Quantitative description of boom-bust cycles in invasions: necessary narrowing of the definition to facilitate communication

Nathan T. Barrus- The Department of Biological Sciences; Florida International University

Abstract:

Many invasions of non-native species undergo boom-bust dynamics where after rapidly reaching high abundances, they have rapid and severe declines. Despite this concept being consistently used in the invasion literature, only qualitative definitions of what constitutes a boom-bust currently exist. A quantitative definition of a boom-bust cycle could aid in exploring and finding generalities as well as facilitate communication. Building off of the established qualitative definition, I define boom-busts cycles in invasions as a sequence of three phases 1) lag/growth phase, 2) boom phase, and 3) bust phase (Figure 1) where the transition between the growth and boom phase must be rapid (ለ ≥ 4; *r* ≥1.386), and the transition from the boom to the bust phase must be rapid (0 < ለ ≤ 0.372; *r* ≤ -0.99), severe (≥ 90%), and sustained (≥3 years). I also present a variety of metrics to describe population growth when making comparisons across taxa and subpopulations. I use my identification to identify 28 studies document boom-bust cycles across taxa and systems with 2 studies documenting repeated boom-bust cycles.

**Introduction**

The boom-bust concept within invasion ecology is one case where quantitative standardizing terminology could potentially lead to finding generalities. Somewhat recently, boom-bust cycles have been described in non-native invasions (Strayer *et al.* 2017). In many invasions, populations undergo a sequence of sharp population increase (sometimes called a Boom; Strayer et al., 2017) until a maximum followed by sudden dramatic decline until a minimum (sometimes called a Bust; Strayer et al., 2017). While solitary boom-bust cycles have been described and identified in many cases of invasions (Strayer *et al.* 2017), the causes and mechanisms responsible for many solitary boom-busts remain unclear (Strayer et al., 2017). With invasive species continually identified as an extreme threat to native biodiversity (Clavero *et al.* 2009; Linders *et al.* 2019), understanding the causes of these solitary boom-bust dynamics in invasions of species is of particular importance. Before a thorough understanding of the mechanisms responsible for boom-bust dynamics can be made, thorough quantitative description of patterns within boom-bust dynamics have to be identified and terms describing these patterns need to be standardized.

Drawing upon previous work in ecology could help aid in quantitatively describing boom-bust cycles of non-native species. Understanding why population size fluctuates rather than reaching an equilibrium has intrigued ecologists for almost a century (Elton 1927)

with primary focus on populations that exhibit cyclic dynamics (Elton & Nicholson 1942; Lindström *et al.* 2007; Myers 2018). In these systems, great effort has been made to demonstrate the importance of mechanisms in producing observable dynamics in unmanipulated populations (Myers 2018; Andreassen *et al.* 2021), and describing patterns quantitatively has helped link mechanisms to population dynamics (Sheriff *et al.* 2015; Myers 2018). For example in the classic lynx-snowshoe hare system of cyclic populations, snowshoe hare populations were identified to remain at population lows even after lynx populations reached their lows in the cycle. During this lag between population lows to population increase, lynx were found to have non-consumptive effects on reproduction of snowshoe hare (i.e., chronic stress from predator avoidance) which limited births from 4 to 2 young per litter (Sheriff *et al.* 2015). These stress effects continued until a generation after the lynx population decline and corresponded to the lag between the population low and the population increase phase in the cycle.

During the first attempt at standardizing terminology when studying boom-bust cycles within invasions, Strayer *et al.* (2017) qualitatively defined a boom-bust cycle as: a rapid, large increase in a population metric (e.g., population size or range size), followed by a rapid, large and sustained decline, and gave four potential problems for adopting a quantitative definition of boom-bust cycles in invasions. Theses problems were: 1) past practices have not provided clear precedents in numerical criteria, 2) different species have different response times (i.e., different generation times), 3) the ability to detect boom-bust dynamics depends strongly on the characteristics of the data set, and 4) the amount of change that is “important” or “dramatic” across systems varies. Here, I review the literature of boom-bust in invasions and draw upon classic work on fluctuating population dynamics of native systems to propose a new quantitative criteria in describing and defining boom-busts in invasions that addresses the concerns presented by Strayer et al., (2017). This work should aid in the communication of boom-bust cycles, and progress towards finding generalities.

**Literature Search**

I searched the literature using Web of Science with the following keywords: boom and bust; explosion and crash; population and explosion; population and outbreak; population and cycles; fluctuat\* populations. I then filtered the results to include only the web of science categories; Environmental Studies; Ecology; Environmental Sciences; Marine Freshwater Biology; Zoology; Evolutionary Biology; Plant Sciences; Biology; Ornithology; Limnology; Forestry; Entomology. I then searched the abstracts of the remaining results to exclude studies that described boom-bust in mining and fossil fuels industries. This gave me a list of 171 studies. Because I wanted to look at the quantitative definition of boom-bust cycles, I then eliminated 46 studies because they did not include time series of any population metric. This first search resulted in 125 studies.

As a second search of the relevant literature I looked through the supplemental material and references of three reviews that potentially related to boom-bust cycles (Strayer *et al.* 2017; McDowell & Sousa 2019; Spear *et al.* 2021). I then filtered these results to find studies that included time series as well. The second search resulted in an additional 120 studies.

I looked through the 245 studies identified by my literature searches to identify characteristics of the time series (i.e., the number of years served, how sporadic or continuous the surveys appeared) the taxonomy of the each species that contained a time series (i.e., some studies had multiple time series), the natives status of the species (native or introduced), as well as the continent (Oecania, S. America, N. America, Europe, Asia, and Antarctica) and the ecosystem (terrestrial, marine, freshwater) of each study. This resulted in 266 identified time series in the 245 studies. I further focused my study to exploring boom-bust cycles in non-native populations. This resulted in 66 studies with 95 identified time series.

**What is a boom-bust?**

*Phase Identification*

Before a quantitative definition of a boom-bust can be made, the different phases of the invasion should be identified (Figure 1). Typically the different phases are qualitatively defined (Mergeay *et al.* 2006; Morris *et al.* 2013; Fernández 2020), but qualitatively defining the phases can be challenging when a boom phase or established phase is highly variable (Kaeuffer *et al.* 2009; Strayer *et al.* 2017). A more objective and quantitative approach would be to implement regime shift detection methods (see, Rodionov & Overland 2005). Regime shift detection methods are often used in fisheries to detect long-term changes within time series (Daskalov *et al.* 2007) and have been used to identify the phases of a boom-bust cycle for introduced populations of Signal crayfish (*Aphanomyces astaci*) in Europe (Sandström *et al.* 2014). I advocate using regime shift detection methods for identifying persistent changes in a times series. This can help identify the phases of a boom-bust cycle, but using these methods solely for defining a boom-bust may be misleading because relatively minor shifts in a regime can be detected (Daskalov *et al.* 2007).

Identifying phases of the invasion can present a challenge when studying boom-bust cycles because it requires longer time series. Data in the early stages of the invasion are often sparse and tend to rely on anecdotal information about introductions and sporadic surveys (Rawlings *et al.* 2007; Witte *et al.* 2010; Cecere *et al.* 2016). An alternative approach that has been taken is to compare time series of locations that have not entered the boom phase to locations that have entered a boom phase (Ferreira *et al.* 2006; Angeler *et al.* 2010; Moore *et al.* 2012; Forsström *et al.* 2018). The added benefit of comparing locations of a boom phase to locations not in a boom phase is that it can provide a “natural experiment” and help elucidate the mechanisms involved during the boom-bust cycle (Moore *et al.* 2012; Sandström *et al.* 2014).

*Quantitative Criteria*

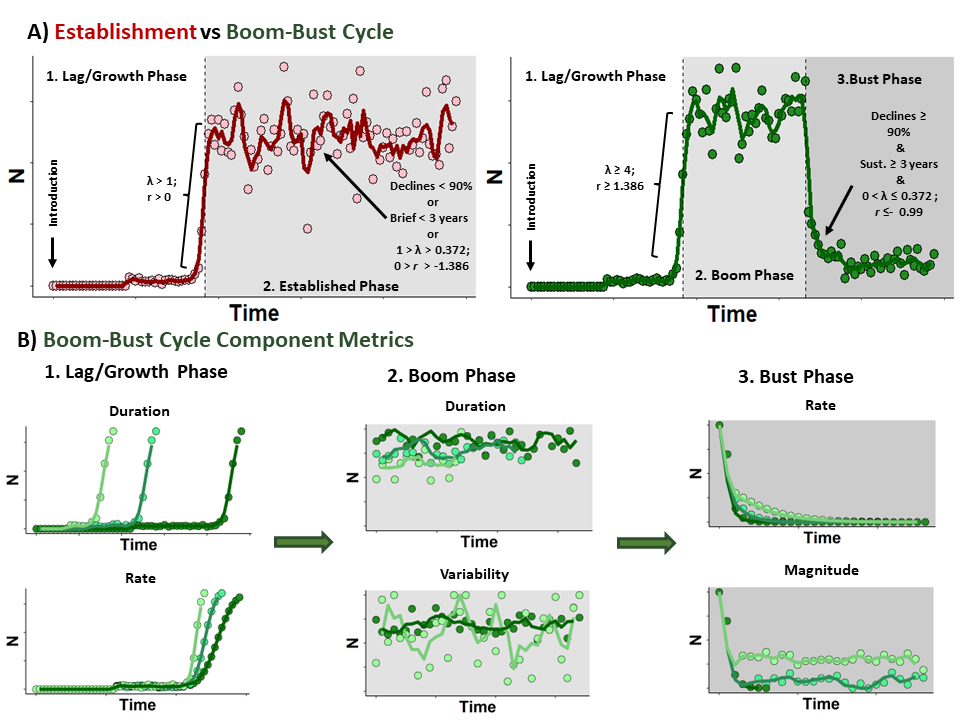
After identifying the different phases of an invasion, identifying a boom-bust cycle further requires a quantitative definition. Strayer *et al.* (2017) defined a boom-bust cycle as a rapid, large increase in a population metric followed by a rapid, large, and sustained decline. For the population metric, I focus on estimates of population size and abundance because relatively few studies have explored boom-bust phases in terms of population expansion and contraction of range size (however for examples see Cooling & Hoffmann 2015; Kauppi *et al.* 2015; Wasson *et al.* 2020). ****

Figure 1. A) Graphical representation of quantified definition of boom-bust cycles and B) proposed metrics of a boom-bust cycle’s components.

Determining quantitative criteria for rapid population growth requires a temporal scale and determination of the rate. I suggest that yearly time scales should be used whenever possible because seasonal fluxes in population size (particular strong in species with short generation times: e.g., phytoplankton - Angeler *et al.* 2010 & zooplankton - Dexter *et al.* 2015) might be misidentified as boom-busts. Seasonal changes in abundance misidentified as boom-bust cycles are likely more common in short-term studies, but if adequate detection of the different phases in the invasion process is made then sampling at finer scales than a year should not be a problem (Angeler *et al.* 2010; Dexter *et al.* 2015; Walsh *et al.* 2016).

There has been virtually no discussion in the invasion literature of how rapid population growth needs to be considered a boom. Perhaps the assumption is that to reach high population sizes, populations of invasive species have had to grow rapidly which isn’t necessarily the case (e.g., Bloch *et al.* 2019). Alternatively, in the marine invertebrate literature a major review of long-term populations dynamics of echinoderms previously defined a boom as a minimum of a four fold increase in a population typically within a year (Uthicke *et al.* 2009). I suggest adopting this criteria in terms of population growth rate (i.e., ለ ≥ 4) which can be extended to instantaneous measures of population growth (i.e., *r* ≥ ln(4) ≥ 1.386). Studying invasions of populations with short generation times might choose to adopt the instantaneous growth rate because it might better represent how fast these populations respond to the environment.

In contrast to the bust, many more studies have attempted to identify to what extent populations need to crash to be considered a bust (Simberloff & Gibbons 2004; Uthicke *et al.* 2009; Cooling *et al.* 2012; Aagaard & Lockwood 2016; Strayer *et al.* 2017). A threshold in magnitude of 90% decline from the maximum population has frequently been adopted for describing busts (Simberloff & Gibbons 2004; Cooling *et al.* 2012; Aagaard & Lockwood 2016; Fernández 2020). The extent (i.e., magnitude of the decline) should also be represented as a rate. Two studies attempted to quantitatively describe the rate with one more rapid (four fold decline in population size within a year: Uthicke *et al.* 2009) than the other (≥90% decline within 10 years; Aagaard & Lockwood 2016). Seeing as the first comes from outside the invasion literature, I suggest adopting the second. However, I recommend representing the rate in terms of population growth which translate to a finite rate of increase 0 < ለ ≤ 0.372 and instantaneous rate of increase *r* ≤ -0.99.

Finally, describing to what extent a bust is sustained is likely the most important quantitative description of a boom-bust cycle because it separates population cycles (i.e., temporary declines in abundance; Strayer & Malcom 2006; Kaeuffer *et al.* 2009; Jaćimović *et al.* 2019) from boom-bust cycles (i.e., populations remain at low abundances, Hurlbert *et al.* 2007; Gherardi *et al.* 2011; Dunlop & Riley 2013; Kauppi *et al.* 2015; Fernández 2020). I suggest using the criteria that declines must be sustained ≥ 3 years, which has been used previously in a study of population crashes in 68 exotic bird species ([Aagaard & Lockwood 2016)](https://www.zotero.org/google-docs/?broken=Nru0H6). Surprisingly many studies that report boom-bust cycles only include a single survey after the population decline (Mouthon 2003; Boggs *et al.* 2006; Morris *et al.* 2013; Forsström *et al.* 2018) which may result in a bias towards studies being falsely identified as boom-bust cycles.

*Necessary narrowing*

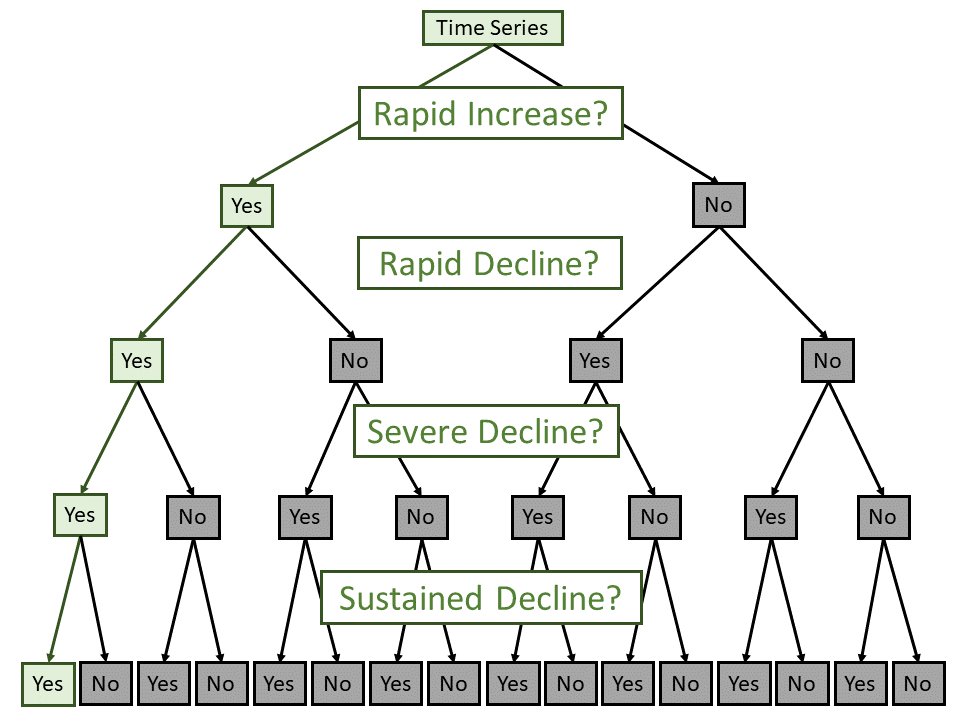
Combining these aspects together I define boom-busts cycles in invasions as a sequence of three phases 1) lag/growth phase, 2) boom phase, and 3) bust phase (Figure 1) where the transition between the growth and boom phase must be rapid (ለ ≥ 4; *r* ≥1.386), and the transition from the boom to the bust phase must be rapid (0 < ለ ≤ 0.372; *r* ≤ -0.99), severe (≥ 90%), and sustained (≥3 years; Figure 1). Using boolean logic, this definition of boom-bust cycles creates a list of 16 mutually exclusive groups with boom-bust cycles occupying only one of the pathways (Figure 2). Narrowing the definition of a boom-bust cycle using my quantitative criteria will facilitate the communication of processes that give rise to this phenomenon. Previously, nine potential mechanisms were hypothesized to give rise to boom-bust cycles (Strayer *et al.* 2017). With a narrower definition of a boom-bust cycle these mechanisms can be tested broadly across ecosystems, continents, and taxon. A narrower definition of a boom-bust cycle could potentially omit population dynamics of invasions previously thought to be boom-busts. The omitted populations just fall into categories of invasive population dynamics other than boom-bust cycles (e.g., slow increase followed by slow decline, [Bloch *et al.* 2019)](https://www.zotero.org/google-docs/?broken=kW7dE2). Identifying alternative population dynamics in invasions will bring greater awareness to these dynamics and the potentially different mechanisms that explain them.

Figure 2. Decision tree using the four quantitative criteria for identifying boom-bust cycles in invasions the green shaded pathway indicates the criteria for a boom-bust.

*Are irruptive dynamics and cyclic populations repeated boom-busts?*

Another important aspect to consider when clarifying terminology of boom-bust is the potential for occurrences of repeated boom-busts cycles. Irruptive population dynamics were first identified in arid small mammal populations where populations can persist at low abundance for many years (Pavey *et al.* 2017; Andreassen *et al.* 2021). Then, in response to stochastic events of high abnormal rainfall, these small mammal populations irrupt to states of high abundances (Letnic & Dickman 2006). In reference to persistence (or sustained) low abundances and the rapid growth and declines exhibited in these dynamics (Andreassen *et al.* 2021) which are a necessary criteria that I previously proposed, I choose to use “irruptive population dynamics” as the term to describe repeated boom-bust cycles in invasions. Furthermore, non-native common house mice (*Mus musculus*) have also been documented to exhibit irruptive population dynamics in these same regions (Breed *et al.* 2017; Bennison *et al.* 2018).

In contrast to irruptive population dynamics, I do not classify cyclic population dynamics in invasive species as repeated boom-bust cycles. Cyclic population dynamics undergo regular fluctuations of population size (Myers 2018). Although the rate of population increase and decline during the fluctuations in abundance might meet the criteria for boom-bust cycles, declines during fluctuations rarely are sustained and severe. I interpret cyclic population dynamics in invasions as the natural variation in the established/boom phases of invasions (Figure 1). Fluctuations akin to cyclic dynamics have been reported in non-native populations during invasions (Strayer & Malcom 2006; Kaeuffer *et al.* 2009; Moncayo-Estrada *et al.* 2012; Dexter *et al.* 2015; Lester *et al.* 2017). Although rare, it may be possible that boom-bust cycles repeat at regular intervals rather than stochastically like population irruptions. In this case, I would name these “cyclic irruptions” in reference to the sustained nature of the population declines between cycles.

**Boom-bust phase metrics**

Comparing invasions of different populations of the sames species (Daskalov *et al.* 2007; Angeler *et al.* 2010; Cooling *et al.* 2012; Morris *et al.* 2013; Sandström *et al.* 2014; Kauppi *et al.* 2015; Aagaard & Lockwood 2016; Lester *et al.* 2017; Haubrock *et al.* 2022) and different species (Kurihara *et al.* 2010; Morris *et al.* 2013; Sandlund *et al.* 2013; Dexter *et al.* 2015; Cecere *et al.* 2016) is relatively useful when trying to find mechanisms that produce boom-bust cycles. Creating metrics that can be used to compare boom-bust cycles will aid these comparisons (Figure 1b). When looking at the lag/growth phase, the duration between introduction and high population growth rates has been suggested which can help determine how common “latent sleeper populations” (i.e.populations that lag due to environmental threshold or completion of mutualism) are in natural systems (Spear *et al.* 2021). I further suggest that a measure of the population growth rate should be used because there may be a correlation with high population growth and the likelihood and/or severity of boom-bust cycles (Duncan *et al.* 2020).

In addition to the lag phase, metrics for the boom and bust phase are important as well (Figure 1b). As previously discussed, variability in boom or establishment phase may indicate cyclic population dynamics (Strayer & Malcom 2006; Kaeuffer *et al.* 2009; Dexter *et al.* 2015; Lester *et al.* 2017), and the duration of high abundances could be an important component in determining the impact that invasive species have on the community and their environment (Strayer & Malcom 2006; Haubrock *et al.* 2022). Considerable consideration has been taken in determining metrics for comparing declines in the bust phase of the boom-bust cycles (Cooling *et al.* 2012; Aagaard & Lockwood 2016). The time from peak density to population bust, the peak probability that a population collapses across different location/subpopulations, the magnitude of decline, and the duration the decline was sustained have previously been used in describing variation between boom-bust cycles (Cooling *et al.* 2012; Aagaard & Lockwood 2016). I further suggest adding the rate of population decline because it represents how fast populations decline.

An additional metric that could be especially important in the context of community ecology is the dominance of the species (i.e., relative abundance). A general rule in community ecology is that the vast majority of species are typically rare in locations with only a few species dominating assemblages (Fisher *et al.* 1943; Brown *et al.* 1995; McGill *et al.* 2007). Dominance is important because it is often related to a species impact in a the system. Although dominance in the boom phase is common (Hurlbert *et al.* 2007; Yerli *et al.* 2013; Duggan 2014), it may be more interesting to understand if a non-native species continues to dominate in the bust phase.

**Boom-Bust Cycles in Natural Populations**

*Identification*

When identifying boom-busts cycles from my literature search, many of the time series I identified did not document the lag/growth phase (Creed & Sheldon 1995; Newman & Biesboer 2000; Strayer & Malcom 2006; Caskey *et al.* 2007; Carbayo *et al.* 2008; Kurihara *et al.* 2010; Dunlop & Riley 2013; McCallum *et al.* 2014; Cooling & Hoffmann 2015; Dexter *et al.* 2015; Gibson-Reinemer *et al.* 2017; Lester *et al.* 2017; Castañeda *et al.* 2018; Jaćimović *et al.* 2019; Wegner *et al.* 2019; Wasson *et al.* 2020), so these studies cannot be classified as boom-bust cycles. Interestingly, in a few of these studies, population abundances fluctuated similar to cyclic populations which could mean that cyclic populations are possible in established population of non-natives (Strayer & Malcom 2006; Lester *et al.* 2017). Many of the other studies with no documentation of the lag/growth phase reported severe (≥ 90%) declines (Creed & Sheldon 1995; Newman & Biesboer 2000; Caskey *et al.* 2007; Carbayo *et al.* 2008; Cooling & Hoffmann 2015; Gibson-Reinemer *et al.* 2017; Castañeda *et al.* 2018). This suggests that declines after reaching high abundances is relatively common in invasive species. Studies that had no documentation of the lag/growth phase also tended to have shorter time series (<10 years) and often would include only one survey was documenting declines (except; Carbayo *et al.* 2008; Dunlop & Riley 2013; Dexter *et al.* 2015; Gibson-Reinemer *et al.* 2017). Shorter time series with fewer studies in the bust phase may overestimate bust like declines.

In contrast to these studies, a substantial number of studies that had documented the lag/growth phase did not exhibit sustained declines (Diederich *et al.* 2005; Ferreira *et al.* 2006; Mergeay *et al.* 2006; Kaeuffer *et al.* 2009; Angeler *et al.* 2010; Witte *et al.* 2010; Morris *et al.* 2013; Sandström *et al.* 2014; Cecere *et al.* 2016; Wegner *et al.* 2019). The primary focus of many of these studies was to document rapid population growth (Ferreira *et al.* 2006; Witte *et al.* 2010; Wegner *et al.* 2019). One study demonstrated that established populations could fluctuate like cyclic population dynamics (Kaeuffer *et al.* 2009).

I identified 28 of taxon that exhibited boom-bust cycles when invading (Mouthon 2003; Bilio & Niermann 2004; Salonen & Mutenia 2004; Boggs *et al.* 2006; Letnic & Dickman 2006; Daskalov *et al.* 2007; Hurlbert *et al.* 2007; Carbayo *et al.* 2008; Eagles-Smith *et al.* 2008; Gerard *et al.* 2010; Hershberger *et al.* 2010; Moncayo-Estrada *et al.* 2012; Moore *et al.* 2012; Dunlop & Riley 2013; Gustaveson & Blommer 2013; Morris *et al.* 2013; Sandlund *et al.* 2013; Yerli *et al.* 2013; Sandström *et al.* 2014; Dexter *et al.* 2015; Kauppi *et al.* 2015; Cecere *et al.* 2016; Korman *et al.* 2017; Wegner *et al.* 2019; Fernández 2020; Haubrock *et al.* 2022). Nine of these studies included only one survey after the population declined (Boggs *et al.* 2006; Letnic & Dickman 2006; Daskalov *et al.* 2007; Hershberger *et al.* 2010; Delefosse *et al.* 2012; Gustaveson & Blommer 2013; Morris *et al.* 2013; Kauppi *et al.* 2015; Forsström *et al.* 2018). Interestingly, I found two cases where boom-bust cycles were repeated (Eagles-Smith *et al.* 2008; Gherardi *et al.* 2011). Finally, there were two studies where populations reached high abundances but population growth and/or population declines were slow (Magnusdottir *et al.* 2014; Bloch *et al.* 2019).

**Conclusions**

Overall, I quantitatively define boom-bust cycles in invasions as a sequence of three phases 1) lag/growth phase, 2) boom phase, and 3) bust phase (Figure 1) where the transition between the growth and boom phase must be rapid (ለ ≥ 4; *r* ≥1.386), and the transition from the boom to the bust phase must be rapid (0 < ለ ≤ 0.372; *r* ≤ -0.99), severe (≥ 90%), and sustained (≥3 years; Figure 1). These criteria narrowed the definition of boom-bust cycles which potentially could help find mechanisms general to these phenomena. I also provide metrics that describe boom-busts cycles that could facilitate comparison across species and locations. Using these criteria, I identified 28 studies demonstrating boom-bust cycles with 2 studies exhibiting repeated boom-bust cycles.

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