

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

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61

62 **Abstract**

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

78 **Introduction**

79 One of the most persistent ideas in invasion biology is the boom-bust concept (Elton
80 1958; Williamson 1996; Simberloff & Gibbons 2004; Lockwood et al. 2013). According to this
81 concept, invaders may go through an initial outbreak (or “boom”) phase, in which their
82 population becomes very large, before declining to a much lower population size (the “bust”,
83 “collapse”, “decline”, or “crash”). Boom-bust dynamics are of fundamental importance to
84 understanding, interpreting, and managing biological invasions. The boom-bust dynamic
85 suggests that the initial outbreak phase may be a transient phenomenon, and focuses attention on
86 the nature, strength, and generality of mechanisms by which the invader and the invaded
87 ecosystem establish a more stable long-term coexistence. It also suggests that the effects of the
88 invader on ecosystem processes and other species in the community, whether harmful or
89 beneficial, are at least partially reversible and do not necessarily represent the new, persistent
90 state of the invaded ecosystem.

91 The boom-bust dynamic has been viewed as a progression from a transient “harmful”
92 phase to a more persistent “harmless” phase. The boom-bust concept is therefore of particular
93 significance in the management of biological invasions. If harmful invasions often turn into
94 harmless invasions on their own, then the best management option might be to take no action at
95 all, and simply let the invader’s population diminish (e.g., Anon. 2011; Thompson 2014; Pearce
96 2015). At most, managers might have to mitigate some undesirable short-term effects of the
97 invasion before it enters the “harmless” phase.

98 Despite the prominence of the boom-bust phenomenon in invasion biology and its
99 importance to management, ecologists disagree about how frequently it occurs. Williamson’s
100 (1996) influential book presented several examples of boom-bust dynamics, mostly from islands,

101 but described such dynamics as “not common”. In perhaps the most detailed examination of the
102 phenomenon, Simberloff & Gibbons (2004) concluded that “spontaneous population crashes are
103 a minor phenomenon in invasion biology”, but lamented the scarcity of reliable long-term data.
104 In contrast, Davis (2009) wrote that a decline in abundance following a period of dominance was
105 a “common dynamic”, and Lockwood et al. (2013) agreed that “boom and bust dynamics may be
106 quite common”. Aagaard & Lockwood (2016) reported population collapses in many non-native
107 bird populations, and concluded that “severe, rapid, and persistent population declines may be
108 common among exotic populations.”

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

118 In addition to the problem of inadequate data, already noted by Simberloff & Gibbons
119 (2004), confusion about the frequency and importance of boom-bust dynamics in biological
120 invasions may have arisen at least in part because of imprecision in defining the basic “boom-
121 bust” dynamic, and from incautious interpretation of inadequate data. In this paper, we (i)
122 describe the common variants of the boom-bust concept; (ii) review multiple mechanisms that
123 could produce a boom-bust dynamic in non-native species; and (iii) describe and evaluate

124 various approaches that have been used or could be used to describe and test for boom-bust
125 dynamics in field data. This overview includes a systematic review of published papers on
126 boom-bust dynamics, as well as analyses of simulated population data to test methods used to
127 describe boom-bust dynamics.

128 **The boom-bust dynamic and its variants**

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

142 Perhaps because of the encouraging implication that invaded systems frequently recover
143 on their own, the solitary boom-bust dynamic, rather than the recurrent boom-bust, has been the
144 chief focus of invasion ecology and management, and will be the main subject of this paper. It
145 has four phases (Fig. 1a): (1) a pre-boom phase (i.e., the pre-invasion phase plus sometimes a lag
146 phase); (2) a boom phase, in which the focal variable (e.g., population size or biomass, range

147 size, ecological impact) increases rapidly; (3) a bust phase, in which the focal variable decreases
148 rapidly; and (4) a post-bust phase, during which the focal variable persists at a value lower than
149 its peak (although it need not be constant), or drops to zero.

150 This simple description hides several complications, the most obvious of which is how
151 large or rapid changes must be to qualify as a boom-bust dynamic (Box 1). Additional
152 complicating factors include the spatial scale of the dynamics and the sampling program used to
153 detect them. Some mechanisms produce local population dynamics that are different from those
154 that occur at large scales (see below), so it is important to specify the spatial scale at which
155 boom-bust dynamics are observed. Depending on the purpose of the analysis, though, local,
156 regional, or global population dynamics may be of interest, so we see no reason to insist that
157 boom-bust dynamics be analyzed at a particular spatial scale, other than to note that boom-bust
158 dynamics at very small spatial scales (e.g., a few m²) are likely to be common but uninteresting
159 to most invasion ecologists and managers. Variables other than population size (or density) may
160 be used to assess boom-bust dynamics. Invasion ecologists may choose to analyze the time-
161 course of range size or ecological impact of the non-native species (Table 1), either because
162 these data are available and population data are not, or because the focus of the study is on range
163 or impacts, both of which have received much attention in invasion ecology (Parker et al. 1999;
164 Simberloff et al. 2013; Jeschke et al. 2014). These different descriptors of the invading
165 population do not necessarily map simply onto one another. Indeed, it has been demonstrated
166 that temporal changes in the population size and range size of species can be positively
167 correlated, uncorrelated, or negatively correlated (e.g., Gaston 2003). Likewise, impacts may not
168 always tightly track population size, for example because the relationship between density and
169 impact is nonlinear (Yokomizo et al. 2009; Dostál et al. 2013), because of trait shifts in the

170 invader's population (e.g., Fig. 2, Pace et al. 2010), or because the impacts may be time-lagged,
171 hysteretic, or even irreversible. Consequently, these different descriptors of invading populations
172 probably should not be combined uncritically with one another into a single analysis.

173 In view of these considerations, we offer the following general definitions. In a *solitary*
174 *boom-bust dynamic*, the response variable rises rapidly from a low baseline or zero value to a
175 high value (the boom), then drops (the bust) to and persists at values substantially lower than the
176 boom, possibly even zero. In a *recurrent boom-bust dynamic*, this up-and-down dynamic is
177 repeated two or more times, possibly with diminishing amplitude, and in a *cyclic boom-bust*
178 *dynamic* (a variant of the recurrent boom-bust dynamic), the booms occur at more or less regular
179 intervals. Although recurring seasonal cycles of population size may technically meet this broad
180 definition of cyclic boom-bust, we follow customary usage and exclude them from further
181 consideration.

182 **Causes of boom-bust dynamics**

183 If we were monitoring a local population of an invader, and observed a dynamic like that
184 shown in Fig. 1a, what could we infer about its cause and meaning? The dynamic shown in Fig.
185 1a is simple and combines three common attributes of biological populations: rapid growth, a
186 large peak population, and a severe decline, each of which can be produced by several causes
187 well known to ecologists. Consequently, boom-bust dynamics could be produced by many
188 different mechanisms, only some of them closely related to the restoration of nature's balance
189 following a biological invasion. It would be difficult to catalog all possible causes of a boom-
190 bust dynamic, but we briefly discuss some of the more likely ones. For convenience, we divide
191 these mechanisms between (A) those that are typically associated with invasions and (B) those

192 that occur broadly in ecology (not just in invasions, but which may affect invaders), recognizing
193 that some of these mechanisms do not fall cleanly into just one of these categories.

194 (A) *Mechanisms typically associated with invasions*

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

197 (A1) *Enemy release followed by enemy accumulation.* Boom-bust dynamics of invaders
198 probably are most often attributed to this mechanism (predator-prey or diseases/parasites in Fig.
199 3; Simberloff & Gibbons, 2004). Invaders often are introduced into a new range without their
200 full complement of enemies such as predators, parasites, and pathogens (the “enemy release
201 hypothesis”; Keane & Crawley 2002). This may allow them to rapidly develop large populations,
202 and divert resources formerly used for defenses against enemies into growth and reproduction
203 (the “evolution of increased competitive ability” [EICA] hypothesis; Blossey & Nötzold 1995).
204 Competitors and prey are not typically included in the enemy release and EICA hypotheses, but
205 could have similar effects. For instance, native prey might be naïve to a newly introduced
206 predator, providing large rewards to the non-native predator (Sih et al. 2010; Saul et al. 2013).
207 Likewise, non-native species might be functionally novel in their new environment, e.g. possess
208 a “novel weapon” (*sensu* Callaway & Ridenour 2004) or consume a resource that is not
209 consumed by resident species, which allows them to be relatively free of competitors. All of
210 these mechanisms could lead to a boom in the early phase of an invasion.

211 These release effects might diminish over time, as (i) enemies or competitors of the
212 invader from its native range arrive (or are deliberately introduced) or (ii) resident species
213 become more effective predators, parasites or competitors of the non-native species (e.g., Strayer
214 et al. 2006; Diez et al. 2010; Mitchell et al. 2010; Strickler et al. 2016), or develop defenses

215 against a non-native predator (e.g., Nunes et al. 2014; Saul & Jeschke 2015), potentially leading
216 to a bust in the invader’s population. However, these compensatory mechanisms can occur
217 without leading to a “bust” in population size or ecosystem effects of the invader. For instance,
218 mortality arising partially from increases in consumption by a native predator (the blue crab,
219 *Callinectes sapidus*) on the non-native *Dreissena polymorpha* (zebra mussel) in the Hudson
220 River increased from 46%/yr to >99%/yr over the first 20 years of the invasion (Carlsson et al.
221 2011), but this dramatic increase did not affect the number of *D. polymorpha* in the river (Strayer
222 et al. 2011; Fig. 2a). Mussel recruitment was sufficient to compensate for these large increases in
223 mortality. The extent, strength, and functional significance of release effects and their possible
224 diminishment over time are still being debated (e.g., Speek et al. 2015).

225 (A2) *Interactions with subsequent invaders.* An interesting special case of enemy
226 accumulation occurs when an earlier invader is displaced by a later invader (termed “over-
227 invasion” by Russell et al. 2014). For instance, among the dreissenid mussels (*D. polymorpha*
228 and *D. rostriformis*, the quagga mussel), *D. rostriformis* disperses less readily than *D.*
229 *polymorpha*, but is typically competitively dominant, often leading to boom-bust dynamics in *D.*
230 *polymorpha* as it arrives first, booms, and is displaced a few years later when *D. rostriformis*
231 arrives (Karatayev et al. 2011). Other examples of displacement of earlier invaders by later ones
232 have been reported from a wide variety of locations and taxa, including plants, insects,
233 crustaceans, and rats (Mack 1989; Russell et al. 2014).

234 This special case of enemy accumulation may have two interesting features. First, it has
235 been suggested that dispersal ability and competitive ability are negatively correlated (e.g.,
236 Tilman et al. 1997). If this is generally true, then frequent invasions such as those that are
237 occurring in many contemporary ecosystems may often produce boom-bust dynamics in the

238 earlier invaders as they are displaced by later invaders with slower dispersal but better
239 competitive abilities.

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

248 (A3) *Time-lags in density-dependent populations.* The population growth of a non-native
249 species introduced into a new environment offers formal similarities to laboratory populations in
250 which a few individuals of a species are inoculated into a microcosm. Introducing time lags into
251 models of such populations can produce repeated oscillations or boom-bust dynamics or even a
252 population boom followed by extinction (e.g., May et al. 1974). The critical attributes that
253 determine the trajectory of a population are its characteristic return time (the rate at which the
254 population approaches an equilibrium following a small perturbation) and the time delays of the
255 system, whether induced by the population itself (e.g., through age- or stage-structure), or
256 interactions with its enemies or resource supply. If the return time is greater than the generation
257 time, the population damps exponentially to equilibrium, following a logistic curve. However, as
258 the return time falls below generation time, populations show a variety of forms of cycles or
259 oscillatory damping which may resemble Fig. 1b. In even more extreme cases (longer lags,
260 shorter return times), populations may go extinct after large fluctuations, resembling Fig. 1a, but

261 with a post-boom density of zero. This mechanism is not specific to species introduced into
262 novel environments, but introduced populations with high growth rates, for example when losses
263 to enemies or opportunities for dispersal are low, or systems with long time-lags, or introductions
264 initiated far from a stable age- or stage-structure (Stott et al. 2010; Iles et al. 2016) may be
265 particularly prone to boom-bust dynamics arising from this mechanism.

266 (A4) *Slow environmental change caused by the invader.* Abundant invaders often
267 substantially change the chemistry, physical structure, or other environmental conditions of
268 invaded habitats (e.g., Levine et al. 2003; Strayer et al. 2006). If these changes are harmful to the
269 invader and occur quickly, they may prevent a boom from occurring in the first place. However,
270 if they are slow and cumulative, produced either by “mining” accumulated resources or
271 engineering the physicochemical environment to the long-term detriment of the invader, they
272 may trigger a (usually solitary) bust after an initial boom phase as environmental quality
273 declines.

274 Probably the best-known examples involve non-native plants and changes to the physical
275 or chemical properties of soils and sediments (pools with slow dynamics that are important to the
276 plants; Van der Putten et al. 2013; Vilà et al. 2013), although it is not always easy to separate the
277 effects of changing soil physicochemistry from those of changing soil microbial communities. A
278 16-year time series of the *Spartina alterniflora* (smooth cordgrass) invasion in the Yangtze River
279 estuary revealed that an initial 5-year growth phase was followed by a decline due to steady
280 decreases in the tidal inundation time and increases in standing litter as the *Spartina* bed
281 gradually accumulated sediment (Tang et al. 2012). In Iceland, the non-native nitrogen-fixing
282 plant *Lupinus nootkatensis* can develop large populations, causing soil nitrogen to increase, after
283 which it may be replaced by *Anthriscus sylvestris*, a plant (also non-native) that needs nitrogen-

284 rich soils (Magnússon et al. 2003). In a similar example involving animals, it has been suggested
285 the populations of some invading earthworms in northeastern North America boom and then bust
286 as they consume stores of accumulated leaf litter on the forest floor and soil (Straube et al. 2009).

287 (A5) *Delayed genetic effects.* Several genetic mechanisms could in principle lead to
288 boom-bust dynamics in invaders. Many biological invasions arise from small inocula with low
289 genetic variation (Simberloff 2009). Invasions of species with vegetative or parthenogenetic
290 reproduction may even arise from single individuals. Such populations may flourish initially, but
291 then collapse when exposed to a new stress (e.g., disease, extreme climatic events). Aghighi et
292 al. (2014) believed that low genetic variability together with apomictic reproduction contributed
293 to the decline of the invasive blackberry *Rubus anglocandicans* in Australia. However, some
294 invaders with very low genetic variation have been very successful (e.g., Bailey & Conolly 2000;
295 Dybdahl & Drown 2011). Likewise, strong selection following invasion may erode initial genetic
296 diversity, and alleles that favor introduction, dispersal, and initial population growth may be less
297 advantageous in later phases of the invasion (Keller & Taylor 2008) or during extreme events.

298 Low initial genetic variability may also make populations of invaders prone to inbreeding
299 depression. The level of equilibrium between the selection and inbreeding may delay the
300 negative effects of inbreeding (Connor & Bellucci 1979). In such circumstances, homozygote
301 production and inbreeding depression would eventually occur, but with a lag proportional to
302 selection strength. In addition, the spread of an invader over a patchy environment may result in
303 inbreeding effects within occupied patches, if the invasion is characterized by a strong
304 directional migration, followed by limited gene flow between populations (Stone & Sunnucks
305 1993). Low abundance within patches may intensify genetic drift and inbreeding, which will
306 occur after a lag from the initial invasion. Increasing levels of gene flow between patches

307 containing locally adapted genotypes may also lead to a genetic regime shift in which
308 maladapted genotypes prevail over these locally adapted genotypes (a transient monopolization,
309 De Meester et al. 2016).

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

318 (A6) *Human control of invaders.* Finally, humans may deliberately suppress troublesome
319 invaders through a wide variety of tools (e.g., classic biological control, including augmentation
320 or re-introduction of native predators or pathogens, harvesting, poisoning, and so on), or
321 inadvertently reduce populations of desirable invaders by overharvesting them (e.g., the edible
322 signal crayfish *Pacifastacus leniusculus* – Jussila et al. 2014). In some cases (e.g., harvest), this
323 suppression is temporary and produces a population bust only as long as active control continues,
324 while other tools (e.g., biological control) may produce a long-lasting or permanent population
325 bust. There are many examples of this kind of human-induced boom-bust cycle of non-native
326 species (e.g., Lockwood et al. 2013), as well as many examples of control or harvest campaigns
327 that failed to produce a bust in the target population (e.g., Syslo et al. 2011). Although
328 documented in a higher proportion of cases than other mechanisms thought to cause population

329 busts (Fig. 3), if an outbreak has been suppressed by deliberate human actions, it does not
330 provide evidence that invaders and their impacts would have disappeared on their own.

331 *(B) General ecological mechanisms*

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

344 *(B1) Succession or recovery from disturbance.* Disturbance is important in driving
345 community dynamics in many ecosystems, with some species flourishing immediately after a
346 disturbance and others peaking only after a long period free from disturbance (e.g., Meiners et al.
347 2015). In such disturbance-controlled systems, local populations will appear to boom and bust in
348 response to disturbance events (although not necessarily at larger spatial scales, if a shifting
349 mosaic of sites at different successional stages exists). Disturbance-related boom-busts may be
350 especially frequent among invaders, because it has been demonstrated that disturbance facilitates
351 invasion, at least among plants (D'Antonio et al. 1999; Davis et al. 2000). Certainly, many non-

352 native plant species are associated with early seral stages, so that they become less abundant or
353 even disappear as succession occurs at a site (e.g., Rejmánek 1989; Meiners et al. 2015).

354 *(B2) Climate change and other changes in the abiotic and biotic environments.* Changes
355 in local environmental conditions and biotic communities often drive changes in local
356 populations. In particular, human-induced climate change has increased to the point that it is
357 affecting many biological populations (e.g., Parmesan 2006; Chen et al. 2011) and will likely
358 become even more important in the future (e.g., Thomas et al. 2004; Bellard et al. 2012). In the
359 specific case of an invader, the initial colonization of a site could cause a boom, followed by a
360 decline as environmental conditions or the biotic community move away from the optimum for
361 the species. Climate change in particular is likely to cause many such declines among
362 populations of non-native species (e.g., Bradley et al., 2009; Wenger et al. 2011), just as for
363 native species. Depending on the details of the relationship between the species and its
364 environment (e.g., thresholds between survival and variables such as rising temperature or
365 declining soil moisture; see White et al. 2016 for an example), these declines could be rapid
366 enough to appear as busts. Changes in local environmental conditions other than human-induced
367 climate change probably will cause many busts in local populations of invaders as well.
368 Likewise, changes in the local biotic communities that interact with invaders (predators,
369 competitors, mutualists, etc.), whatever the cause, probably will also drive local busts in non-
370 native populations.

371 *(B3) Shifts between alternative stable states.* Some ecosystems exhibit alternative stable
372 states, in which multiple stable equilibria are possible under identical environmental conditions
373 (Scheffer et al. 2001; Beisner et al. 2003). These stable states can be reinforced by positive
374 feedbacks and result in hysteresis, so that backward and forward transitions between states occur

375 at different levels of environmental drivers, and large perturbations are required to overcome
376 thresholds between states (Beisner et al. 2003). Several examples of ecological systems with
377 multiple stable states have been offered (see Petraitis 2013 for a critical review).

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

388 *General remarks about mechanisms*

389 Mechanisms producing boom-bust dynamics in local populations operate so frequently
390 and are so varied that observing such dynamics in an invader does not by itself allow us to infer
391 the underlying mechanism(s), whether it is particularly related to the invasion, the long-term
392 prospects for that population, or the actions that should be taken to manage that population or its
393 impacts. Even our brief survey shows that booms and busts can be produced by mechanisms
394 intrinsic to the population or by external factors; by changing vital parameters of the system or
395 without any change in these parameters; and that they can be solitary, cyclic, or recurring but
396 irregular. Different kinds of management responses (including no response at all) would be
397 appropriate for addressing booms caused by different mechanisms. Finally, there is no need for a

398 boom-bust dynamic to be the result of a single mechanism. Indeed, it would be unusual for an
399 invader to be subject to only one of the mechanisms that we have described, so combined and
400 interactive effects probably are common. Instead, we will need to gather additional information
401 about the invader, such as detailed demographic information, response to experimental
402 interventions, invasion history in other regions, and so on. Nevertheless, it is striking how
403 frequently that causative mechanisms are assumed rather than demonstrated in published
404 analyses of boom-bust dynamics (Fig. 3).

405 We hypothesize that small, isolated environments such as islands or lakes may be
406 especially likely to foster boom-bust dynamics in invaders. Such habitats may have reduced
407 populations of natural enemies, be more prone to local resource depletion, and have fewer
408 opportunities for local overpopulation to be relieved by emigration (or low genetic variation to
409 be relieved by immigration) than more open or networked habitats (e.g., Elton 1958; Carlquist
410 1974; Holt 2010). This could make mechanisms such as enemy release and accumulation,
411 environmental degradation or resource depletion, time lags, delayed genetic effects, deliberate
412 human intervention, and shift between stable states more likely, so that boom-bust observations
413 may be especially characteristic of islands, lakes and similar habitats. Further studies of the
414 prevalence of boom-bust dynamics in species introduced into open and closed, or isolated and
415 networked, habitats could be informative.

416 **Quantitative analysis of boom-bust dynamics**

417 Ecologists concerned with boom-bust dynamics have not extensively discussed how the
418 characteristics of such dynamics might be quantitatively described. Studies of boom-bust
419 dynamics often are made without applying any quantitative criteria, and when quantitative
420 criteria are used, a wide range of values have been applied (Table 1). We describe six

421 alternatives that have been used or might be useful, and use original, simulated data to test or
422 illustrate three of them. The first of these, based on the observed decline from a peak value, has
423 been widely used, but our original simulations show that it is prone to severe bias in noisy data
424 sets. We discuss two alternative methods (regime shift detection and tests of deviations from
425 expected population trajectories) that appear to have broad potential for analyzing boom-bust
426 dynamics, although neither has yet been widely used by invasion ecologists. Finally, we briefly
427 describe three additional methods (Bayesian detection of population collapse, randomization
428 tests and analysis of the temporal sequence of peaks) that might be useful in special situations.
429 The different methods provide different information (e.g., size vs. statistical significance of bust)
430 and are suited to different kinds of data sets.

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

437 Although this criterion appears to be simple to apply and interpret, it is sensitive to the
438 length of the data set and the amount of noise (spatiotemporal variation in population size,
439 observation or sampling error) in the data. In particular, our simulations show that it tends to
440 overestimate the severity of boom-bust dynamics, sometimes badly (Fig. 4). This metric
441 frequently detects booms-and-busts in runs of data that have no underlying boom-bust dynamic,
442 particularly if the data are noisy (shown in the left-hand bar in Fig. 4a). Bias is least in cases
443 where the data are not very variable, with longer periods of record, and with most severe actual

444 decline. Bias can be reduced by averaging or smoothing data. Nevertheless, simple metrics based
445 on the observed decline from peak to subsequent trough produce accurate estimates of the
446 amount of bust only under the most favorable combination of circumstances. Except in such
447 ideal cases, they are likely to greatly overestimate the frequency and severity of busts. Therefore,
448 these metrics should be used very carefully, if at all. It is likely that some reports of boom-bust
449 dynamics based on this criterion have been exaggerated or are entirely spurious (cf. Fig. 4a).

450 *Regime shift and change-point detection.* Methods developed to detect and describe
451 regime shifts and thresholds in time series could be adapted to describe and detect booms and
452 busts. The most common methods have been used to detect step-changes (e.g., Rodionov &
453 Overland 2005; Andersen et al. 2009), and their utility drops if the change is gradual (Rodionov
454 2004). Nevertheless, such methods were used successfully by Sandström et al. (2014) to detect
455 boom-bust dynamics in introduced crayfish populations. In our tests of this method on simulated
456 data (Fig. 5), we found that it typically identified two regime shifts, the first (at $t \sim 6$) associated
457 with the shift from the growth phase to the stationary phase, and the second (at $t \sim 14-15$, lagged
458 several years after the bust actually began) associated with the population bust. As with the
459 decline-from-peak metrics, this test was more likely to detect the bust and produced fewer false
460 positives for more severe busts (Fig. 5a), less noisy data (Fig. 5b), and longer runs of data (Fig.
461 5c). In contrast to the decline-from-peak methods, this method did not produce a large number of
462 false positives for populations that were not actually declining (red line in Fig. 5a), and generally
463 performed satisfactorily. The results shown in Fig. 5 should not be interpreted as applying to all
464 regime-shift methods, because the performance of these methods could be improved by better
465 matching the model to the dynamics of the target population (e.g., sudden vs. gradual collapse),
466 but our findings about the influence of noise and length of record should apply broadly. There is

467 a rich literature on methods to detect change points and regime shifts, some of which can
468 accommodate changes other than step-changes (e.g., Carstensen & Weydmann 2012), so it seems
469 very likely that some of these methods will be useful for analyzing boom-bust dynamics.
470 Andersen et al. (2009) provided a critical review of methods that have been proposed to detect
471 ecological change points, including available software.

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

487 Economists, especially those concerned with temporal trends in real estate prices, identify
488 the timing and size of booms and busts (which they sometimes call “bubbles” and “crashes”) as
489 deviations from running time-series predictions (e.g., Hui et al. 2010). Although powerful, these

490 methods require such long data runs (typically thousands of data points) that they are unlikely to
491 be very useful in invasion ecology.

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

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

510
$$B_k = \frac{\sum_1^{n-k} N_t / (n - k) - \sum_{n-k+1}^n N_t / k}{\sum_1^{n-k} N_t / (n - k)}$$

511 B_k equals 0 for no change in mean population size and 1 for a complete bust to extinction, and
512 will be negative if mean population size has increased rather than decreased during the supposed
513 bust period. It can be tested for statistical significance by comparing observed values to values
514 generated by randomly shuffling the time-series (bootstrapping). The resulting plot (Fig. 6)
515 shows the severity and statistical significance of the bust. This test seems simple and easy to
516 understand, and details of the test could be modified to fit the hypothesis and the data set being
517 tested, but may be biased by using the observed data to choose the first data point to include in
518 the calculation of B_k . If we choose the observed maximum of the time-series, for example, this
519 test seems likely to overestimate the size and significance of the bust. Because of this problem,
520 and because randomization tests have not been tested for their ability to detect and describe
521 boom-bust dynamics, any randomization test will need to be evaluated carefully before it is
522 applied to real data.

523 *Temporal sequence of peaks.* Methods adapted from those developed to use a temporal
524 sequence of sightings of a rare animal to estimate the probability that extinction has occurred
525 (e.g., Solow & Roberts 2003; Boakes et al. 2015) might be applied to boom-bust dynamics. The
526 approach would be to define a boom as any value of N_t above some threshold value N_{thres} , and a
527 bust as any value below that threshold. One could then use the temporal sequence of booms to
528 estimate the probability that booms have stopped. One could either choose a single value of N_{thres}
529 that is of special interest (e.g., the threshold above which economic impacts occur), or test a
530 series of values of N_{thres} . This method is well developed in conservation biology (Boakes et al.
531 2015) and relatively simple, but would have to be modified to take temporal autocorrelation into
532 account (they were developed for independent observations, but see Lindén et al. 2013). It seems
533 most applicable to populations having recurrent booms and busts, and will have low power

534 unless the number of years of observation is high (Boakes et al. 2015). One situation for which
535 this method may be especially suited is where the data consist simply of the dates of outbreaks,
536 rather than of quantitative measures of population size or impact. Such data sometimes are
537 available for pest species, for example. Methods might also be adapted from hydrology and
538 climatology (e.g., Katz et al. 2002; Zhang et al. 2004) to test for busts (declining peak values) in
539 recurrent boom-bust dynamics.

540 **Conclusions**

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

553 The analytical method chosen then needs to match this definition as well as the
554 characteristics of the data. As we have cautioned, simple metrics based on the observed decline
555 from a peak value to a subsequent trough are likely to be badly biased, and rarely will be
556 appropriate for detecting or describing boom-bust dynamics. Instead, one of the alternative

557 analyses that we have described, or a new analysis well suited to the question and the data set, is
558 more likely to be useful.

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

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

576 One of the difficulties with current methods for detecting boom-bust dynamics is that
577 they are backward-looking (trailing indicators), so it typically is not possible to demonstrate a
578 bust until several years after it has occurred, leading to delays and uncertainty in management
579 actions. Field data or experiments might help to provide more timely indicators of population

580 busts. For instance, a time-series of exclosure experiments might provide information about
581 critical changes in predation rates on the invader, or interaction strengths with the local biota,
582 and measurements of resource availability could show that limiting resources are being depleted.
583 Alternatively, it may be possible to borrow from the literature on regime shifts (e.g., Carpenter &
584 Brock 2006; Scheffer et al. 2015) or population collapses (e.g., Clements & Ozgul 2016) to
585 develop real-time or leading indicators of busts in nature.

586 *Coda: The way forward*

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

599 In the near term, the conceptual and computational difficulties associated with the boom-
600 bust dynamic can be reduced by careful attention to definitions and computations, along with
601 more critical consideration of underlying mechanisms. We have provided many specific
602 suggestions in this paper for improving the application of the boom-bust concept. It should thus

603 be possible to make considerable progress in understanding boom-bust dynamics in invading
604 species through critical application of the concepts and tools that are now at hand.

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

618

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631

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869

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

871 Our definition of boom-bust dynamics is frustratingly vague, and couched in terms like
872 “high value”, “rapidly”, and “substantially lower”. Why not simply adopt numerical criteria
873 (population growth $>X\%$ /year, rising to a value $\geq Y$, falling to a value $\leq Z$ within N years of
874 peaking)?

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

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

891 Second, different species and ecological processes have different characteristic response
892 times. Rates of population change, expressed as % per year, will vary with the generation time of

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

900 Third, the amount of change in population size that would qualify as “important” or
901 “dramatic” will vary across systems, depending on the interests of the scientist or manager. A
902 20% decline in population could be highly interesting or important in one system but trivial in
903 another.

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

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

916 define a bust as a $Z\%$ decline in population density within K generations. These are very
917 different definitions of bust, but all are specific and measurable.

918

919 Table 1. Selected characteristics of published scientific studies on boom-bust dynamics of non-
 920 native populations ($n=56$ papers). Some studies fit into more than one category (e.g., used more
 921 than one metric of population size) or had missing data, so the number of studies does not always
 922 sum to 56. Some studies used multiple data sets; the length of study given below is an average
 923 for the data sets used in the study. More details about this analysis, including a description of
 924 methods, are given in Appendix 1.

	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 hypothesized	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

925

926

927 **Figure legends**

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

933

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

940

941 Fig. 3. Causes offered for population busts by authors of papers included in our systematic
942 review (see Appendix 1), and whether these mechanisms were actually demonstrated. Studies in
943 which a cause was hypothesized but not demonstrated are represented as the difference between
944 the white and black bars. Because some studies suggested that busts were the result of multiple
945 causes, the number of causes offered sums to more than the number of studies ($n=56$).

946

947 Fig. 4. Bias produced by decline-from-peak metrics, based on analysis of simulated data sets
948 with different known characteristics. Red lines show true characteristics of the data, and boxes
949 and whiskers show estimated values. Unless otherwise noted, simulated population is subject to a
950 50% bust beginning in year 10, has normally distributed error with SD = 30% of mean, is

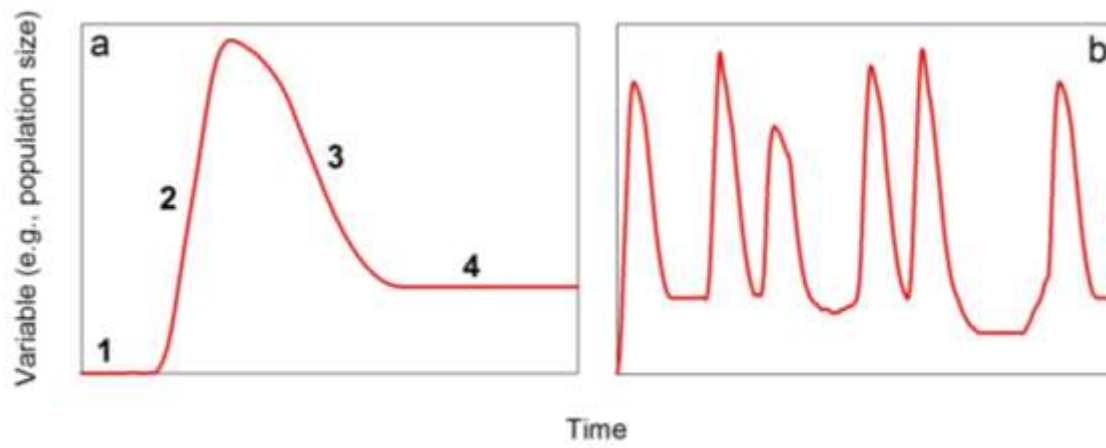
951 smoothed by calculating 3-year running means, and extends for 30 years after the peak; (a)
952 populations with different degrees of bust, including a population that has no bust (i.e., logistic
953 growth); (b) populations with different amounts of normally distributed error (SD/mean = 10%,
954 30%, and 100% for low, medium, and high, respectively); (c) different lengths of record; and (d)
955 different metrics of decline (from left to right, difference between single highest year and single
956 lowest year after that peak using unsmoothed data [single, un]; same for data smoothed by
957 calculating 3-year running means [single, sm]; difference between peak year and mean of next
958 10 years using unsmoothed data [avg, un]; same for data smoothed by calculating 3-year running
959 means [avg, sm]. See Appendix 2 for details.

960

961 Fig. 5. Tests of the performance of the sequential *t*-test of Rodionov & Overland (2005), based
962 on analysis of simulated data sets with different known characteristics. Graphs show the
963 percentage of simulations for which a significant regime shift was detected at each time. Unless
964 otherwise noted, the simulated population is subject to a 50% bust beginning in year 10, has
965 normally distributed error with SD = 30% of mean, is smoothed by calculating 3-year running
966 means, and extends for 30 years after the peak; (a) populations with different degrees of bust,
967 including a population that has no bust (i.e., logistic growth); (b) populations with different
968 amounts of normally distributed error (SD/mean = 10%, 30%, and 100% for low, medium, and
969 high, respectively); and (c) different lengths of record after the peak. We ran 100 trials for each
970 scenario, and used the default parameters of $p=0.1$, cut-off length=10, and Huber's weight
971 parameter=1. See Appendix 2 for more details.

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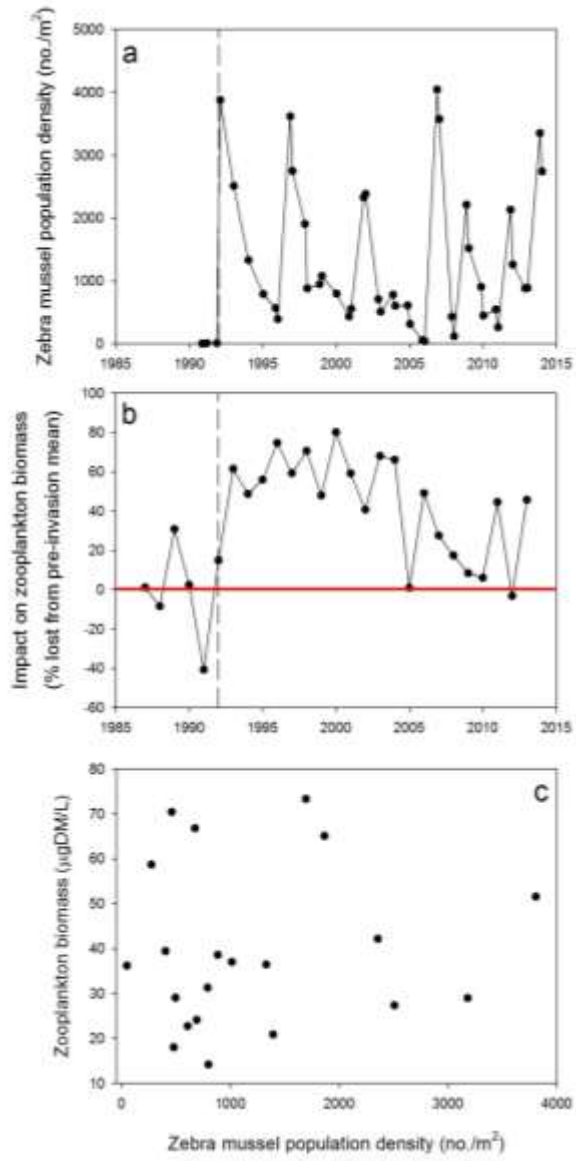
973 Fig. 6. Example of the use of a randomization test on a simulated data set: (a) the time-course of
974 population size N_t ; (b): calculations of the test statistic B_k (see text for definition) from the data
975 (black line and dots), and the 95th percentile of values derived from 100 randomizations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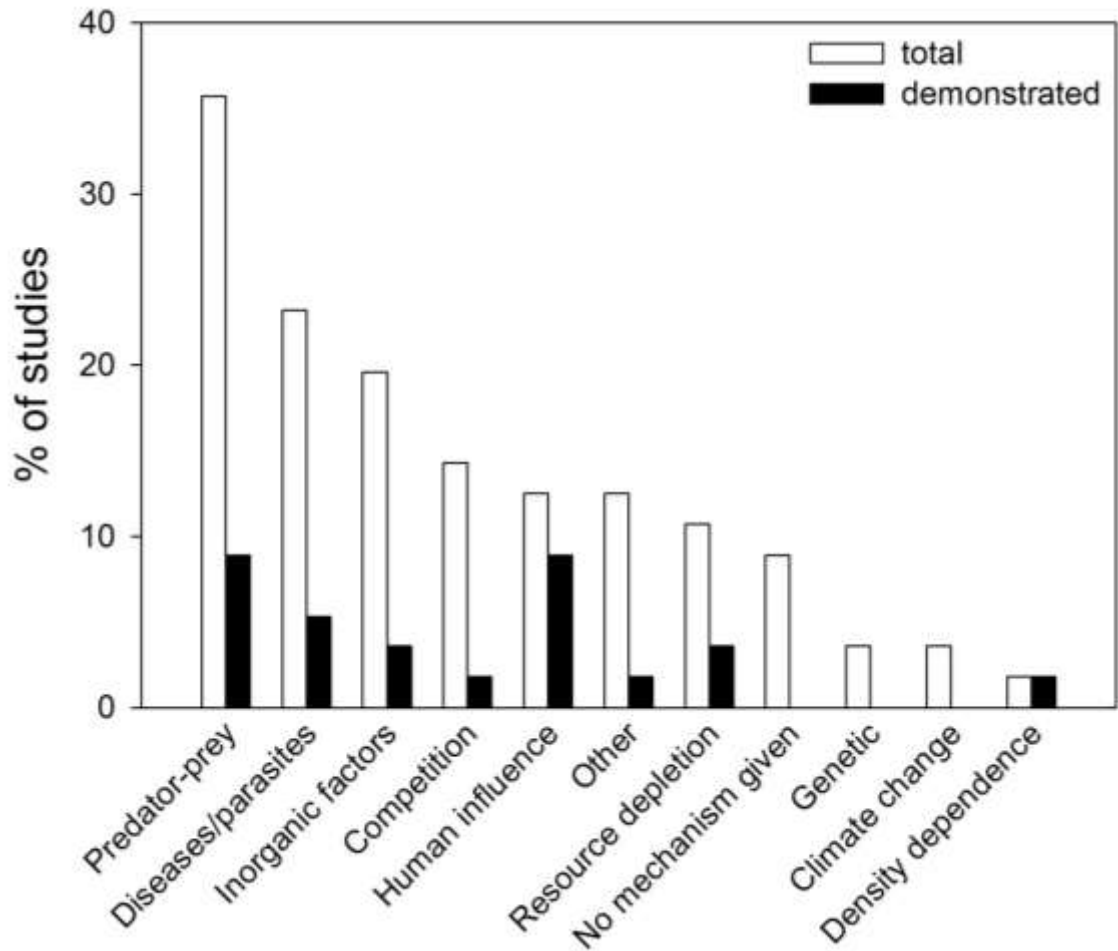
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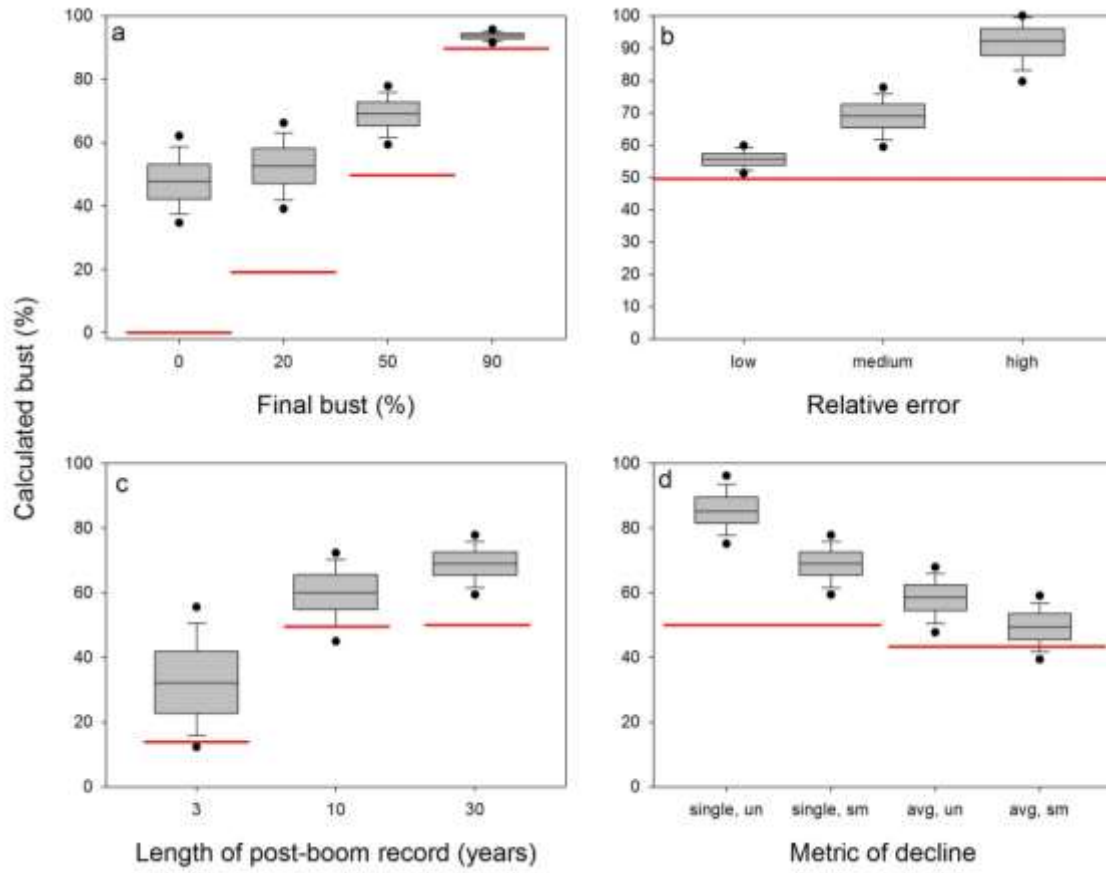
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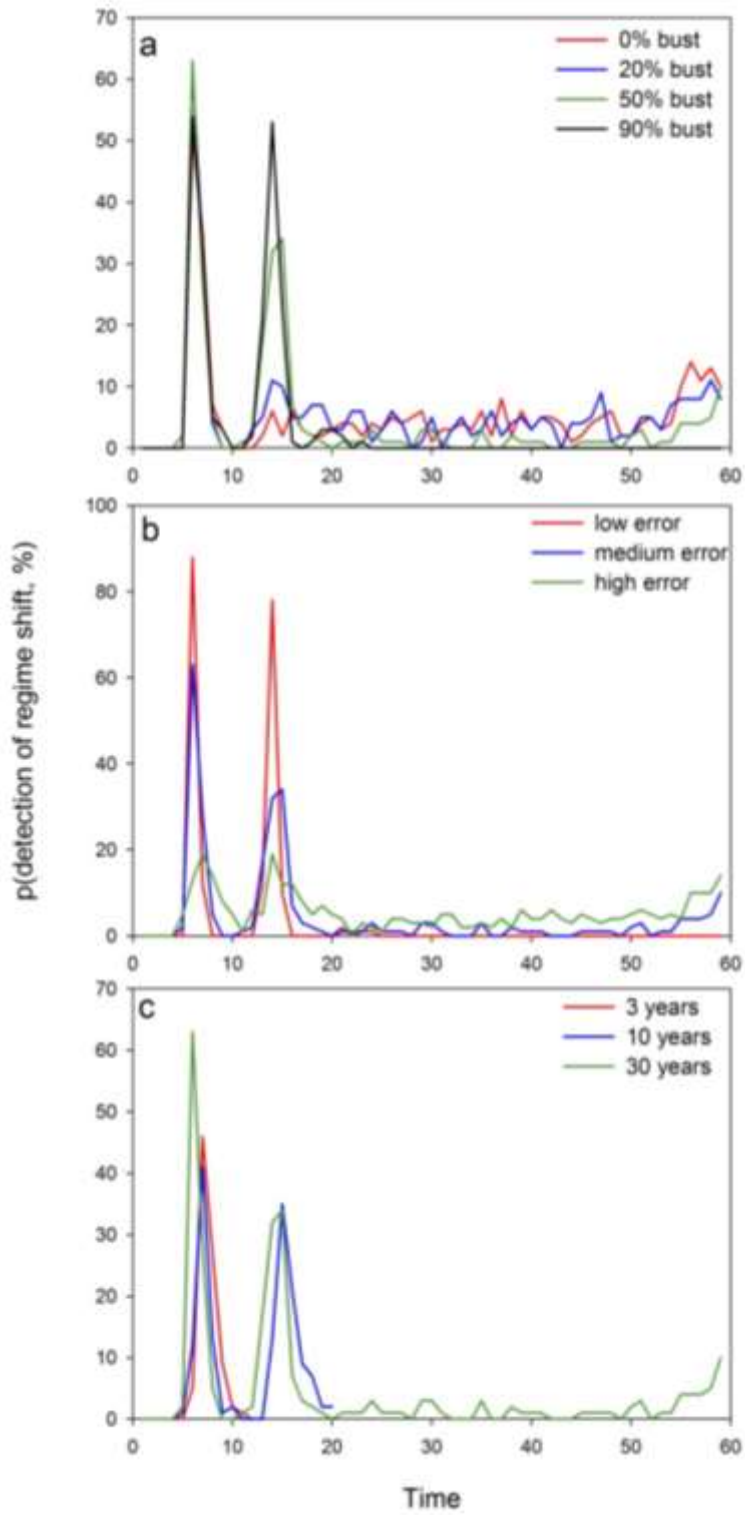
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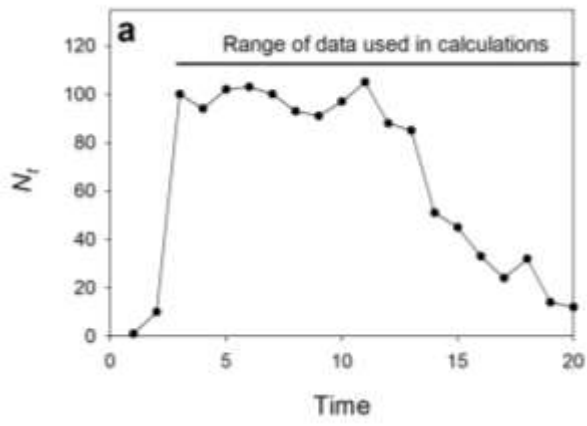
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