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Scale invariance in the spatial-dynamics of biological invasions

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Abstract

Despite the enormous negative consequences of biological invasions, we have a limited understanding of how spatial demography during invasions creates population patterns observed at different spatial scales. Early stages of invasions, arrival and establishment, are considered distinct from the later stage of spread, but the processes of population growth and dispersal underlie all invasion phases. Here, we argue that the spread of invading species, to a first approximation, exhibits scale invariant spatial-dynamic patterns that transcend multiple spatial scales. Dispersal from a source population creates smaller satellite colonies, which in turn act as sources for secondary invasions; the scale invariant pattern of coalescing colonies can be seen at multiple scales. This self-similar pattern is referred to as "stratified diffusion" at landscape scales and the "bridgehead effect" at the global scale. The extent to which invasions exhibit such scale-invariant spatial dynamics may be limited by the form of the organisms' dispersal kernel and by the connectivity of the habitat. Recognition of this self-similar pattern suggests that certain concepts for understanding and managing invasions might be widely transferable across spatial scales.

Keywords

bridgehead effect, coalescing colonies, invasion framework, self-similarity, spread, stratified dispersal

Introduction

The phenomenon of biological invasions occurs among a wide variety of organisms representing virtually all major animal, plant and microbial taxa (Lockwood et al. 2013). Though the details of invasions vary considerably among different species, the existence of common biological processes during all invasions is widely recognized. One of the earliest, simplest and widely applied frameworks for stages through which all invasions pass was proposed by Dobson and May (1986) who recognized three discrete stages: arrival of the species beyond its native range, followed by establishment of the population to a level beyond which extinction is unlikely, and spread into surrounding unoccupied patches. Several variants on this framework have been proposed, but the most widely applied of these break up the arrival stage into two successive stages: transport (movement of propagules from the native to non-native habitat) and introduction (escape or release of individuals following transport) (Duncan et al. 2003; Richardson et al. 2000; Blackburn et al. 2011). In these frameworks, species pass through various population processes and barriers as they move between successive invasion stages.

Here we argue that while these widely applied invasion frameworks have been tremendously useful, they emphasize distinct invasion stages even though all stages biologically ensue from just two demographic processes-dispersal and population growth. This, in turn, may produce scale-invariant properties that characterize invasions across all spatial scales. Given these common underlying mechanisms, different invasion stages can be considered manifestations of similar processes operating at different spatial scales. And as such, the spatial-dynamics of many invasions exhibit common structures that are evident at multiple spatial scales, leading to a self-similar or fractal spatial structure. Below we present the theoretical basis for the emergence of these scale invariance patterns and discuss the resulting practical implications.

Scale invariance

Population growth and dispersal are the two basic population processes that underlie invasions across all stages. These two processes form the basis for both the “early” phase of invasions (arrival / establishment) and the “later” phase (spread) and there is a fundamental similarity in the way these processes are expressed at multiple spatial scales. Inter-continental movement of propagules that found new reproducing colonies is inherently similar to the movement and growth of populations along an expanding population front within a continent. This coupling of dispersal with population growth is a fundamental dynamic occurring at multiple spatial scales to produce both the arrival / establishment and spread invasion phases. Recognizing this underlying similarity suggests that there is a continuum of spatial scales over which these recurring processes operate.

The concept of scale invariance has been widely applied in physics and statistics and refers to characteristics or processes that are constant across multiple scales or energy levels (Stanley et al. 2000). Scale invariance is also referred to as ‘self-similarity’ which represents the concept that when viewing an object, as one zooms in or out, the spatial structure of objects appears the same. An example of self-similarity are fractals which are geometrical figures in which each part has the same properties as the whole.

Fractals have been applied in many different scientific disciplines and among these, fractals have proven useful for describing spatial patterns in ecology (Keitt and Stanley 1998; Keitt et al. 2002; Marquet et al. 2005). Compared to rigorous theoretical definitions, ecological systems generally do not exhibit true fractals or scale invariance but these concepts do provide insight for describing ecological patterns at multiple scales (Halley et al. 2004). Survey data characterizing the spatial-dynamics of invasions at various spatial scales suggest that biological invasion may be characterized by scale invariant patterns (Fig. 1B–E). Although relatively few studies have compared invasion spread patterns across spatial scales and though radial rates of spread may vary depending upon the scale at which it is measured, there is evidence of similarity in the geometry of spread across scales ranging from intercontinental to local (Mack et al. 2007; Pyšek et al. 2008). Furthermore, recent theoretical work on the mechanisms driving the spatial-dynamics of invasions provides insight into processes responsible for scale invariance (Hallatschek and Fisher 2014). Cannas et al. (2006) used a theoretical model to demonstrate that long-distance dispersal can create a fractal invasion front; they related the fractal dimension of this pattern to the characteristics of the dispersal function. Below, we describe two processes, stratified dispersal and the bridgehead effect; while these processes function at very different spatial scales, their underlying topologies and resultant patterns share a remarkable similarity. As part of both processes, isolated colonies are founded via jump dispersal; these colonies grow and spawn more colonies which ultimately coalesce (Fig. 1A).

Stratified dispersal

As pointed out by Cannas et al. (2006) dispersal plays a key role in creating self-similarity in invasion fronts across multiple spatial scales. The existence of long-distance dispersal coupled with localized dispersal was described as "stratified dispersal" by Hengeveld (1989) who noted that such a phenomenon is common in invading populations. Often, localized dispersal is caused by natural movement of organisms while long-distance dispersal is typically the result of anthropogenic movement of organisms, though human-mediated dispersal can contribute to both long- and short distance dispersal (Wilson et al. 2009; Gippet et al. 2019). Such coupling of long- and short-distance dispersal driving invasion spread has been observed in a variety of organisms ranging from plants to insects (Suarez et al. 2001; Trakhtenbrot et al. 2005; Pyšek et al. 2008; Lockwood et al. 2013). The gypsy moth, *Lymantria dispar*, provides a classic example; over short distances (0–100 m) movement occurs via windborne dispersal of young caterpillars, while long-distance dispersal (5–5000 km) occurs by accidental transport of life stages by humans (Sharov and Liebhold 1998). Theoretical ecologists often describe such movement patterns using leptokurtic "fat-tailed" dispersal kernels (Kot et al. 1996; Hallatschek and Fisher 2014). This same spatial-dynamic pattern of

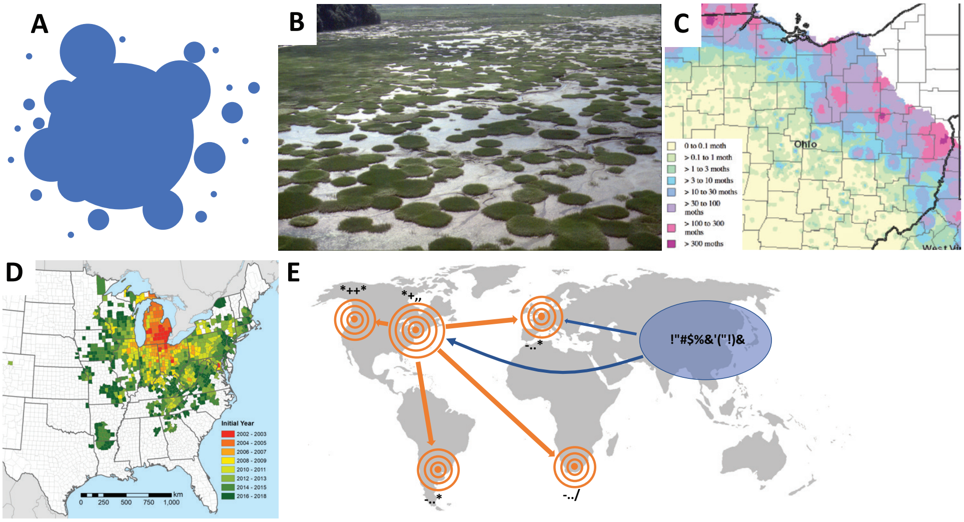

Figure 1. Examples of coalescing colonies seen in the invasions of different species viewed at varying scales **A** conceptual representation of invasion via coalescing colonies **B** aerial photo showing *Spartina alterniflora* invasion into Willapa Bay, WA, (photo by Fritzi Grevstad) **C** spread of the gypsy moth, *Lymantria dispar*, in Ohio, USA. Interpolated pheromone trap captures from 2019 (data at http://yt.ento.vt.edu/da/) **D** spread of the emerald ash borer, *Agrilus planipennis*, in the eastern USA showing year of first discovery by county (data from USDA APHIS) **E** historical global spread of the Harlequin ladybird *Harmonia axyridis* (modified from Lombaert et al. 2010). Eastern North America has functioned as a bridgehead region from which colonization of other continents has originated.

invasion via long-distance dispersal founding coalescing colonies is sometimes referred to as "nucleation" or "nascent foci" in the plant invasion literature (Moody and Mack 1988; Pausas et al. 2006; Milton et al. 2007)

Regardless of the term, stratified dispersal is well known to play a key role in invasion spread. Simple models show that stratified dispersal creates a pattern in which isolated populations form ahead of the invasion front (via long-distance dispersal); these colonies then expand as isolated colonies that ultimately coalesce with each other and the main invasion front (Kot et al. 1996; Shigesada et al. 1995; Hallatschek and Fisher 2014) (Figure 1A). These studies demonstrate that the existence of long-range dispersal plays a key role in elevating rates of range expansion above levels that would occur through simple diffusive dispersal (Higgins and Richardson 1999). This phenomenon of coalescing colonies is a space-time pattern commonly observed in the spread of many types of organisms. Figure 1B–D shows examples in several organisms.

Bridgehead effect

The bridgehead effect is a term used to describe large-scale (global) patterns of invasion in which organisms initially invade one region but this invaded region then becomes a source of propagules for invading more regions (Figure 1E). This phenomenon has been documented in historical global patterns of invasions for several individual plant and animal species using genetic markers (e.g. Lombaert et al. 2010). Bertelsmeier et al. (2018) characterized the bridgehead effect for an entire taxonomic group consisting of ants (Hymenoptera: Formicidae) invading the USA; most ant species arriving at US ports are native to Africa, but they predominantly arrive on shipments originating from previously invaded portions of Central America which function as bridgehead regions. While theories have been proposed to explain the bridgehead effect based upon evolution of greater invasiveness in bridgehead populations, Bertelsmeier and Keller (2018) found little evidence supporting these theories and showed that the phenomenon more likely results from purely demographic reasons in which initial invasion of bridgehead regions results in dense populations which then serve as sources of propagules that invade other regions. Bridgehead dynamics are also driven by global transportation networks that channel invasions into hubs from which populations subsequently spread into surrounding regions (Tatam 2009). Bertelsmeier et al. (2017) describe a global pattern recurrently seen among various ant species; alien populations establish in multiple continents followed by expansion of these populations into adjacent regions.

Though operating at a much larger scale, the bridgehead effect shows a remarkable resemblance to stratified dispersal. Both processes are characterized by initial founding of isolated colonies which grow, spawn more colonies and ultimately coalesce. The net result of the bridgehead effect is the creation of invasion patterns at large spatial scales that are similar to that of coalescing colonies resulting from stratified dispersal seen at smaller spatial scales.

Not all invasions exhibit either stratified dispersal or the bridgehead effect and the reasons for this may be varied. For one, dispersal of some species is not characterized by long-distance dispersal. For example, the historical spread of muskrats, *Ondatra zibethica*, in Europe (Ulbrich 1930) was continuous, without jumps, apparently due to the lack of long-distance dispersal (dispersal is relatively short ranged with little anthropogenic movement in this species). Another factor that profoundly affects spatial-dynamics during the spread of invading species, is habitat connectivity (With 2002). Connectivity of habitats may vary with spatial scale and the constraints that connectivity places on spread may limit the spatial dynamics of invading populations from exhibiting scale invariance.

Implications

Introduction of alien species through human agency is a major component of global change, affecting biodiversity patterns and composition at multiple scales of organization. Here we describe a phenomenon frequently seen in the spatial-dynamics of biological invasions that reflects a scale invariant pattern operating across scales ranging from continents to landscapes. The existence of these consistent patterns of spatial-dynamics suggests that the stages of arrival, establishment and spread can be considered descriptions of a fundamentally similar scale invariant process at different spatial scales. While several invasion frameworks provide extensive detail of the various phases through which invasions progress, our description here of scale invariant patterns suggest an underlying similarity among invasion phases and future frameworks may be able to incorporate these similarities in a simpler structure.

There are implications that emerge from this scale-invariant perspective on invasions. First is the suggestion that approaches currently applied to model invasion spread at relatively small spatial scales could be applied to characterize the spatial dynamics of global (intercontinental) invasions. Several types of models have been developed to describe the role of stratified dispersal in the spatial dynamics of invading populations during the spread stage (e.g., Shigesada et al. 1995; Kot et al. 1996; Lewis and Pacala 2000). Similarly, gravity models are often applied to model localized invasion spread (Potapov et al. 2011). New insight may be gained by applying these approaches to model bridgehead dynamics in invasions at global scales.

Another implication of scale invariance is that some of the strategies applied to manage invasions at large global spatial scales could potentially also be applied to manage spread at more local scales. For example, surveillance and eradication are widely applied by national governments to detect and eliminate nascent invading populations in their countries. Though there are relatively few examples of successful barrier-zone programs within countries or regions (Liebhold and Kean 2019), this strategy could be applied at smaller spatial scales to contain local invasion spread. One of the few examples of such application of surveillance and eradication at a local level to contain spread is the current program to contain gypsy moth spread in North America by deploying thousands of traps along the expanding population front to detect isolated populations that are eradicated in order to contain populations (Tobin and Blackburn 2007). These types of strategies have sometimes been applied to contain the spread of plants (Moody and Mack 1988) but rarely considered for animal invasions.

Identification of the roles of bridgehead effects and stratified dispersal have both been consequential developments that have improved our understanding of biological invasions. Recognition that these are self-similar phenomena, reflecting the scale invariance of invasions, may lead to further insights into the study of invasions. Ultimately, such developments in our understanding of invasions can lead to more effective biosecurity measures and ultimate mitigation of the impacts of biological invasions in the future.

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