et al.* 2013) by representing population dynamics and dispersal behaviours in an individual-based framework and allowing them to be simulated on landscapes at different scales. Furthermore, it accommodates inter-individual variability and is fully stochastic, enabling necessary consideration of different sources of uncertainty (Conlisk *et al.* 2013).

In three exemplary studies, we illustrated some of the capabilities and features of the software. We showed its potential for modelling real systems from national to local scales, accounting for habitat heterogeneity, landscape structure and environmental stochasticity. The platform provides flexibility for modelling species in terms of the complexity included in population dynamics and dispersal. As the first two examples show, biological details and consideration of environmental stochasticity and landscape heterogeneity can strongly influence conclusions regarding range expansion and landscape connectivity. This emphasizes how utilizing a modelling plat-

form, which can account for such complexity, is crucial to assess and potentially improve the reliability of projections as a basis for conservation planning.

The third example was illustrative of the many potential theoretical applications of RangeShifter. We explored the eco-evolutionary dynamics of a species range during shifting of an environmental gradient. We showed how RangeShifter can be used to model inter-individual variability in, and evolution of, different traits. This exemplified the likely complexity of evolutionary responses to environmental changes and highlights how this software, with the capability of providing individual-based outputs at high spatio-temporal resolution, can help in gaining better understanding of these dynamics.

The design of RangeShifter exploits recent advances in population dynamics and dispersal theory. Dispersal is clearly a key determinant of species' spatial dynamics and responses to rapid changes. However, an insufficient representation of dispersal is still a major limitation in many methods dealing with species' distribution and local connectivity (Baguette & Van Dyck 2007; Bullock *et al.* 2012; Travis *et al.* 2013). In contrast, RangeShifter allows researchers to model dispersal explicitly in its three phases and consider different context dependencies and responses to landscape structure. Promisingly, understanding of and data related to these three phases are increasing in number rapidly. This is being accelerated by recent experimental developments, such as the Metatron (Legrand *et al.* 2012), specifically established to study dispersal processes and spatial dynamics under the same theoretical framework adopted in RangeShifter. Furthermore, technological advances facilitate the collection of increasing quantities of

movement data, and thus, high-quality data on how multiple species move across complex landscapes during dispersal will soon become available (Cagnacci *et al.* 2010). RangeShifter provides an ideal complement to these empirical advances, which will provide data and understanding to better parameterize the model. In turn, RangeShifter can help to generate hypothesis to be tested empirically.

RangeShifter is already a complex platform, which integrates several components recognized as fundamental for tackling problems related to species' spatial dynamics under environmental changes. Importantly, it also provides a solid foundation on which further components can be added. Here, we identify three key areas for future progress. The first is the explicit incorporation of climate. Gradients that can represent climate are already available for use and RangeShifter could be easily modified to read a time-series of changing landscapes to be used as a 'hybrid' model by coupling it with SDM projections (Conlisk *et al.* 2013). This immediately provides advantages over many existing exercises taking this approach owing to its greater detail in population dynamics and, especially, dispersal. However, we believe that properly integrating climate requires building explicit functional relationships between species' life-history traits and climatic variables. Methods to estimate parameters for such relationships are currently developing, and one, which makes use of a hierarchical Bayesian framework, has been demonstrated *in silico* (Pagel & Schurr 2012; Schurr *et al.* 2012). A promising avenue could be enhancing RangeShifter such that it can be used with approximate Bayesian computation methods (Beaumont 2010; Hartig *et al.* 2011). This would allow the direct estimation of model parameters, especially of the species' traits/climate relationships, from relatively common data such as species' distributions and abundance. A more data-demanding possibility would be to estimate the functional relationships with climate empirically and build them directly into the model. While this might be tractable for modelling a handful of data-rich species, it is likely to be difficult to generalize and apply for multi-species modelling.

The second area where we envisage progress is incorporating interspecific interactions. In many cases, they are known to influence species persistence locally as well as range dynamics (Hellmann, Prior & Pelini 2012; Urban, Zarnetske & Skelly 2013; Wisz *et al.* 2013). RangeShifter has the potential to add interspecific interactions, but the current challenge is to understand the level of complexity required to represent them. In a recent theoretical exercise (Bocedi *et al.* 2013), a trial version of RangeShifter was extended to incorporate simple competitive interactions and local adaptation to climate. This exploratory work demonstrates that the interplay between these two processes can lead to unexpected range dynamics of two competing species during a period of climate change.

Thirdly, RangeShifter has started incorporating evolutionary processes, which are increasingly recognized as being as important as ecological processes for species' responses to environmental changes (Norberg *et al.* 2012; Thuiller *et al.* 2013; Travis *et al.* 2013). Importantly, the individual-based nature of this platform opens the possibility for including a fully

mechanistic genetic module, both for neutral and for adaptive genetics, where genetic architecture (e.g. linkage, dominance, epistasis, pleiotropy) and processes (e.g. point mutations, recombination) can be explicitly and stochastically modelled (Hoban, Bertorelle & Gaggiotti 2011). This development, together with the increasing amount of available genetic data, will provide many opportunities for both theoretical and applied studies. These include understanding the causes and consequences of local adaptation as a function of genetic architecture, landscape structure and species demographic and dispersal traits, *in silico* testing of existing methods for inferring dispersal from landscape genetic data, and improved ability to predict the likelihood that species will adapt quickly enough in response to projected environmental changes.

In conclusion, RangeShifter fills a major gap in the field of eco-evolutionary research by providing a user-friendly platform that will make individual-based simulation of species' dynamics on realistic landscapes much more accessible to stakeholders. We anticipate that the development of RangeShifter will have a similar positive impact on this field that genetic simulation packages have had on population, evolutionary and landscape genetics (Hoban, Bertorelle & Gaggiotti 2011). Importantly, the platform also provides a vehicle for bringing theoretical eco-evolutionary dynamics and applied modelling for conservation closer together, reducing the lag between development of theory and its uptake for ecosystem management (Benton *et al.* 2007).

Acknowledgements

We are grateful to all the colleagues who helped in testing RangeShifter v1.0 during its development. GB, GP, RKH and YGM were supported by the SCALES project (Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal, and Ecological Scales) funded by the European Commission as a Large-scale Integrating Project within FP 7 under grant 226 852 (Henle *et al.* 2010; www.scales-project.net). MJT, SCFP and KW were supported by the Natural Environment Research Council, UK.

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Received 24 August 2013; accepted 24 December 2013

Handling Editor: Robert Freckleton

Supporting Information

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

Appendix S1. The RangeShifter software executable, *RangeShifter_v1-0-5.exe*.

Appendix S2. *RangeShifter_v1-0_User Manual.pdf*.

Appendix S3. Tables summarizing the methods (main options and functions) implemented in RangeShifter v1.0.

Appendix S4. Methods for the three example applications presented in the paper.