

Spread dynamics of invasive species

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Species invasions are a principal component of global change, causing large losses in biodiversity as well as economic damage. Invasion theory attempts to understand and predict invasion success and patterns of spread. However, there is no consensus regarding which species or community attributes enhance invader success or explain spread dynamics. Experimental and theoretical studies suggest that regulation of spread dynamics is possible; however, the conditions for its existence have not yet been empirically demonstrated. If invasion spread is a regulated process, the structure that accounts for this regulation will be a main determinant of invasion dynamics. Here we explore the existence of regulation underlying changes in the rate of new site colonization. We employ concepts and analytical tools from the study of abundance dynamics and show that spread dynamics are, in fact, regulated processes and that the regulation structure is notably consistent among invasions occurring in widely different contexts. We base our conclusions on the analysis of the spread dynamics of 30 species invasions, including birds, amphibians, fish, invertebrates, plants, and a virus, all of which exhibited similar regulation structures. In contrast to current beliefs that species invasions are idiosyncratic phenomena, here we provide evidence that general patterns do indeed exist.

conservation | invasion | population dynamics | range expansion | regulation

Species invasions are a principal component of global change, given that they can cause habitat degradation, extinction of native flora and fauna, changes in ecosystem functioning, and facilitation of subsequent invasions that reinforce the aforementioned damage (1). The magnitude of the problem is such that invasive species threaten almost 60% of the species listed in the U.S. Endangered Species Act (1). Large economic impacts are also associated with many invasive species, which can provoke agricultural losses, disrupt ecosystem services, and lead to disease proliferation (2). Consequently, a prime objective of invasion theory is to understand and predict invasion success and patterns of spread (2). Since the early works of Fisher to the present (e.g., refs. 2–8) invasion theory has principally focused on identifying common features shared among invaders to explain their successful establishment outside their native ranges. In this regard, many alternative approaches have been explored, including theoretical models (reviewed in ref. 3), experimental studies (9), and the search for statistical associations between invasion success and attributes of the invading species or the invaded community (10). Despite the great advances achieved thus far, many aspects of real invasion dynamics continue to be poorly understood. In particular, commonalities among invaders have remained elusive, and idiosyncratic explanations of invasions have been more emphasized (11–13). Unfortunately, this lack of generality is of little use for control and management purposes, and a more profound understanding of the spreading process is urgently needed to develop wide-ranging strategies for coping with the impacts caused by biological invasions (2).

Although specific, taxa-independent characteristics that facilitate successful establishment and expansion have not been unambiguously identified, the invasion process itself has been

observed to roughly follow the same sequence of stages regardless of the taxonomic identity of the invader: (i) an initial establishment phase with low spread, (ii) an expansion phase marked by increasing spread rates, and (iii) a saturation phase when spread rates reach a plateau (4). During the expansion phase, successful invaders present unregulated exponential growth in abundance until space becomes saturated (4). However, before saturation, invasion advancement can be weakened by biological constraints. This weakening may occur for several reasons, e.g., (i) individuals must grow to maturity at newly invaded sites before generating propagules for further invasion; (ii) Allee effects may constrain growth at low abundances (9, 14); and (iii) time delays associated with the production and dispersal of propagules potentially impose limits on totally unregulated spread (15, 16). The existence of a reproductive lag, such as that recently reported for *Spartina alterniflora*, illustrates a biological constraint that determines the observed pattern of invasion (17, 18). This type of lag might account for the existence of regulation mechanisms operating during spread; however, conditions for its existence have not yet been empirically demonstrated. Regulation of spread may arise as a consequence of the mechanisms mentioned above (e.g., reproductive lag), or other mechanisms that are yet to be explored, as long as the mechanism acts to establish a relationship between current and future spreading rates (19, 20). However, despite the fact that the scenario for regulation of spread dynamics is theoretically possible, conditions for its existence have not yet been empirically demonstrated.

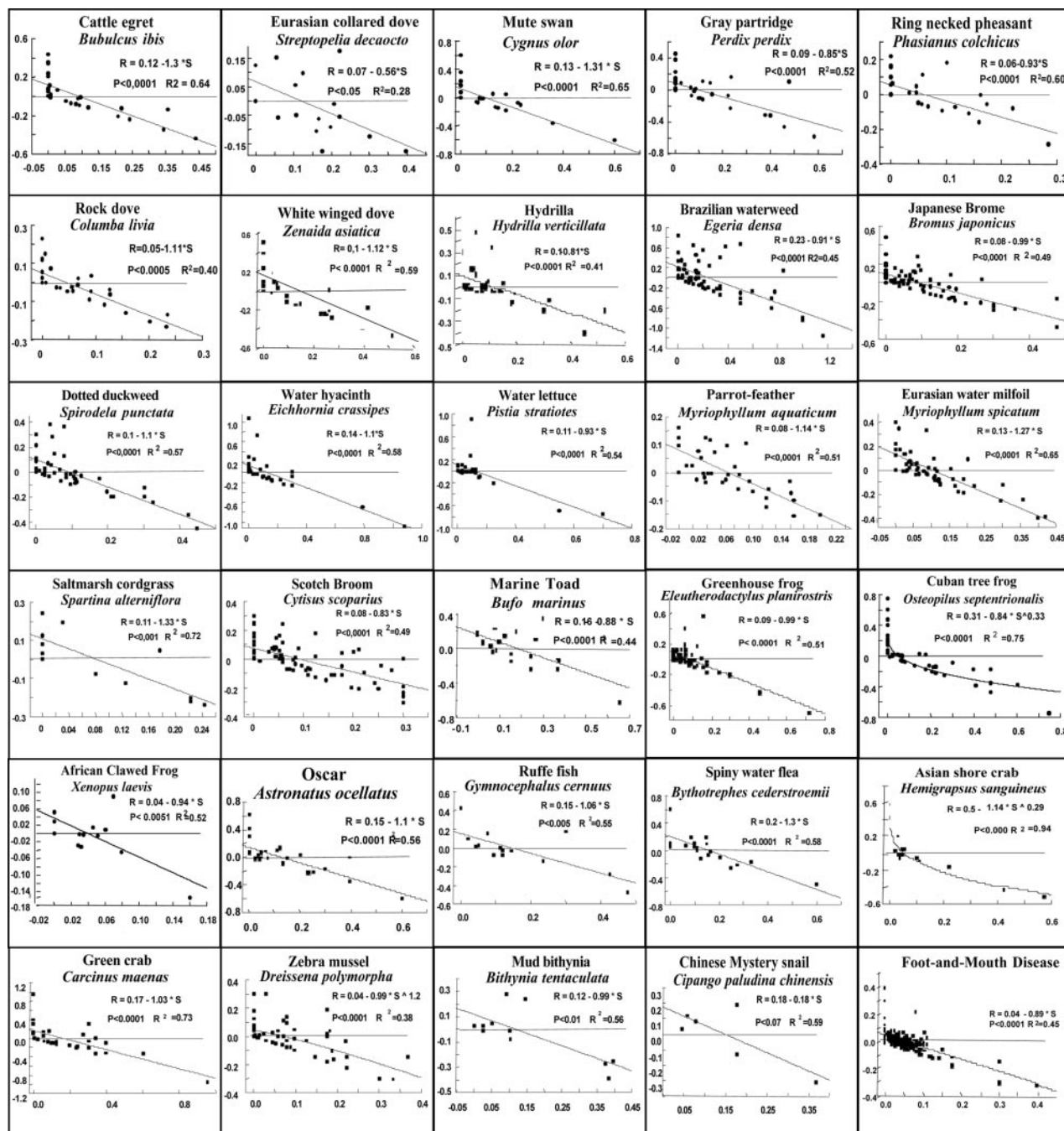
The topic of population regulation has been the focus of an historical debate in ecology (density-dependent versus density-independent population dynamics), which has generated a strong theoretical framework, with a clear definition of regulation, and tools for its detection and analysis (19–24). Population regulation has been defined as the existence of a negative feedback in population abundance with an internal equilibrium condition (20, 24), that is, a negative slope for the relationship between the state variable (e.g., density and spread) and its rate of change, and a 0 rate of change for some value of the state variable. Different types of feedback structures are illustrated in Fig. 1 and explained in more detail elsewhere (see refs. 19, 20, and 24). In this article we assess the existence of these conditions and the functional structure of regulation in the spreading process. The detection of regulation and its structure is in practice estimated by means of a plot that relates the observed rate of change in the variable with the variable itself; following previous terminology, we will refer to these graphs as *R*-functions (20). This approach further allows for the discrimination of unregulated processes (e.g., exponential growth and random walks) from regulated ones (Fig. 1). For example, the *R*-function of deterministic exponential growth is a straight line with a 0 slope (Fig. 1*A*), and a random walk shows a cloud of points with a 0 slope and 0 intercept (Fig. 1*B*). In contrast, the *R*-function of a regulated

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to as first-order dynamics and is typically the result of competition among individuals for a limited resource (20). A similar process could be invoked for spread dynamics, although the precise mechanisms operating on this process still need to be established.

Only two of the species analyzed were best described by markedly nonlinear R -functions (the Cuban tree frog *Osteopilus septentrionalis* and the Asian shore crab *Hemigrapsus sanguineus*). Interestingly, the parameters observed for these R -functions imply the existence of eruptive invasion dynamics. These dynamics originate from three attributes of their R -

function. First, the function is very concave and the equilibrium point is very near to the origin. Second, the slope to the left of the equilibrium point is very steep. Third, the slope to the right of the equilibrium point is shallow. These features imply that negative deviations from equilibrium are largely overcompensated, forcing spread rate to very high values. In contrast, equilibrium is recovered at a slow rate over several time steps after positive deviations. This asymmetry in response to deviations from equilibrium can produce a huge explosion in advancement followed by periods of invasion fade-out tending toward equilibrium. Without knowledge of the regulation structure,

available to better understand patterns of invasion, its underlying mechanisms, and the role played by the environment.

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