

Landscape Effects on the Spread of Invasive Species

Andrew O'Reilly-Nugent¹ · Rakhi Palit¹ · Angelica Lopez-Aldana¹ ·
Margarita Medina-Romero¹ · E. Wandrag¹ · Richard P. Duncan¹

Published online: 12 August 2016
© Springer International Publishing AG 2016

Abstract Landscapes differ in the composition and configuration of habitats, and this heterogeneity can influence the manner in which invasive species spread in complex ways. To understand this complexity, we outline a framework that identifies how landscape heterogeneity influences spread by causing dispersal behaviour and local population growth to vary across the landscape. We use this framework to review progress over the last 5 years in understanding landscape effects on invasive spread, focussing on the role of interactions between landscape heterogeneity, dispersal and population processes.

Keywords Landscape heterogeneity · Dispersal · Invasion · Population growth · Stochasticity · Density-dependence

Introduction

Species introduced to regions outside their native range become invasive when they spread away from the site of initial introduction to establish self-sustaining populations in new locations [1]. Understanding the processes that control the pattern and rate at which invasive species spread is key to forecasting and managing their potential impacts [2–4].

Much of our understanding of spread dynamics comes from mathematical models of populations expanding across

homogeneous landscapes [5–7]. However, invasions typically unfold across more complex landscapes, and attention has shifted toward understanding how landscape heterogeneity (the composition and configuration of habitats) can influence the pattern and rate of invasive species spread [8–11]. Perhaps the dominant theme to emerge from this research is the wide variation in outcomes obtained from relatively simple spread models, with this complexity arising for three key reasons. The first is that the pattern and rate of species spread is context specific, depending on both the traits of the species concerned and individual landscape composition and configuration. Second, theoretical studies show that the key demographic processes driving spread, including rates of dispersal and local population growth, can have non-linear responses and both interact and feedback on one another, leading to highly variable outcomes given slight changes to demographic parameters, landscape configuration or starting conditions [12]. Finally, recent work has highlighted the role that demographic and environmental stochasticity can play in affecting spread rates, with their influence mediated by interactions with other demographic processes [13, 14]. These complex interactions and the varied outcomes they generate make it difficult to identify general principles governing the effect of landscape structure on invasive spread [15, 16].

Our aim in this review is twofold. First, to illustrate the potentially complex interactions that can drive spread we develop a framework that aims to capture the key processes underlying spread, and use this framework to identify the ways in which landscape heterogeneity can influence the spread of invasive species. Second, using this framework we review progress over the last five years in understanding landscape effects on invasive spread.

To do this, we conducted a systematic review of studies published since 2010 as indexed by Web of Science and Google Scholar, using the following Web of Science keywords:

This article is part of the Topical Collection on *Effects of Landscape Structure on Undesired/Over-Abundant Species and Ecological Processes*

✉ Richard P. Duncan
Richard.Duncan@canberra.edu.au

¹ Institute for Applied Ecology, University of Canberra, Canberra, ACT, Australia

TOPIC: ((invas* OR alien OR exotic) AND (land*)) AND (spread OR expansion) AND YEAR PUBLISHED: (2010–2015). This returned 809 articles, which we refined to 503 by specifying the following Web of Science fields: ENVIRONMENTAL SCIENCES ECOLOGY OR PLANT SCIENCES OR BIODIVERSITY CONSERVATION OR ZOOLOGY OR AGRICULTURE OR MARINE FRESHWATER BIOLOGY. These 503 articles were further narrowed to 180 based on their title. We reviewed the abstracts of these 180 articles and identified a subset we considered most relevant to the aims of this review. Our choice was selective: there have been several excellent reviews of landscape effects on invasive spread [6, 11, 17], and rather than covering much of the same ground, we focus on recent developments in understanding how landscape heterogeneity and interactions between spread processes generate variation in spread dynamics, using the framework we develop.

Conceptual Framework for Spread

Spread involves an increase in the number of locations or area occupied by a species [12]. At its core, spread is a population process that can be understood as a repetitive sequence of events (Fig. 1): individuals arrive and settle at a location, with settlement implying that arriving individuals persist at that location. Given conditions suitable for reproduction, those individuals then produce propagules that either contribute to local population growth or disperse to new locations. If conditions are suitable at these new locations, dispersed propagules settle and reproduce, producing propagules that are dispersed to further locations, and so forth [18]. Figure 1 illustrates these events, with arrows identifying the steps between dispersal, settlement and local population growth that result in spread.

We include settlement and local population growth as separate events to accommodate sink habitats: locations where arriving individuals can survive (settle) but local reproduction is insufficient for positive population growth, and occupancy relies on the continued arrival of individuals from elsewhere [19]. This distinction is important when considering the spread of invasive species, because sink habitats will usually be included in the area an invader has occupied, and thus contribute to measures of spread, although in reality it is difficult to distinguish sink from non-sink locations [20]. The transition from settlement to population growth implies that conditions are suitable for the establishment of a self-sustaining population at a given locality.

A large body of theory shows that in homogeneous landscapes, the rate at which an invasive species spreads is critically dependent on its dispersal capability and its rate of population growth when rare [5, 7, 21]. Real landscapes are not homogeneous, and typically comprise a variety of habitats with different characteristics. For a given species, habitats can differ both in their suitability for movement, with some habitats facilitating and others impeding dispersal [22], and in their suitability for survival and reproduction, leading to spatial variation in local population growth rates [23]. Landscape heterogeneity can thus directly affect spread through variation in habitat suitability that results in varying rates of dispersal, settlement and local population growth across the landscape. The direct effects of habitat suitability on these demographic processes are shown as arrows in Fig. 1.

Although habitat variation can affect spread directly by causing dispersal and local population growth rates to vary, complex spread dynamics often arise through interactions between these processes, creating the potential for non-linear responses, feedback and thresholds in spread behaviour, leading to highly variable outcomes [12]. While the arrows in

Fig. 1 Conceptual framework for understanding landscape effects on the spread of invasive species. Landscapes differ in the composition and configuration of habitats. For a given invader, landscapes comprise habitats of varying suitability for movement, survival and reproduction, which influences spread by generating spatiotemporal heterogeneity in both dispersal behaviour and local population dynamics (settlement and population growth)

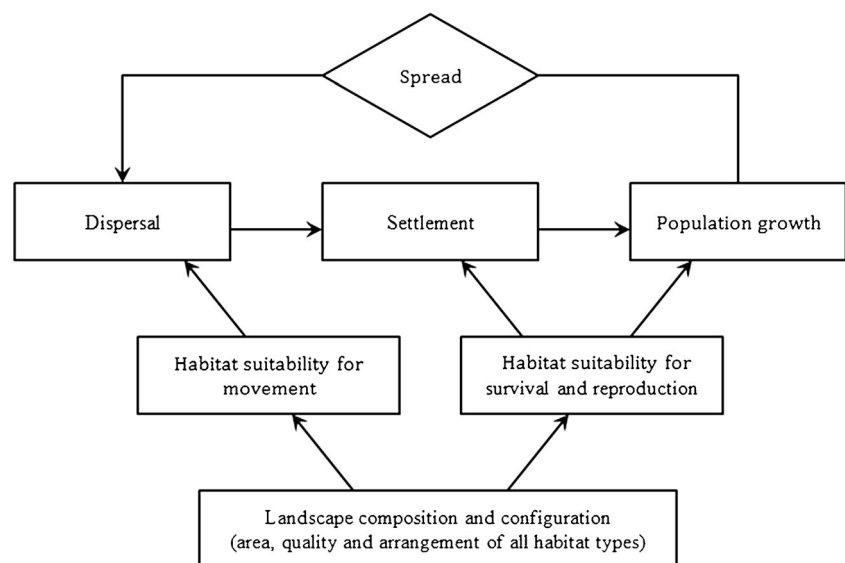


Fig. 1 identify the direct effects of one process on another, multiple arrows pointing to the same process identify the potential for interactions, meaning outcomes could exhibit greater variability because they depend on the joint effects of two processes whose effects may not be additive. Settlement and the transition to population growth, for example, depend on both dispersal and habitat suitability for survival and reproduction (Fig. 1). Rather than acting independently, however, it is the interaction between these processes that determines the probability that a population will establish at a new location [24, 25]. Low rates of dispersal, for example, may allow populations to settle in patches of suitable habitat, but may not provide sufficient propagules for establishment in patches of less suitable habitat [25], resulting in spread being strongly influenced by the make-up of habitat patches that differ in their suitability for population growth. In contrast, high rates of dispersal may provide sufficient propagules to overcome establishment barriers [26], meaning spread is much less affected by differences among habitat patches in their suitability for population growth. As a consequence, while landscape heterogeneity may cause dispersal behaviour and local population growth to vary across the landscape somewhat independently, spread is critically dependent on how these processes interact to jointly determine outcomes. Here we use the framework shown in Fig. 1 to review progress over the last 5 years in understanding how landscape-level heterogeneity in dispersal behaviour and population growth can influence spread dynamics, first by considering the direct effects of heterogeneity on each of these processes separately, and second by examining the importance of interactions.

Direct Effects of Landscape Heterogeneity on Dispersal Behaviour

The rate at which invasive species spread is known to be highly sensitive to variation in dispersal parameters, with spread rate increasing as both mean dispersal distance and the frequency of long-distance dispersal events increase [12, 21]. Nevertheless, for a given species, spread is often modelled assuming a fixed dispersal kernel that does not vary across the landscape. Relative to this, patterns of spread are likely to differ if, instead, a landscape comprises habitats or has features that differentially affect the movement of individuals, leading to spatial and/or temporal heterogeneity in dispersal behaviour. Spatially, dispersal behaviour may vary if propagule movement is facilitated in some habitats but not others, resulting in more propagules able to move a greater distance through some parts of the landscape [22]. If the mean dispersal distance remains the same, introducing spatial heterogeneity in dispersal behaviour should increase invasion speed, because this will increase the frequency of

longer-distance dispersal events, which have a disproportionate influence on spread rates [21, 27]. Ellner and Schreiber [27] have shown that this is the case for temporal variation, with increasing variation in dispersal rates accelerating invasive spread because this results in an increase in the frequency of longer-distance dispersal events. We expect the same outcome given spatial heterogeneity, whereby the addition of landscape features or vectors that facilitate long-distance dispersal will increase invasion speed. Human-assisted dispersal can play a key role in this regard, with even occasional long-distance movements by humans substantially accelerating the spread of invasive species [28, 29].

Empirical studies of invasive spread highlight the importance of landscape features that influence propagule movement. Caplat et al. [30] and Jongejans et al. [14], for example, show that invasion speed in two wind-dispersed species is highly sensitive to variation in wind speed, implying that the strength and direction of wind patterns across the landscape are likely to be critical determinants of spread dynamics [31]. Data on how wind patterns vary across the landscape can be used to identify areas connected by high rates of dispersal, which is where management may be most effective in limiting spread [32]. Similarly, Miller et al. [33] show that variation in local vegetation structure affects spread by creating barriers to movement. They show a steeper decline in the density of the wind-dispersed invasive herb *Hieracium lepidulum* away from stream habitat, which acts as a propagule source, when the surrounding vegetation is forest rather than grassland. The ability of *H. lepidulum* to spread more rapidly into grassland habitat is most likely due to greater dispersal distances across low-growing grassland vegetation relative to forest, which creates a taller barrier (see also [34]). This suggests that management to reduce spread would be most effective if it targeted control in parts of the landscape acting as a source for rapid dispersal into surrounding areas (in this case grassland stream habitat [33]).

Nevertheless, relative to settlement and population growth, which we discuss below, few invasion studies have quantified the extent to which landscape heterogeneity affects dispersal behaviour, and fewer still have explored the consequences of such heterogeneity for spread dynamics [35]. This is most likely due to the difficulty in measuring dispersal, but highlights an important gap in understanding. The increasing availability of genetic data allowing the spatial locations of parents and their offspring to be matched [36] provides a way of quantifying rates of dispersal across the landscape and identifying landscape features that act as barriers or facilitate movement [37]. Such approaches are starting to be applied to invasion questions [38].

Direct Effects of Landscape Heterogeneity on Local Population Processes

In simple spread models across homogeneous landscapes, rate of spread depends on population growth rate when rare: all else being equal, higher rates of population growth result in faster spread [39], because more rapidly growing local populations are able to supply greater numbers of propagules that then disperse and settle (Fig. 1). Variation across the landscape in local population growth rates should therefore directly affect spread dynamics.

Many studies that have explored how heterogeneity in local population processes affect invasive spread have employed spatially explicit simulation models, because the added complexity of allowing population processes to vary means analytical approaches are less tractable or require strongly simplifying assumptions [40–42]. While simulation models are informative, it is not always clear whether the findings from modelling a given scenario are system-specific or provide more general insights. Significant progress has been made recently, however, in deriving analytical solutions for spread dynamics across landscapes where population growth rates vary spatially. Perhaps the most accessible treatment is by Dewhurst and Lutscher [43], who derive several important results that generalise findings from earlier simulation studies. A key outcome is that the relationship between landscape heterogeneity and rate of spread can be highly non-linear. Simulation models, for example, have previously identified the existence of ‘invasion thresholds’ whereby invasive spread occurs most rapidly and extensively across landscapes with some minimum proportion and distribution of suitable habitat [11]. Dewhurst and Lutscher [43] show that, as a rule of thumb, in a landscape comprising suitable and less-suitable habitat patches, the minimum proportion of suitable habitat, p_{\min} , required for an invader to spread is:

$$p_{\min} = \frac{1-r_2}{r_1-r_2}$$

where r_1 and r_2 are the population growth rates when rare in suitable and less suitable habitat patches, respectively (assuming $r_2 < 1$). When $r_2 = 0$ (i.e., populations are unable to establish in unsuitable patches,) the proportion of suitable habitat required for spread is $1/r_1$, implying that much larger areas of suitable habitat are required for invasive spread if that suitable habitat has relatively low rates of population growth. These outcomes depend on the shape of the invader species’ dispersal kernel, and the above rules apply when the variance, and hence the mean dispersal distance, is large relative to the average distance between suitable habitat patches, meaning that suitable patches are well connected by dispersal. As the mean

dispersal distance declines relative to the distance between habitat patches, the probability that some suitable patches may not be colonised increases, and p_{\min} also increases.

Dewhurst and Lutscher [43] also show that, in the absence of Allee effects, the rate of invasive spread across a landscape comprising habitat patches that differ in suitability for population growth is a function of the spatially weighted average population growth rate of the different patches. This confirms the intuitive idea that increasing the area of habitat unsuitable for population growth should slow invader spread by creating habitat sinks that effectively act as dispersal barriers. Rigot et al. [44] provide a recent demonstration, showing that the rate of spread of the pine bark scale *Matsucoccus feytaudi* is slower in diverse landscapes having patches of suitable and unsuitable habitat, relative to more homogeneous landscapes.

What remains less well understood analytically is how the spatial arrangement of habitat patches, as opposed to the proportion of suitable habitats or degree of fragmentation, affects spread (but see [45]). Spatial simulation models reinforce what we might anticipate: that spatial aggregation of suitable habitat can slow the rate of spread, with more spread occurring across greater distances where suitable habitat forms corridors or stepping stones that allow rapid movement or jumps through unsuitable habitat [18]. This highlights the importance of habitat corridors and stepping stones in facilitating invasive spread, and the potential for management to slow spread by targeting populations in these habitats [2, 3, 46].

A further source of heterogeneity in population processes are temporal fluctuations due to demographic and environmental stochasticity. Recent work has identified two important consequences of temporal stochasticity. First, while theoretical studies have shown that temporal variability in dispersal can lead to increased rates of invasive spread [27], the opposite is true for population growth, where temporal variation in growth rates causes spread to slow relative to a temporally stable landscape [27]. This occurs because long-term mean population growth rates at localities will decline with increasing variance in local population growth rates [47], meaning invasion speed will slow as temporal variability increases. Fitzpatrick et al. [48], for example, show that spread of the hemlock woolly adelgid *Adelges tsugae* is slowed substantially by cold winter temperatures, and that regions with greater temperature variability, leading to extremes lethal to populations, have slower spread rates.

Second, temporal stochasticity means that invasive spread is not a deterministic process: any real-life invasion represents one outcome contingent on a series of probabilistic events, such that we could see a different outcome if we reran the process. How important is this variation? Melbourne and Hastings [16] show that spread of the flour beetle (*Tribolium castaneum*) is remarkably variable in replicate landscapes comprising identical habitat patches. This variability arises in part through demographic stochasticity, but also through

other stochastic processes perhaps related to the initial conditions in small founding populations [16]. The implication is that stochasticity makes it inherently difficult to predict the trajectory of any given invasion, even under laboratory-controlled homogeneous conditions. In contrast, Giometto et al. [49] show much higher levels of repeatability in the spread of the freshwater ciliate *Tetrahymena* under similar controlled conditions, although any uncertainty will almost certainly be magnified in heterogeneous landscapes (e.g. [48]).

Interactions Between Landscape Heterogeneity, Dispersal and Population Processes

The previous two sections considered how landscape-induced variation in dispersal and population processes can independently affect spread dynamics. While heterogeneity in these processes alone can generate substantial variation in patterns of spread, recent work has emphasised that interactions between these processes have the potential to generate even greater complexity.

Central to understanding the variability in outcomes that can result from interactions between dispersal and population processes is the role of stochasticity. While deterministic models treat population density and spread as continuously varying, in reality, spread involves the dispersal of a discrete number of individuals. When only a few individuals disperse to a new locality, the resulting small founding population will be prone to extinction through fluctuations in size due to demographic and environmental stochasticity [24]. As a consequence, spread via the establishment of new populations is a probabilistic process, with the probability of a new population establishing jointly dependent on the number of individuals that disperse and settle (the size of the founding population) and the suitability of the locality for survival and reproduction (see Fig. 1 and [24, 25, 50]).

Relative to a deterministic spread model, the inclusion of stochasticity should slow the spread of an invasive species, because small founding populations just beyond the edge of the invasion front can go extinct in even suitable localities. Eventually, however, these localities should be colonised as populations at the edge of the invasion front grow and supply a greater number of propagules, leading to more frequent colonisation events and larger founding populations, resulting in higher probabilities of establishment. The potential to colonise beyond the invasion front, however, depends on the ability of established populations near the front to produce sufficient propagules, and hence on the degree to which reproductive output is density-dependent.

In homogeneous landscapes, the combined effects of density dependence and demographic stochasticity have been shown to result in only a modest slowing of invasion

speed [51]. In heterogeneous landscapes, however, these processes can interact to have large effects on spread rates [13]. In a fragmented landscape comprising patches that are both suitable and unsuitable for population growth, spread will slow if populations on the edge of the invasion front cannot produce enough dispersing propagules to successfully colonise suitable habitat patches that are sufficiently far away. Without density-dependent regulation, initially small populations at the invasion front will grow and increase their propagule output, eventually producing sufficient numbers of propagules that disperse across a habitat gap to ensure colonisation of distant patches. However, if density-dependent regulation causes per capita reproductive output to decline as populations increase in size, total propagule output may not increase greatly as edge populations grow, meaning distant patches continue to receive few propagules, resulting in a low probability of colonisation and greatly slowing the rate of spread [13].

While we are not aware that this effect has been demonstrated in real populations, Warren et al. [50] have shown that the relevant conditions arise in the invasive grass *Microstegium vimineum*. This species shows variable recruitment across the landscape (equivalent to settlement in Fig. 1) that is jointly dependent on the number of seeds arriving at a locality and the suitability of that locality, such that the probability of colonisation increases with greater seed supply and in more favourable habitats. Subsequent reproductive output, however, is strongly density-dependent, with low-density populations producing roughly the same number of seeds as high-density populations. While the number of seeds produced by an initially low-density population is sufficient for positive local population growth [50], strong density dependence then limits the number of seeds available for dispersal as the population grows, potentially limiting its ability to provide sufficient seeds to colonise more distant localities. This potential for density dependence to interact with heterogeneity in suitability for population growth has implications for the traits we associate with species having high rates of invasive spread. While previous work has emphasised the importance of traits linked to rapid population growth rate when rare, Pachepsky and Levine [13] show that traits associated with reproduction at both high and low densities may be important.

The importance of interactions between landscape heterogeneity, dispersal and population processes is likely to depend on the extent to which rates of dispersal and population growth are correlated across the landscape, with strong correlations potentially accelerating rates of spread through positive feedback between dispersal and population growth. For example, while Ellner and Schreiber [27] showed that temporal variation in population growth rate

slows spread, such variation will increase the rate of spread if it is positively correlated with dispersal variability. In other words, invasive spread will accelerate if favourable years for local population growth are also associated with favourable years for dispersal. Similarly, Schreiber and Lloyd-Smith [15] show that spread rates increase when dispersal and population growth rates are positively correlated in spatially heterogeneous landscapes, and slow when they are negatively correlated. These findings are important because it may be relatively common for good years or good habitat patches to provide conditions favourable for both population growth and dispersal. Many animal species, for example, exhibit density-dependent dispersal [52], such that patches of higher population growth may lead to greater dispersal distance among animals to avoid crowding effects. Similarly, roadsides are often identified as conduits for the rapid spread of invasive species because they provide corridors of suitable habitat, but also because human-mediated transport along road corridors can facilitate long distance dispersal [38, 53].

The implication is that spatiotemporal heterogeneity in environmental conditions can result in windows of opportunity where conditions are particularly favourable for both population growth and dispersal [54], and that even brief windows of opportunity could play a critical role in accelerating the spread of invasive species. Such heterogeneity also provides a plausible mechanism for the widely observed time lag between establishment and the start of rapid population growth and spread in invasive species [15, 55].

If spatial variation in dispersal and population growth are positively correlated, then management aimed at reducing spread may be most effective if it targets habitats with high suitability for both [32]. Without detailed knowledge of how dispersal and population growth vary across the landscape, it is less clear which should be targeted. Coutts et al. [12] found that dispersal was the main factor driving spread in a spatially explicit invasive plant simulation model, implying that management aimed at limiting dispersal at key locations in the landscape may be the most effective way to slow invasions. Nevertheless, they also found that interactions between drivers could result in habitat manipulations having highly variable and unpredictable outcomes. Indeed, we suspect there is no universal answer as to the relative importance of dispersal versus population growth in influencing spread, given the potential for these processes to both interact and covary across the landscape. In pine species, for example, Caplat et al. [30] found that intraspecific variation in seed terminal velocity had the largest effect on spread rate via wind, while Nathan et al. [56], using a similar approach, found that wind velocity was more important. The differing results were attributed to stronger mean

wind velocity in the Nathan et al. [56] study, emphasising the importance of landscape context and highlighting that spread dynamics result from interactions between landscape conditions and demographic processes.

Conclusion

Figure 1 provides a framework identifying how landscape heterogeneity affects invasive spread, both as a direct consequence of variations in dispersal, settlement and population growth across the landscape, and because the joint effects of these processes are not additive, resulting in interactions that increase the range of possible outcomes. Our review has identified areas of recent progress in understanding how these processes combine to determine invasive spread, but has also highlighted gaps in our understanding that provide avenues for further research:

1. Relative to understanding how variation in population processes affect spread, we understand less about how dispersal behaviour varies across the landscape and the implications of this for spread dynamics.
2. Interactions between landscape heterogeneity, dispersal and population processes appear key to understanding spread, and demographic and environmental stochasticity play a central role in these interactions.
3. Spread dynamics should be influenced by the degree to which variation in dispersal behaviour and population processes are correlated across the landscape, because this can result in positive feedback that disproportionately drives spread.

Acknowledgements This work was supported by ARC grant LP150100375.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

References

1. Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ. Naturalization and invasion of alien plants: concepts and definitions. *Divers Distrib.* 2000;6(2):93–107.
2. Tingley R, Phillips BL, Letnic M, Brown GP, Shine R, Baird SJ. Identifying optimal barriers to halt the invasion of cane toads *Rhinella marina* in arid Australia. *J Appl Ecol.* 2013;50:129–37.
3. Letnic M, Webb JK, Jessop TS, Dempster T. Restricting access to invasion hubs enables sustained control of an invasive vertebrate. *J Appl Ecol.* 2015;52:341–7.

4. Caplat P, Coutts S, Buckley YM. Modeling population dynamics, landscape structure, and management decisions for controlling the spread of invasive plants. *Ann N Y Acad Sci.* 2012;1249(1):72–83.
5. Skellam JG. Random dispersal in theoretical populations. *Biometrika.* 1951;38:196–218.
6. Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA. The spatial spread of invasions: new developments in theory and evidence. *Ecol Lett.* 2005;8:91–101.
7. van den Bosch F, Hengeveld R, Metz JAJ. Analysing the velocity of animal range expansion. *J Biogeogr.* 1992;19(2):135–50.
8. Higgins S, Richardson D, Cowling R. Modeling invasive plant spread: the role of plant-environment interactions and model structure. *Ecology.* 1996;77(7):2043–54.
9. Marco D, Páez S. Invasion of *Gleditsia triacanthos* in *Lithraea ternifolia* montane forests of Central Argentina. *Environ Manage.* 2000;26(4):409–19.
10. Shigesada N, Kawasaki K. Biological invasions: theory and practice (Oxford University Press). 1997.
11. With KA. The landscape ecology of invasive species. *Conserv Biol.* 2002;16(5):1192–203.
12. Coutts SR, van Klinken RD, Yokomizo H, Buckley YM. What are the key drivers of spread in invasive plants: dispersal, demography or landscape: and how can we use this knowledge to aid management? *Biol Invasions.* 2011;13(7):1649–61.
13. Pachepsky E, Levine JM. Density dependence slows invader spread in fragmented landscapes. *Am Nat.* 2011;177(1):18–28.
14. Jongejans E, Shea K, Skarpaas O, Kelly D, Ellner SP. Importance of individual and environmental variation for invasive species spread: a spatial integral projection model. *Ecology.* 2011;92(1):86–97.
15. Schreiber SJ, Lloyd-Smith JO. Invasion dynamics in spatially heterogeneous environments. *Am Nat.* 2009;174:490–505.
16. Melbourne BA, Hastings A. Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science.* 2009;325:1536–9.
17. Vilà M, Ibáñez I. Plant invasions in the landscape. *Landsc Ecol.* 2011;26(4):461–72.
18. Hodgson JA, Thomas CD, Dytham C, Travis MJJ, Cornell SJ. The speed of range shifts in fragmented landscapes. *PLoS One.* 2012;7(10), e47141.
19. Pulliam HR. On the relationship between niche and distribution. *Ecol Lett.* 2000;3(4):349–61.
20. Meffin R, Duncan RP, Hulme PE. Landscape-level persistence and distribution of alien feral crops linked to seed transport. *Agric Ecosyst Environ.* 2015;203:119–26.
21. Kot M, Lewis MA, Van Den Driessche P. Dispersal data and the spread of invading organisms. *Ecology.* 1996;77(7):2027–42.
22. Bullock JM, Moy IL, Coulson SJ, Clarke RT. Habitat-specific dispersal: environmental effects on the mechanisms and patterns of seed movement in a grassland herb *Rhinanthus minor*. *Ecography.* 2003;5:692–704.
23. Pulliam H. Sources, sinks and population regulation. *Am Nat.* 1988;132:652–61.
24. Duncan RP, Blackburn TM, Rossinelli S, Bacher S. Quantifying invasion risk: the relationship between establishment probability and founding population size. *Methods Ecol Evol.* 2014;5:1255–63.
25. Duncan RP. How propagule size and environmental suitability jointly determine establishment success: a test using dung beetle introductions. *Biol Invasions.* 2016;18(4):985–96.
26. Von Holle B, Simberloff D. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology.* 2005;86(12):3212–8.
27. Ellner SP, Schreiber SJ. Temporally variable dispersal and demography can accelerate the spread of invading species. *Theor Popul Biol.* 2012;82(4):283–98.
28. Carrasco LR, Mumford JD, MacLeod A, Harwood T, Grabenweger G, Leach AW, Knight JD, Baker RH. Unveiling human-assisted dispersal mechanisms in invasive alien insects: integration of spatial stochastic simulation and phenology models. *Ecol Modell.* 2010;221:2068–75.
29. Liebhold AM, Tobin PC. Population ecology of insect invasions and their management. *Annu Rev Entomol.* 2008;53:387–408.
30. Caplat P, Nathan R, Buckley YM. Seed terminal velocity, wind turbulence, and demography drive the spread of an invasive tree in an analytical model. *Ecology.* 2012;93(2):368–77.
31. Cousens R, Heydel F, Giljohann K, Tackenberg O, Mesgaran M, Williams N, Eldershaw V. Predicting the dispersal of hawkweeds (*Hieracium aurantiacum* and *H. praealtum*) in the Australian Alps. *18th Australas Weeds Conf:*5–8. 2012.
32. Williams NSG, Hahs AK, Morgan JW. A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. *Ecol Appl.* 2008;18:347–59.
33. Miller AL, Wiser SK, Sullivan JJ, Duncan RP. Creek habitats as sources for the spread of an invasive herb in a New Zealand mountain landscape. *N Z J Ecol.* 2015. 39:in press.
34. Gelbard JL, Harrison S. Roadless habitats as refuges for native grasslands: interactions with soil, aspect, and grazing. *Ecol Appl.* 2003;13(2):404–15.
35. Driscoll DA, Banks SC, Barton PS, Ikin K, Lentini P, Lindenmayer DB, Smith AL, Berry LE, Burns EL, Edworthy A, Evans MJ. The trajectory of dispersal research in conservation biology. Systematic review. *PLoS One.* 2014;9(4):e95053.
36. Manel S, Gaggiotti OE, Waples RS. Assignment methods: matching biological questions with appropriate techniques. *Trends Ecol Evol.* 2005;20(3):136–42.
37. Zeller KA, McGarigal K, Whiteley AR. Estimating landscape resistance to movement: a review. *Landsc Ecol.* 2012;27:777–97.
38. Medley KA, Jenkins DG, Hoffman EA. Human-aided and natural dispersal drive gene flow across the range of an invasive mosquito. *Mol Ecol.* 2015;24(2):284–95.
39. Fisher RA. The wave of advance of advantageous genes. *Ann Eugen.* 1937;7:355–69.
40. Pitt JPW, Womer SP, Suarez AV. Predicting Argentine ant spread over the heterogeneous landscape using a spatially-explicit stochastic model. *Ecol Appl.* 2009;19(5):1176–86.
41. Keeling MJ. Dynamics of the 2001 UK Foot and Mouth epidemic: Stochastic dispersal in a heterogeneous landscape. *Science.* 2001;294:813–7.
42. Sebert-Cuvillier E, Simon-Goyheneche V, Paccaut F, Chabrierie O, Goubet O, Decocq G. Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model. *Landsc Ecol.* 2008;23(7):787–801.
43. Dewhurst S, Lutscher F. Dispersal in heterogeneous habitats: thresholds, spatial scales, and approximate rates of spread. *Ecology.* 2009;90(5):1338–45.
44. Rigot T, van Halder I, Jactel H. Landscape diversity slows the spread of an invasive forest pest species. *Ecography.* 2014;37(7):648–58.
45. Kinezaki N, Kawasaki K, Shigesada N. The effect of the spatial configuration of habitat fragmentation on invasive spread. *Theor Popul Biol.* 2010;78(4):298–308.
46. Resasco J, Haddad NM, Orrock JL, Shoemaker D, Brudvig LA, Damschen EI, Tewksbury JJ, Levey DJ. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species reports. *Ecology.* 2014;95(8):2033–9.
47. Dennis B, Munholland P, Scott M. Estimation of growth and extinction parameters for endangered species. *Ecology.* 1991;61:115–43.
48. Fitzpatrick MC, Preisser EL, Porter A, Elkinton J, Ellison AM. Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. *Ecol Appl.* 2012;22(2):472–86.
49. Giometto A, Rinaldo A, Carrara F, Altermatt F. Emerging predictable features of replicated biological invasion fronts. *Proc Natl Acad Sci U S A.* 2014;111(1):297–301.

50. Warren RJ, Bahn V, Bradford MA. The interaction between propagule pressure, habitat suitability and density-dependent reproduction in species invasion. *Oikos*. 2012;121(6):874–81.
51. Snyder RE. How demographic stochasticity can slow biological invasions. *Ecology*. 2003;84(5):1333–9.
52. Matthysen E. Density-dependent dispersal in birds and mammals. *Ecography*. 2005;28:403–16.
53. Warren RJ, Ursell T, Keiser AD, Bradford MA. Habitat, dispersal and propagule pressure control exotic infilling within an invaded range. *Ecosphere*. 2013;4:1–12.
54. Johnstone I. Plant invasion windows: a time-based classification of invasion potential. *Biol Rev*. 1986;61:369–94.
55. Aikio S, Duncan RP, Hulme PE. Lag phases in alien plant invasions: separating the facts from the artefacts. *Oikos*. 2010;119:370–8.
56. Nathan R, Safriel U, No-Meir I. Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology*. 2001;82:374–88.