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REVIEW AND SYNTHESIS

Boom-bust dynamics in biological invasions: towards an improved application of the concept

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Abstract

Boom-bust dynamics – the rise of a population to outbreak levels, followed by a dramatic decline – have been associated with biological invasions and offered as a reason not to manage troublesome invaders. However, boom-bust dynamics rarely have been critically defined, analyzed, or interpreted. Here, we define boom-bust dynamics and provide specific suggestions for improving the application of the boom-bust concept. Boom-bust dynamics can arise from many causes, some closely associated with invasions, but others occurring across a wide range of ecological settings, especially when environmental conditions are changing rapidly. As a result, it is difficult to infer cause or predict future trajectories merely by observing the dynamic. We use tests with simulated data to show that a common metric for detecting and describing boom-bust dynamics, decline from an observed peak to a subsequent trough, tends to severely overestimate the frequency and severity of busts, and should be used cautiously if at all. We review and test other metrics that are better suited to describe boom-bust dynamics. Understanding the frequency and importance of boom-bust dynamics requires empirical studies of large, representative, long-term data sets that use clear definitions of boom-bust, appropriate analytical methods, and careful interpretations.

Keywords

alien species, biological invasions, concepts, exotic species, invasive species, long-term, management, non-native species, population collapse, population crash, population dynamics, reckless invaders, systematic review.

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INTRODUCTION

One of the most persistent ideas in invasion biology is the boom-bust concept (Elton 1958; Williamson 1996; Simberloff & Gibbons 2004; Lockwood *et al.* 2013). According to this concept, invaders may go through an initial outbreak (or 'boom') phase, in which their population becomes very large, before declining to a much lower population size (the 'bust', 'collapse', 'decline', or 'crash'). Boom-bust dynamics are of fundamental importance to understanding, interpreting, and managing biological invasions. The boom-bust dynamic suggests that the initial outbreak phase may be a transient phenomenon, and focuses attention on the nature, strength, and generality of mechanisms by which the invader and the invaded ecosystem establish a more stable long-term coexistence. It also suggests that the effects of the invader on ecosystem processes and other species in the community, whether harmful or beneficial, are at least partially reversible

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and do not necessarily represent the new, persistent state of the invaded ecosystem.

The boom-bust dynamic has been viewed as a progression from a transient 'harmful' phase to a more persistent 'harmless' phase. The boom-bust concept is therefore of particular significance in the management of biological invasions. If harmful invasions often turn into harmless invasions on their own, then the best management option might be to take no action at all, and simply let the invader's population diminish (e.g. Anon. 2011; Thompson 2014; Pearce 2015). At most, managers might have to mitigate some undesirable short-term effects of the invasion before it enters the 'harmless' phase.

Despite the prominence of the boom-bust phenomenon in invasion biology and its importance to management, ecologists disagree about how frequently it occurs. Williamson's (1996) influential book presented several examples of boom-bust dynamics, mostly from islands, but described such dynamics as 'not common'. In perhaps the most detailed examination of the phenomenon, Simberloff & Gibbons (2004) concluded that 'spontaneous population crashes are a minor phenomenon in invasion biology', but lamented the scarcity of reliable long-term data. In contrast, Davis (2009) wrote that a decline in abundance following a period of dominance was a 'common dynamic', and Lockwood *et al.* (2013) agreed that 'boom and bust dynamics may be quite common'. Aagaard & Lockwood (2016) reported population collapses in many non-native bird populations, and concluded that 'severe, rapid, and persistent population declines may be common among exotic populations'.

It appears that the boom-bust concept is widely accepted among non-scientists, perhaps because it accords with an underlying 'balance of nature' paradigm. For example, Verbrugge *et al.* (2013) found that an overwhelming majority of people surveyed in the Netherlands believed that nature tended to return to its original state after biological invasions. Certainly, materials written for the general public about biological invasions, such as books by Marris (2013), Thompson (2014), and Pearce (2015) often assert some variant of the boom-bust concept. For example: 'most of the time, the tens of thousands of introduced species usually swiftly die out or settle down and become model eco-citizens' (Pearce 2015), or '[a]ny introduced species tends to boom at first, then decline and level off, experts say' (Lavey 2016).

In addition to the problem of inadequate data, already noted by Simberloff & Gibbons (2004), confusion about the frequency and importance of boom-bust dynamics in biological invasions may have arisen at least in part because of imprecision in defining the basic 'boom-bust' dynamic, and from incautious interpretation of inadequate data. In this paper, we (1) describe the common variants of the boom-bust concept, (2) review multiple mechanisms that could produce a boom-bust dynamic in non-native species and (3) describe and evaluate various approaches that have been used or could be used to describe and test for boom-bust dynamics in field data. This overview includes a systematic review of published papers on boom-bust dynamics, as well as analyses of simulated population data to test methods used to describe boom-bust dynamics.

THE BOOM-BUST DYNAMIC AND ITS VARIANTS

Several related but not identical dynamics have been described as 'boom-bust' in invasion ecology and other fields. These dynamics fall into two broad classes: solitary and recurring boom-busts (Fig. 1). In a solitary boom-bust (Fig. 1a), the variable of interest (e.g. population size of the invader) undergoes a rapid, large increase followed by a rapid, large, and sustained decline. It does not recover, and in some formulations, may fall to zero (i.e. the invading population is extirpated). In a recurring boom-bust dynamic (Fig. 1b), which is the usual formulation in economics and sociology (e.g. Hui *et al.* 2010; Angeletos & La'O 2013) but also used in ecology (e.g. Arthington & Balcome 2011), the variable undergoes repeated episodes of boom and bust. Such recurrent booms may be regularly cyclic or irregularly repeated. If booms do recur, they may or may not diminish in size over time (i.e. damped oscillations). Because solitary, cyclic, and irregularly recurring boom-busts can have such different causes, characteristics and management implications, it is worth distinguishing among them.

Perhaps because of the encouraging implication that invaded systems frequently recover on their own, the solitary boom-bust dynamic, rather than the recurrent boom-bust, has been the chief focus of invasion ecology and management, and will be the main subject of this paper. It has four phases (Fig. 1a): (1) a pre-boom phase (i.e. the pre-invasion phase plus sometimes a lag phase), (2) a boom phase, in which the focal variable (e.g. population size or biomass, range size, ecological impact) increases rapidly, (3) a bust phase, in which the focal variable decreases rapidly and (4) a post-bust phase, during which the focal variable persists at a value lower than its peak (although it need not be constant), or drops to zero.

This simple description hides several complications, the most obvious of which is how large or rapid changes must be to qualify as a boom-bust dynamic (Box 1). Additional complicating factors include the spatial scale of the dynamics and the sampling program used to detect them. Some mechanisms produce local population dynamics that are different from those that occur at large scales (see below), so it is important to specify the spatial scale at which boom-bust dynamics are

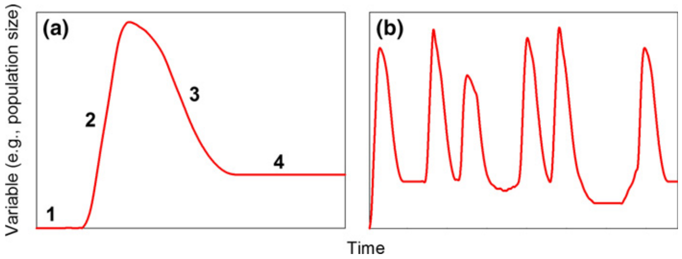

Figure 1 Essential characteristics of (a) solitary and (b) recurring boom-bust dynamics. The four phases of the solitary boom-bust dynamic are 1 = pre-boom (i.e. pre-invasion and lag phase), 2 = boom, 3 = bust, 4 = post-bust; these phases can be repeated in the recurring boom-bust. Real population data typically are noisier than these idealised curves because of environmental variability, year-class interactions, sampling error, and so on.

Box 1 How big do booms and busts have to be to count as a boom-bust?

Our definition of boom-bust dynamics is frustratingly vague, and couched in terms like ‘high value’, ‘rapidly’, and ‘substantially lower’. Why not simply adopt numerical criteria (population growth >X%/year, rising to a value ≥Y, falling to a value ≤Z within N years of peaking)?

To begin with, past practice does not provide clear precedents from which numerical criteria for boom-busts or population declines could be developed. Simberloff & Gibbons (2004) restricted their analysis to ‘cases in which population numbers or densities were believed to have fallen by at least 90% in less than 30 years’, but such rigorous definition is unusual (Table 1). Most authors have used ‘boom-bust’ in a much looser sense simply to mean a dramatic increase in a population followed by a dramatic, persistent decline, without specifying numerical thresholds for rates or amounts of change. When numerical thresholds are specified for boom-busts or population declines, they do not agree with one another (Table 1).

In addition, several complications make it difficult (and probably counterproductive) to specify general numerical criteria for boom-bust dynamics from first principles. First, the underlying basis for the criteria could be how unusual the dynamic is, compared to all observed population dynamics; how large or rapid the population change is, compared to its usual temporal variation; or whether the dynamic is large enough to cross thresholds of ecological or economic damage (see Sandström *et al.* 2014 for such an application). It would be hard to argue that any one of these approaches is always superior to the others, and the different approaches are not necessarily congruent with one another.

Second, different species and ecological processes have different characteristic response times. Rates of population change, expressed as % per year, will vary with the generation time of the organism or where it is located on the fast-slow continuum of life histories (e.g. Jeschke & Kokko 2009), so a tree population undergoing boom-bust dynamics could have very different rates of change than a booming-and-busting zooplankton population. One solution to this problem would be to rescale the *x*-axis to generation times rather than years. However, if we expand the definition of boom-bust to include impacts or range size as well as population size, there may be more than one characteristic time scale involved in the dynamics, so it may not be simple to identify an appropriate temporal rescaling that is equivalent to generation time.

Third, the amount of change in population size that would qualify as ‘important’ or ‘dramatic’ will vary across systems, depending on the interests of the scientist or manager. A 20% decline in population could be highly interesting or important in one system but trivial in another.

Finally, as a practical matter, our ability to detect boom-bust dynamics depends strongly on the characteristics (length, variability) of the data set. It hardly seems useful to set universal numerical criteria for boom-bust dynamics that would be readily detectable in some data sets but entirely undetectable in others.

For all of these reasons, it does not seem worthwhile to include numerical criteria in the general definition of boom-bust dynamics. Nevertheless, in any individual analysis of biological invasions it will be essential to go beyond vague notions of what constitutes boom-bust dynamics, and carefully specify what is meant by ‘boom-bust’. For instance, an ecologist studying an invading zooplankton species that has several generations per year may define a bust as a decline to a population density of <X individual/L (a threshold of economic damage) within I years of invasion, a forest ecologist may choose to define a bust as a decline of Y% in standing biomass of a non-native tree within J years, and a demographer doing a cross-taxon analysis may define a bust as a Z% decline in population density within K generations. These are very different definitions of bust, but all are specific and measurable.

observed. Depending on the purpose of the analysis, though, local, regional, or global population dynamics may be of interest, so we see no reason to insist that boom-bust dynamics be analyzed at a particular spatial scale, other than to note that boom-bust dynamics at very small spatial scales (e.g. a few m^2) are likely to be common but uninteresting to most invasion ecologists and managers. Variables other than population size (or density) may be used to assess boom-bust dynamics. Invasion ecologists may choose to analyse the time-course of range size or ecological impact of the non-native species (Table 1), either because these data are available and population data are not, or because the focus of the study is on range or impacts, both of which have received much attention in invasion ecology (Parker *et al.* 1999; Simberloff *et al.* 2013; Jeschke *et al.* 2014). These different descriptors of the invading population do not necessarily map simply onto one another. Indeed, it has been demonstrated that temporal changes in the population size and range size of species can be positively correlated, uncorrelated, or negatively correlated (e.g. Gaston 2003). Likewise, impacts may not always tightly track population size, for example because the relationship between density and impact is nonlinear (Yokomizo *et al.* 2009; Dostál *et al.* 2013), because of trait shifts in the invader’s population (e.g. Fig. 2, Pace *et al.* 2010), or because the impacts may be time-lagged, hysteretic, or even irreversible. Consequently, these different descriptors of invading populations probably should not be combined uncritically with one another into a single analysis.

In view of these considerations, we offer the following general definitions. In a *solitary boom-bust dynamic*, the response variable rises rapidly from a low baseline or zero value to a high value (the boom), then drops (the bust) to and persists at values substantially lower than the boom, possibly even zero. In a *recurrent boom-bust dynamic*, this up-and-down dynamic is repeated two or more times, possibly with diminishing amplitude, and in a *cyclic boom-bust dynamic* (a variant of the

Table 1 Selected characteristics of published scientific studies on boom-bust dynamics of non-native populations (*n* = 56 papers)

	Number of studies (%)
Metric used to describe population (*n* = 53)	
Population density (areal)	24 (45)
Population size (abundance)	13 (25)
Biomass	7 (13)
Catch-per-unit-effort	7 (13)
Range size	6 (11)
% cover	3 (6)
Total catch	3 (6)
Population density (volumetric)	1 (2)
Criterion used to support claim of boom-bust (*n* = 56)	
Quantitative	31 (55)
Narrative	23 (41)
Not given	3 (5)
Decline reported, in quantitative studies (*n* = 29)	
50–74%	9 (31)
75–89%	4 (14)
90–98%	6 (21)
>98%	10 (34)
Evidence for cause (*n* = 56)	
Causes hypothesised	35 (63)
Causes demonstrated	16 (29)
Causes not given	5 (9)
Length of study (years) (*n* = 54)	
≤5	11 (20)
6–10	11 (20)
11–20	10 (19)
21–40	11 (20)
41–80	8 (15)
81–157	3 (6)

Some studies fit into more than one category (e.g. used more than one metric of population size) or had missing data, so the number of studies does not always sum to 56. Some studies used multiple data sets; the length of study given below is an average for the data sets used in the study. More details about this analysis, including a description of methods, are given in Appendix S1.

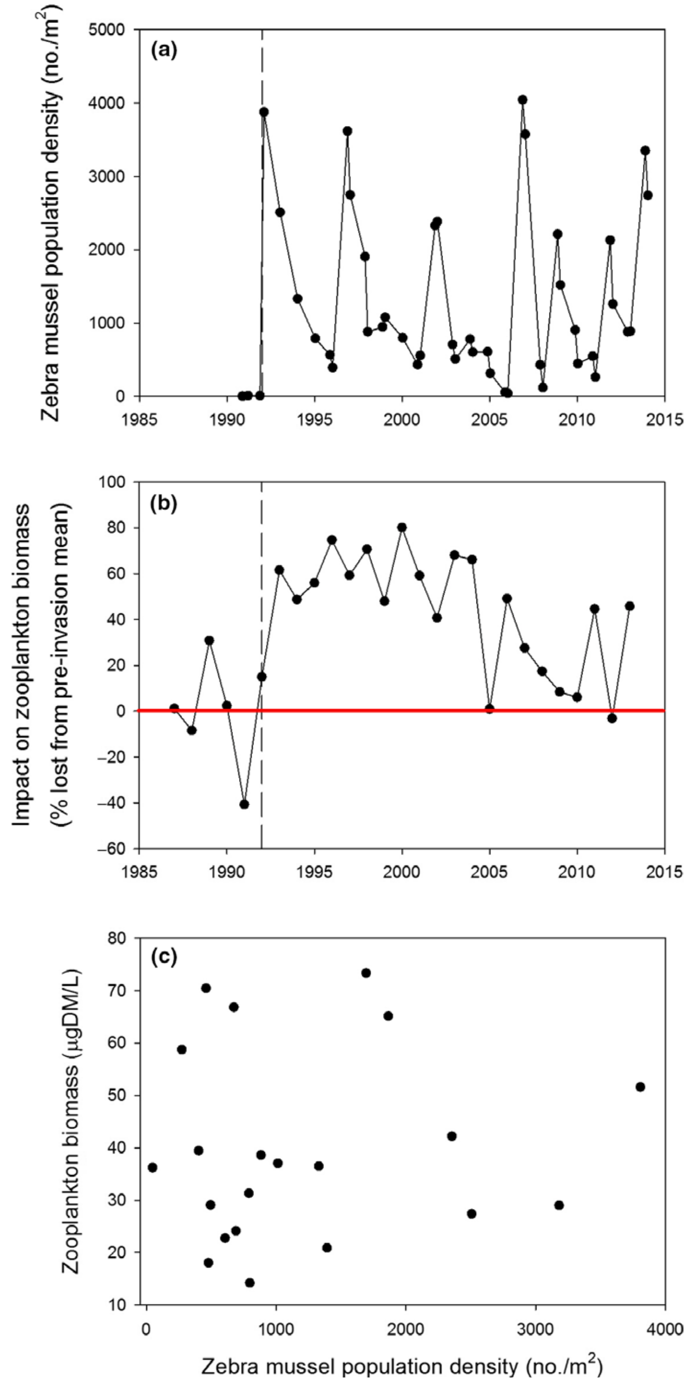

Figure 2 Example showing non-congruence of population size and impacts of a non-native species, extended from Pace *et al.* (2010). (a) population density of zebra mussels (*Dreissena* spp.) in the Hudson River estuary; (b) boom and bust of impacts on zooplankton biomass; and (c) lack of correlation ($r^2 < 0.01$) between these two variables for the post-invasion period (1993–2013). This lack of correlation is apparently a result of shifts in the body sizes of zebra mussels in the river (Pace *et al.* 2010; Carlsson *et al.* 2011).

recurrent boom-bust dynamic), the booms occur at more or less regular intervals. Although recurring seasonal cycles of population size may technically meet this broad definition of cyclic boom-bust, we follow customary usage and exclude them from further consideration.

CAUSES OF BOOM-BUST DYNAMICS

If we were monitoring a local population of an invader, and observed a dynamic like that shown in Fig. 1a, what could we infer about its cause and meaning? The dynamic shown in Fig. 1a is simple and combines three common attributes of biological populations: rapid growth, a large peak population, and a severe decline, each of which can be produced by several causes well known to ecologists. Consequently, boom-bust dynamics could be produced by many different mechanisms, only some of them closely related to the restoration of nature's balance following a biological invasion. It would be difficult to catalogue all possible causes of a boom-bust dynamic, but we briefly discuss some of the more likely ones. For convenience, we divide these mechanisms between (A) those that are typically associated with invasions and (B) those that occur broadly in ecology (not just in invasions, but which may affect invaders), recognising that some of these mechanisms do not fall cleanly into just one of these categories.

(A) Mechanisms typically associated with invasions

Some mechanisms leading to boom-bust dynamics are characteristically if not exclusively associated with invasions of new ranges.

(A1) Enemy release followed by enemy accumulation

Boom-bust dynamics of invaders probably are most often attributed to this mechanism (predator-prey or diseases/parasites in Fig. 3; Simberloff & Gibbons 2004). Invaders often are introduced into a new range without their full complement of enemies such as predators, parasites and pathogens (the 'enemy release hypothesis'; Keane & Crawley 2002). This may allow them to rapidly develop large populations, and divert resources formerly used for defences against enemies into growth and reproduction (the 'evolution of increased competitive ability' [EICA] hypothesis; Blossey & Nötzold 1995). Competitors and prey are not typically included in the enemy release and EICA hypotheses, but could have similar effects. For instance, native prey might be naïve to a newly introduced predator, providing large rewards to the non-native predator (Sih *et al.* 2010; Saul *et al.* 2013). Likewise, non-native species might be functionally novel in their new environment, e.g. possess a 'novel weapon' (*sensu* Callaway & Ridenour 2004) or consume a resource that is not consumed by resident species, which allows them to be relatively free of competitors. All of these mechanisms could lead to a boom in the early phase of an invasion.

These release effects might diminish over time, as (1) enemies or competitors of the invader from its native range arrive (or are deliberately introduced) or (2) resident species become more effective predators, parasites or competitors of the non-native species (e.g. Strayer *et al.* 2006; Diez *et al.* 2010; Mitchell *et al.* 2010; Strickler *et al.* 2016), or develop defences against a non-native predator (e.g. Nunes *et al.* 2014; Saul & Jeschke 2015), potentially leading to a bust in the invader's population. However, these compensatory mechanisms can occur without leading to a 'bust' in population size or ecosystem effects of the invader. For instance, mortality arising partially from increases in consumption by a native predator (the blue crab, *Callinectes sapidus* Rathbun) on the non-native *Dreissena polymorpha* (Pallas) (zebra mussel) in the Hudson River increased from 46%/year to > 99%/year over the first 20 years of the invasion (Carlsson *et al.* 2011), but this dramatic increase did not affect the number of *D. polymorpha* in the river (Strayer *et al.* 2011; Fig. 2a). Mussel recruitment was sufficient to compensate for these large increases in mortality. The extent, strength, and functional significance of release effects and their possible diminishment over time are still being debated (e.g. Speek *et al.* 2015).

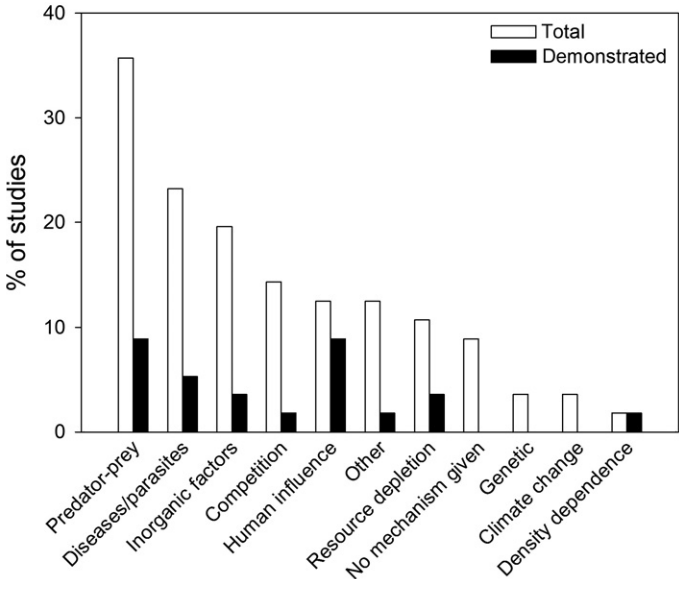

Figure 3 Causes offered for population busts by authors of papers included in our systematic review (see Appendix S1), and whether these mechanisms were actually demonstrated. Studies in which a cause was hypothesised but not demonstrated are represented as the difference between the white and black bars. Because some studies suggested that busts were the result of multiple causes, the number of causes offered sums to more than the number of studies ($n = 56$).

(A2) Interactions with subsequent invaders

An interesting special case of enemy accumulation occurs when an earlier invader is displaced by a later invader (termed 'over-invasion' by Russell *et al.* 2014). For instance, among the dreissenid mussels (*D. polymorpha* and *D. rostriformis* (Deshayes), the quagga mussel), *D. rostriformis* disperses less readily than *D. polymorpha*, but is typically competitively dominant, often leading to boom-bust dynamics in *D. polymorpha* as it arrives first, booms, and is displaced a few years later when *D. rostriformis* arrives (Karatayev *et al.* 2011). Other examples of displacement of earlier invaders by later ones have been reported from a wide variety of locations and taxa, including plants, insects, crustaceans and rats (Mack 1989; Russell *et al.* 2014).

This special case of enemy accumulation may have two interesting features. First, it has been suggested that dispersal ability and competitive ability are negatively correlated (e.g. Tilman *et al.* 1997). If this is generally true, then frequent invasions such as those that are occurring in many contemporary ecosystems may often produce boom-bust dynamics in the earlier invaders as they are displaced by later invaders with slower dispersal but better competitive abilities.

Second, although this mechanism may produce boom-bust dynamics in populations of the early invaders, it does not necessarily allow recovery of native species and ecosystems as these initial invaders fade away. In addition to the problem of persistent effects of some invaders (see section A4 below), the impacts of the first invader may be replaced or augmented by the later invaders, resulting in continued effects on native species and ecosystems. For instance, the replacement of *D. polymorpha* by *D. rostriformis* throughout much of the Laurentian Great Lakes vastly increased the overall population size of dreissenid mussels and their impacts on other parts of the ecosystem (Madenjian *et al.* 2015).

(A3) Time-lags in density-dependent populations

The population growth of a non-native species introduced into a new environment offers formal similarities to laboratory populations in which a few individuals of a species are inoculated into a microcosm. Introducing time lags into models of such populations can produce repeated oscillations or boom-bust dynamics or even a population boom followed by extinction (e.g. May *et al.* 1974). The critical attributes that determine the trajectory of a population are its characteristic return time (the rate at which the population approaches an equilibrium following a small perturbation) and the time delays of the system, whether induced by the population itself (e.g. through age- or stage-structure), or interactions with its enemies or resource supply. If the return time is greater than the generation time, the population damps exponentially to equilibrium, following a logistic curve. However, as the return time falls below generation time, populations show a variety of forms of cycles or oscillatory damping which may resemble Fig. 1b. In even more extreme cases (longer lags, shorter return times), populations may go extinct after large fluctuations, resembling Fig. 1a, but with a post-boom density of zero. This mechanism is not specific to species introduced into novel environments, but introduced populations with high growth rates, for example when losses to enemies or opportunities for dispersal are low, or systems with long time-lags, or introductions initiated far from a stable age- or stage-structure (Stott *et al.* 2010; Iles *et al.* 2016) may be particularly prone to boom-bust dynamics arising from this mechanism.

(A4) Slow environmental change caused by the invader

Abundant invaders often substantially change the chemistry, physical structure, or other environmental conditions of invaded habitats (e.g. Levine *et al.* 2003; Strayer *et al.* 2006). If these changes are harmful to the invader and occur quickly, they may prevent a boom from occurring in the first place. However, if they are slow and cumulative, produced either by 'mining' accumulated resources or engineering the physicochemical environment to the long-term detriment of the invader, they may trigger a (usually solitary) bust after an initial boom phase as environmental quality declines.

Probably the best-known examples involve non-native plants and changes to the physical or chemical properties of soils and sediments (pools with slow dynamics that are important to the plants; Van der Putten *et al.* 2013; Vilà *et al.* 2011), although it is not always easy to separate the effects of changing soil physicochemistry from those of changing soil microbial communities. A 16-year time series of the *Spartina alterniflora* Loisel (smooth cordgrass) invasion in the Yangtze River estuary revealed that an initial 5-year growth phase was followed by a decline due to steady decreases in the tidal inundation time and increases in standing litter as the *Spartina* bed gradually accumulated sediment (Tang *et al.* 2012). In Iceland, the non-native nitrogen-fixing plant *Lupinus nootkatensis* Donn ex Sims can develop large populations, causing soil nitrogen to increase, after which it may be replaced by *Anthriscus sylvestris* (L.) Hoffmann, a plant (also non-native) that needs nitrogen-rich soils (Magnússon *et al.* 2003). In a similar example involving animals, it has been suggested the populations of some invading earthworms in northeastern North America boom and then bust as they consume stores of accumulated leaf litter on the forest floor and soil (Straube *et al.* 2009).

(A5) Delayed genetic effects

Several genetic mechanisms could in principle lead to boom-bust dynamics in invaders. Many biological invasions arise from small inocula with low genetic variation (Simberloff 2009). Invasions of species with vegetative or parthenogenetic reproduction may even arise from single individuals. Such populations may flourish initially, but then collapse when exposed to a new stress (e.g. disease, extreme climatic events). Aghighi *et al.* (2014) believed that low genetic variability together with apomictic reproduction contributed to the decline of the invasive blackberry *Rubus anglocandicans* A. Newton in Australia. However, some invaders with very low genetic variation have been very successful (e.g. Bailey & Conolly 2000; Dybdahl & Drown 2011). Likewise, strong selection following invasion may erode initial genetic diversity, and alleles that favour introduction, dispersal, and initial population growth may be less advantageous in later phases of the invasion (Keller & Taylor 2008) or during extreme events.

Low initial genetic variability may also make populations of invaders prone to inbreeding depression. The level of equilibrium between the selection and inbreeding may delay the negative effects of inbreeding (Connor & Bellucci 1979). In such circumstances, homozygote production and inbreeding depression would eventually occur, but with a lag proportional to selection strength. In addition, the spread of an invader over a patchy environment may result in inbreeding effects within occupied patches, if the invasion is characterised by a strong directional migration, followed by limited gene flow between populations (Stone & Sunnucks 1993). Low abundance within patches may intensify genetic drift and inbreeding, which will occur after a lag from the initial invasion. Increasing levels of gene flow between patches containing locally adapted genotypes may also lead to a genetic regime shift in which maladapted genotypes prevail over these locally adapted genotypes (a transient monopolisation, De Meester *et al.* 2016).

Invasions may also occur as multiple waves from genetically distinct source populations. This may in principle result in introgressions of different genotypes through later introductions, which may produce outbreeding depression and reduce overall fitness (Tymchuk *et al.* 2007). If such introgressions are characterised by an increasing propagule pressure over time, outbreeding depression will be more likely to occur. Furthermore, outbreeding depression by itself may be delayed if it arises from the disruption of the linkage arrangement of co-adapted allele complexes, especially if they consist of strongly associated genes that require many generations of recombination to break apart (Tymchuk *et al.* 2007).

(A6) Human control of invaders

Finally, humans may deliberately suppress troublesome invaders through a wide variety of tools (e.g. classic biological control, including augmentation or re-introduction of native predators or pathogens, harvesting, poisoning, and so on), or inadvertently reduce populations of desirable invaders by overharvesting them (e.g. the edible signal crayfish *Pacifastacus leniusculus* (Dana) – Jussila *et al.* 2014). In some cases (e.g. harvest), this suppression is temporary and produces a population bust only as long as active control continues, while other tools (e.g. biological control) may produce a long-lasting or permanent population bust. There are many examples of this kind of human-induced boom-bust cycle of non-native species (e.g. Lockwood *et al.* 2013), as well as many examples of control or harvest campaigns that failed to produce a bust in the target population (e.g. Syslo *et al.* 2011). Although documented in a higher proportion of cases than other mechanisms thought to cause population busts (Fig. 3), if an outbreak has been suppressed by deliberate human actions, it does not provide evidence that invaders and their impacts would have disappeared on their own.

(B) General ecological mechanisms

Several common ecological mechanisms not specifically tied to biological invasions may lead to local boom-bust dynamics – sustained collapse of a population after a period of rapid growth. We include them here because an ecologist observing a boom-bust cycle in a non-native population may mistakenly interpret the boom-bust as a feature of the invasion, when in fact a general ecological mechanism unrelated to invasions is the cause. In addition, a biologist observing a fluctuating population (subject to repeated rises and falls) may mistakenly interpret these fluctuations as a boom-bust if the period of record is so short that it includes just a single rise and fall of the population. Mechanisms producing population fluctuations are too numerous to discuss here (see Turchin 2003 for a summary), but ecologists observing an apparent boom-bust in a short record should always be aware of the possibility that they are merely observing a short part of a fluctuating population trajectory, driven by any of many causes unrelated to the invasion *per se*.

(B1) Succession or recovery from disturbance

Disturbance is important in driving community dynamics in many ecosystems, with some species flourishing immediately after a disturbance and others peaking only after a long period free from disturbance (e.g. Meiners *et al.* 2015). In such disturbance-controlled systems, local populations will appear to boom and bust in response to disturbance events (although not necessarily at larger spatial scales, if a shifting mosaic of sites at different successional stages exists). Disturbance-related boom-busts may be especially frequent among invaders, because it has been demonstrated that disturbance facilitates invasion, at least among plants (D'Antonio *et al.* 1999; Davis *et al.* 2000). Certainly, many non-native plant species are associated with early seral stages, so that they become less abundant or even disappear as succession occurs at a site (e.g. Rejmánek 1989; Meiners *et al.* 2015).

(B2) Climate change and other changes in the abiotic and biotic environments

Changes in local environmental conditions and biotic communities often drive changes in local populations. In particular, human-induced climate change has increased to the point that it is affecting many biological populations (e.g. Parmesan 2006; Chen *et al.* 2011) and will likely become even more important in the future (e.g. Thomas *et al.* 2004; Bellard *et al.* 2012). In the specific case of an invader, the initial colonisation of a site could cause a boom, followed by a decline as environmental conditions or the biotic community move away from the optimum for the species. Climate change in particular is likely to cause many such declines among populations of non-native species (e.g. Bradley *et al.* 2009; Wenger *et al.* 2011), just as for native species. Depending on the details of the relationship between the species and its environment (e.g. thresholds between survival and variables such as rising temperature or declining soil moisture; see White *et al.* 2016 for an example), these declines could be rapid enough to appear as busts. Changes in local environmental conditions other than human-induced climate change probably will cause many busts in local populations of invaders as well. Likewise, changes in the local biotic communities that interact with invaders (predators, competitors, mutualists, etc.), whatever the cause, probably will also drive local busts in non-native populations.

(B3) Shifts between alternative stable states

Some ecosystems exhibit alternative stable states, in which multiple stable equilibria are possible under identical environmental conditions (Scheffer *et al.* 2001; Beisner *et al.* 2003). These stable states can be reinforced by positive feedbacks and result in hysteresis, so that backward and forward transitions between states occur at different levels of environmental drivers, and large perturbations are required to overcome thresholds between states (Beisner *et al.* 2003). Several examples of ecological systems with multiple stable states have been offered (see Petraitis 2013 for a critical review).

These shifts between stable states can produce boom-bust (or bust-boom) dynamics in biological populations as stable states alternate. In the case of invasions, population growth following initial colonisation into a favourable state followed by a shift to a state that is unfavourable to the invader would produce a boom-and-bust. Shifts between alternative stable states involving invasive species have been reported for a number of systems, e.g. shifts between the non-native *Orconectes rusticus* (Girard) (rusty crayfish), and native *Lepomis* spp. (sunfishes) in Wisconsin lakes (Hansen *et al.* 2013), shifts in fallow Romanian arable fields with native vegetation to a dominance of the non-native Canada goldenrod (*Solidago canadensis* L.) (Fenesi *et al.* 2015), or shifts in lakes between a turbid, phytoplankton-dominated state and a clear-water state with non-native macrophytes (Hilt *et al.* 2006).

General remarks about mechanisms

Mechanisms producing boom-bust dynamics in local populations operate so frequently and are so varied that observing such dynamics in an invader does not by itself allow us to infer the underlying mechanism(s), whether it is particularly related to the invasion, the long-term prospects for that population, or the actions that should be taken to manage that population or its impacts. Even our brief survey shows that booms and busts can be produced by mechanisms intrinsic to the population or by external factors; by changing vital parameters of the system or without any change in these parameters; and that they can be solitary, cyclic, or recurring but irregular. Different kinds of management responses (including no response at all) would be appropriate for addressing booms caused by different mechanisms. Finally, there is no need for a boom-bust dynamic to be the result of a single mechanism. Indeed, it would be unusual for an invader to be subject to only one of the mechanisms that we have described, so combined and interactive effects probably are common. Instead, we will need to gather additional information about the invader, such as detailed demographic information, response to experimental interventions, invasion history in other regions, and so on. Nevertheless, it is striking how frequently that causative mechanisms are assumed rather than demonstrated in published analyses of boom-bust dynamics (Fig. 3).

We hypothesise that small, isolated environments such as islands or lakes may be especially likely to foster boom-bust dynamics in invaders. Such habitats may have reduced populations of natural enemies, be more prone to local resource depletion, and have fewer opportunities for local overpopulation to be relieved by emigration (or low genetic variation to be relieved by immigration) than more open or networked habitats (e.g. Elton 1958; Carlquist 1974; Holt 2010). This could make mechanisms such as enemy release and accumulation, environmental degradation or resource depletion, time lags, delayed genetic effects, deliberate human intervention, and shift between stable states more likely, so that boom-bust observations may be especially characteristic of islands, lakes and similar habitats. Further studies of the prevalence of boom-bust dynamics in species introduced into open and closed, or isolated and networked, habitats could be informative.

QUANTITATIVE ANALYSIS OF BOOM-BUST DYNAMICS

Ecologists concerned with boom-bust dynamics have not extensively discussed how the characteristics of such dynamics might be quantitatively described. Studies of boom-bust dynamics often are made without applying any quantitative criteria, and when quantitative criteria are used, a wide range of values have been applied (Table 1). We describe six alternatives that have been used or might be useful, and use original, simulated data to test or illustrate three of them. The first of these, based on the observed decline from a peak value, has been widely used, but our original simulations show that it is prone to severe bias in noisy data sets. We discuss two alternative methods (regime shift detection and tests of deviations from expected population trajectories) that appear to have broad potential for analyzing boom-bust dynamics, although neither has yet been widely used by invasion ecologists. Finally, we briefly describe three additional methods (Bayesian detection of population collapse, randomisation tests and analysis of the temporal sequence of peaks) that might be useful in special situations. The different methods provide different information (e.g. size vs. statistical significance of bust) and are suited to different kinds of data sets.

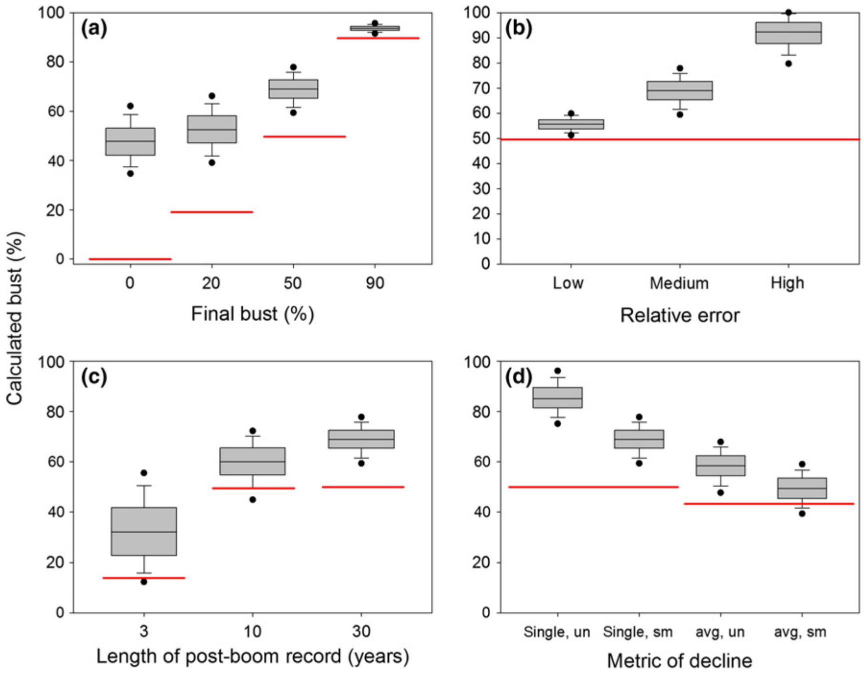

Figure 4 Bias produced by decline-from-peak metrics, based on analysis of simulated data sets with different known characteristics. Red lines show true characteristics of the data, and boxes and whiskers show estimated values. Unless otherwise noted, simulated population is subject to a 50% bust beginning in year 10, has normally distributed error with SD = 30% of mean, is smoothed by calculating 3-year running means, and extends for 30 years after the peak; (a) populations with different degrees of bust, including a population that has no bust (i.e. logistic growth); (b) populations with different amounts of normally distributed error (SD/mean = 10%, 30%, and 100% for low, medium, and high respectively); (c) different lengths of record; and (d) different metrics of decline (from left to right, difference between single highest year and single lowest year after that peak using unsmoothed data [single, un]; same for data smoothed by calculating 3-year running means [single, sm]; difference between peak year and mean of next 10 years using unsmoothed data [avg, un]; same for data smoothed by calculating 3-year running means [avg, sm]. See Appendix S2 for details.

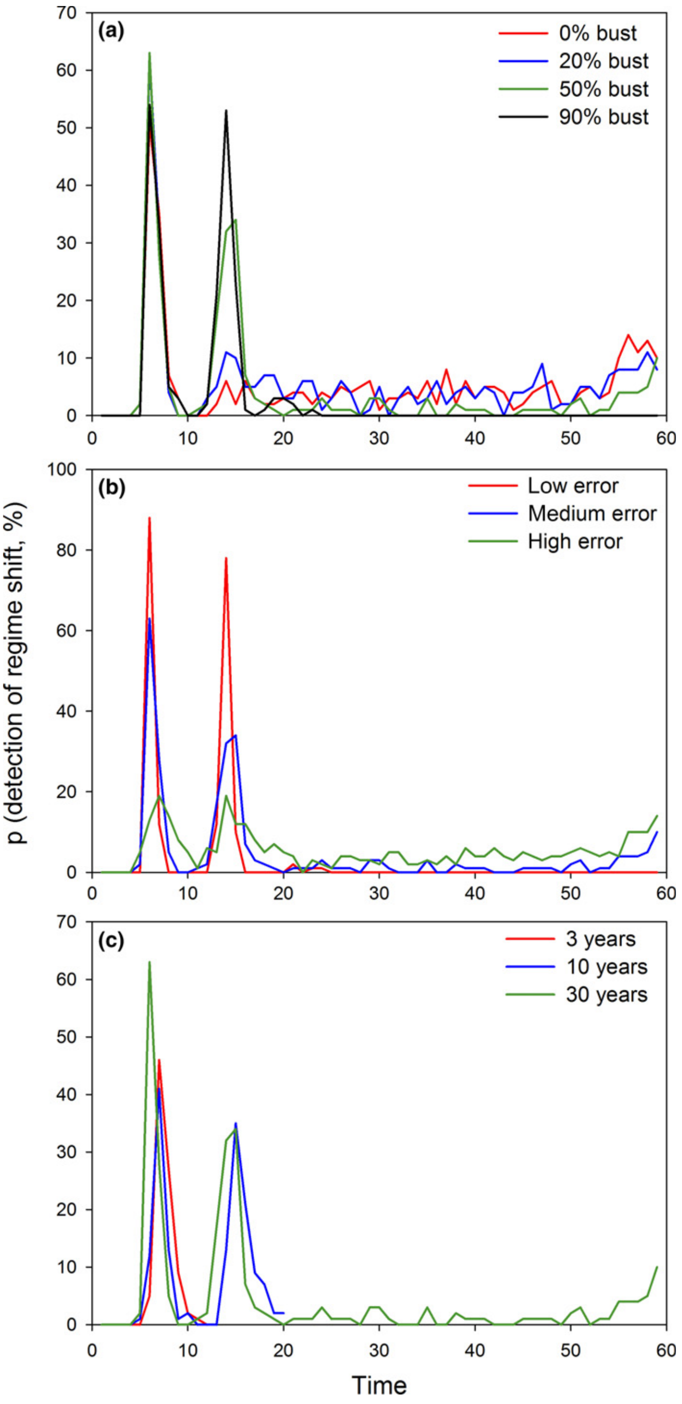

Figure 5 Tests of the performance of the sequential *t*-test of Rodionov & Overland (2005), based on analysis of simulated data sets with different known characteristics. Graphs show the percentage of simulations for which a significant regime shift was detected at each time. Unless otherwise noted, the simulated population is subject to a 50% bust beginning in year 10, has normally distributed error with SD = 30% of mean, is smoothed by calculating 3-year running means, and extends for 30 years after the peak; (a) populations with different degrees of bust, including a population that has no bust (i.e. logistic growth); (b) populations with different amounts of normally distributed error (SD/mean = 10%, 30% and 100% for low, medium, and high respectively); and (c) different lengths of record after the peak. We ran 100 trials for each scenario, and used the default parameters of $p = 0.1$, cut-off length=10, and Huber's weight parameter=1. See Appendix S2 for more details.

Amount of decline from peak

When ecologists have described a boom-bust dynamic quantitatively, they usually have simply calculated the size of the observed decline from the peak value during the boom to the subsequent bust value (e.g. Simberloff & Gibbons 2004; Uthicke *et al.* 2009), occasionally in combination with other criteria (e.g. regime shift detection, Sandström *et al.* 2014). Different authors have used different thresholds of decline in deciding whether the data qualify as a boom-bust.

Although this criterion appears to be simple to apply and interpret, it is sensitive to the length of the data set and the amount of noise (spatiotemporal variation in population size, observation or sampling error) in the data. In particular, our simulations show that it tends to overestimate the severity of boom-bust dynamics, sometimes badly (Fig. 4). This metric frequently detects booms-and-busts in runs of data that have no underlying boom-bust dynamic, particularly if the data are noisy (shown in the left-hand bar in Fig. 4a). Bias is least in cases where the data are not very variable, with longer periods of record, and with most severe actual decline. Bias can be reduced by averaging or smoothing data. Nevertheless, simple metrics based on the observed decline from peak to subsequent trough produce accurate estimates of the amount of bust only under the most favourable combination of circumstances. Except in such ideal cases, they are likely to greatly overestimate the frequency and severity of busts. Therefore, these metrics should be used very carefully, if at all. It is likely that some reports of boom-bust dynamics based on this criterion have been exaggerated or are entirely spurious (cf. Fig. 4a).

Regime shift and change-point detection

Methods developed to detect and describe regime shifts and thresholds in time series could be adapted to describe and detect booms and busts. The most common methods have been used to detect step-changes (e.g. Rodionov & Overland 2005; Andersen *et al.* 2009), and their utility drops if the change is gradual (Rodionov 2004). Nevertheless, such methods were used successfully by Sandström *et al.* (2014) to detect boom-bust dynamics in introduced crayfish populations. In our tests of this method on simulated data (Fig. 5), we found that it typically identified two regime shifts, the first (at $t \sim 6$) associated with the shift from the growth phase to the stationary phase, and the second (at $t \sim 14$–15, lagged several years after the bust actually began) associated with the population bust. As with the decline-from-peak metrics, this test was more likely to detect the bust and produced fewer false positives for more severe busts (Fig. 5a), less noisy data (Fig. 5b), and longer runs of data (Fig. 5c). In contrast to the decline-from-peak methods, this method did not produce a large number of false positives for populations that were not actually declining (red line in Fig. 5a), and generally performed satisfactorily. The results shown in Fig. 5 should not be interpreted as applying to all regime-shift methods, because the performance of these methods could be improved by better matching the model to the dynamics of the target population (e.g. sudden vs. gradual collapse), but our findings about the influence of noise and length of record should apply broadly. There is a rich literature on methods to detect change points and regime shifts, some of which can accommodate changes other than step-changes (e.g. Carstensen & Weydmann 2012), so it seems very likely that some of these methods will be useful for analysing boom-bust dynamics. Andersen *et al.* (2009) provided a critical review of methods that have been proposed to detect ecological change points, including available software.

Testing for deviations from expected population trajectories

If we define an expected population trajectory in the absence of a bust as $N(t) = f(t)$, we could test whether including a bust function $g(t)$ [such that $N(t) = f(t), g(t)$] improves the fit to a real data set, and estimate the parameters of $g(t)$ to describe the size and timing of the bust. For a new invader, we might choose $f(t)$ to be a logistic curve (or perhaps a delayed logistic, in the case of a cyclic population). Depending on the nature of the supposed bust, $g(t)$ could be a step-function, a linear decline, or an exponential decline to a constant, for example. Although this method seems flexible and straightforward, it would require a long run of data to estimate the many model parameters with any precision, and might be compromised by temporal autocorrelations in the data (although these can sometimes be accounted for, Lindén *et al.* 2013). Alternatively, one could test for systematic deviations of data points from the expected trajectory, as was done in archaeology by Shennan *et al.* (2013). We are not aware of any uses of such approaches to test for or describe busts in ecological data. We cannot test this method on our simulated data because we know the actual underlying dynamic that generated the simulated time-series, which will not generally be the case with real data.

Economists, especially those concerned with temporal trends in real estate prices, identify the timing and size of booms and busts (which they sometimes call 'bubbles' and 'crashes') as deviations from running time-series predictions (e.g. Hui *et al.* 2010). Although powerful, these methods require such long data runs (typically thousands of data points) that they are unlikely to be very useful in invasion ecology.

Bayesian detection of population collapse

Aagaard *et al.* (2016) recently published a Bayesian method that takes into account observed uncertainty when analysing a noisy record for evidence of population collapse. This method uses a Markov chain Monte Carlo method to generate a large number of population trajectories from the observed data. This collection of generated trajectories can then be analysed for the frequency of collapses that meet a specified criterion. This method is especially designed to deal with apparent zeroes (non-detections) in the data set, so it seems more likely to be useful in conservation biology than invasion biology. Aagaard & Lockwood (2016) defined collapse (bust) as a 90% decline in abundance from a peak value within 10 years of that peak, and found that populations of non-native birds frequently underwent severe population collapses.

Randomisation test

Randomisation tests might be useful in some cases, for instance if only a few data are available. If a population has busted, the mean values of population size N_t observed late in the time-series should be lower than the mean values of N_t earlier in the sequence. As one example of a randomisation test, consider a time-series of n evenly spaced observations of population size N_t that starts at the end of the initial period of logistic growth (Fig. 6). Divide the data into the final k observations and the initial (n-k) observations. One simple measure of the severity of the bust would be the relative difference in average population size between these two groups of observations, which we will call B_k. Specifically,

$$B_k = \frac{\sum_1^{n-k} N_t/(n-k) - \sum_{n-k+1}^{n} N_t/K}{\sum_1^{n-k} N_t/(n-k)}$$

B_k equals 0 for no change in mean population size and 1 for a complete bust to extinction, and will be negative if mean population size has increased rather than decreased during the supposed bust period. It can be tested for statistical significance by comparing observed values to values generated by randomly shuffling the time-series (bootstrapping). The resulting plot (Fig. 6) shows the severity and statistical significance of the bust. This test seems simple and easy to understand, and details of the test could be modified to fit the hypothesis and the data set being tested, but may be biased using the observed data to choose the first data point to include in the calculation of B_k. If we choose the observed maximum of the time-series, for example, this test seems likely to overestimate

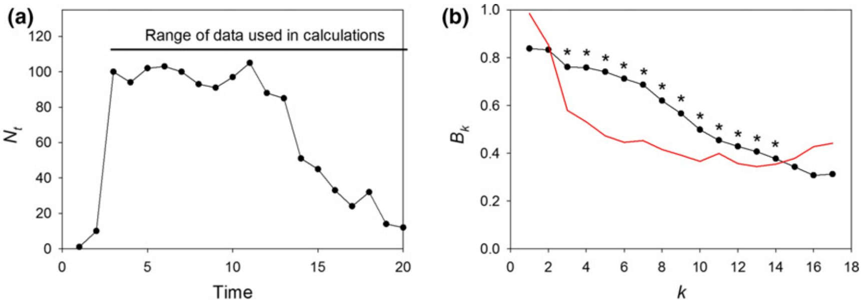

Figure 6 Example of the use of a randomisation test on a simulated data set: (a) the time-course of population size N_t; (b): calculations of the test statistic B_k (see text for definition) from the data (black line and dots), and the 95th percentile of values derived from 100 randomisations (red line). Asterisks show where values of B_k in real data are significantly different from randomised data at $p < 0.05$.

the size and significance of the bust. Because of this problem, and because randomisation tests have not been tested for their ability to detect and describe boom-bust dynamics, any randomisation test will need to be evaluated carefully before it is applied to real data.

Temporal sequence of peaks

Methods adapted from those developed to use a temporal sequence of sightings of a rare animal to estimate the probability that extinction has occurred (e.g. Solow & Roberts 2003; Boakes *et al.* 2015) might be applied to boom-bust dynamics. The approach would be to define a boom as any value of N_t above some threshold value N_{thres}, and a bust as any value below that threshold. One could then use the temporal sequence of booms to estimate the probability that booms have stopped. One could either choose a single value of N_{thres} that is of special interest (e.g. the threshold above which economic impacts occur), or test a series of values of N_{thres}. This method is well developed in conservation biology (Boakes *et al.* 2015) and relatively simple, but would have to be modified to take temporal autocorrelation into account (they were developed for independent observations, but see Lindén *et al.* 2013). It seems most applicable to populations having recurrent booms and busts, and will have low power unless the number of years of observation is high (Boakes *et al.* 2015). One situation for which this method may be especially suited is where the data consist simply of the dates of outbreaks, rather than of quantitative measures of population size or impact. Such data sometimes are available for pest species, for example. Methods might also be adapted from hydrology and climatology (e.g. Katz *et al.* 2002; Zhang *et al.* 2004) to test for busts (declining peak values) in recurrent boom-bust dynamics.

CONCLUSIONS

Boom-bust dynamics must be defined, analyzed, and interpreted carefully. Although we have argued that it probably is counterproductive to develop an all-encompassing, quantitative definition of boom-bust dynamics (Box 1), it is essential that individual studies include a clear and defensible definition. Is the criterion based on how large the population decline is relative to background variation, whether the population falls below a threshold of economic or ecological damage, or some other standard? Is it based on population size, density, or biomass, cover, range size, or ecological or economic impacts, or some mixture of variables? How long must a bust last before it is considered ‘the new normal’ rather than a transient condition? Do the time-period and spatial scale of the analysis match the motivations of the study and the temporal and spatial characteristics of the species or impact under consideration? Quantitative criteria for describing or testing for boom-bust dynamics should be chosen deliberately, not fitted *post hoc* to a data set that was chosen especially because it showed a decline.

The analytical method chosen then needs to match this definition as well as the characteristics of the data. As we have cautioned, simple metrics based on the observed decline from a peak value to a subsequent trough are likely to be badly biased, and rarely will be appropriate for detecting or describing boom-bust dynamics. Instead, one of the alternative analyses that we have described, or a new analysis well suited to the question and the data set, is more likely to be useful.

Even if boom-bust dynamics are carefully defined and detected, they should be interpreted cautiously. Many mechanisms, singly or in combination, can cause boom and busts. Just because a non-native species has undergone boom-bust dynamics does not imply that a particular mechanism is at work. Specifically, a boom-bust does not necessarily mean that the balance of nature is being restored, or that the non-native species will cease to pose management problems. This caveat is especially important because although some of the mechanisms (e.g. enemy accumulation) are likely to cause long-lasting busts that may satisfy management needs, others (e.g. succession, shifts between stable states) produce only local or temporary busts, so that the harmful effects of the non-native species have not been permanently suppressed.

Instead, identifying the mechanism behind a boom-and-bust will require additional information. Depending on the mechanism being tested, such information might include field data such as demographic parameters of the non-native species, diet analyses or population trends of interacting species, or environmental measurements, or the results of experiments specifically designed to distinguish between mechanisms (cf. Peery *et al.*’s (2004) parallel discussion on diagnosing the causes of population declines). Because it may be unethical or illegal to perform field experiments at scale with non-native species, these investigations may be more constrained and therefore more difficult than for other species.

One of the difficulties with current methods for detecting boom-bust dynamics is that they are backward-looking (trailing indicators), so it typically is not possible to demonstrate a bust until several years after it has occurred, leading to delays and uncertainty in management actions. Field data or experiments might help to provide more timely indicators of population busts. For instance, a time-series of exclosure experiments might provide information about critical changes in predation rates on the invader, or interaction strengths with the local biota, and measurements of resource availability could show that limiting resources are being depleted. Alternatively, it may be possible to borrow from the literature on regime shifts (e.g. Carpenter & Brock 2006; Scheffer *et al.* 2015) or population collapses (e.g. Clements & Ozgul 2016) to develop real-time or leading indicators of busts in nature.

Coda: The way forward

In view of the conceptual and practical difficulties with defining and parameterising boom-bust dynamics, one might be tempted to dispense with the concept altogether. The concept, however, is so deeply rooted in the scientific literature and public narrative of biological invasions that it is unlikely to disappear, regardless of what we write here. Furthermore, it is clear that at least some invading species do undergo boom-bust dynamics (e.g. Aagaard & Lockwood 2016), which is of obvious scientific and management importance. Understanding how often invading populations boom and bust, the circumstances (taxa, ecosystems) under which such dynamics occur, and the mechanisms responsible for these dynamics seems to us to be a valid scientific challenge. Finally, many important concepts in ecology are beset by conceptual or practical problems, or are frequently misused (e.g. sustainability, competition, diversity and ecosystem function, and ecosystem engineering, to name just a few), so the mere existence of such difficulties is not sufficient reason to dismiss the boom-bust concept.

In the near term, the conceptual and computational difficulties associated with the boom-bust dynamic can be reduced by careful attention to definitions and computations, along with more critical consideration of underlying mechanisms. We have provided many specific suggestions in this paper for improving the application of the boom-bust concept. It should thus be possible to make considerable progress in understanding boom-bust dynamics in invading species through critical application of the concepts and tools that are now at hand.

Over the longer term, we badly need more empirical analyses of long-term data sets and better understanding of the mechanisms that drive long-term interactions between invaders and their ecosystems. As our literature analysis (Tables 1 and A2, Fig. 3) shows, empirical studies are few, highly non-representative in terms of geography, habitat, and taxonomy, and often have not included rigorous, quantitative analysis. Furthermore, variation in definitions and uses of terms (e.g. boom-bust, collapse, decline), as well as quantitative descriptors of population trajectories, which often are not clearly stated in the published papers that we reviewed, frustrate any attempts to synthesise findings across studies. Such future studies can lay the groundwork for a more satisfactory understanding of the long-term population dynamics of invaders, and better decisions about their management. Until we have built this foundation, it seems imprudent to discard current concepts, and it seems particularly unwise to adopt a 'do nothing' management strategy based on the assumption that problematic non-native species will soon go away on their own.

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AUTHORSHIP

All authors participated in initial discussions about the content of the paper, contributed ideas, and reviewed and edited drafts of the paper; DLS, JMJ and AWL led in organizing these ideas; MvS, IJ and RAS conducted the WoS analysis; DLS ran the population simulations; and DLS, IJ, MvS, and JMJ drafted the paper.

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