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Direct experimental evidence for alternative stable states: a review

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MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Direct experimental evidence for alternative stable states: a review

Arne Schröder, Lennart Persson and André M. De Roos

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A large number of studies have presented empirical arguments for the existence of alternative stable states (ASS) in a wide range of ecological systems. However, most of these studies have used non-manipulative, indirect methods, which findings remain open for alternative explanations. Here, we review the direct evidence for ASS resulting from manipulation experiments. We distinguish four conclusive experimental approaches which test for predictions made by the hysteresis effect: (1) discontinuity in the response to an environmental driving parameter, (2) lack of recovery potential after a perturbation, (3) divergence due to different initial conditions and (4) random divergence. Based on an extensive literature search we found 35 corresponding experiments. We assessed the ecological stability of the reported contrasting states using the minimum turnover of individuals in terms of life span and classified the studies according to 4 categories: (1) experimental system, (2) habitat type, (3) involved organisms and (4) theoretical framework. 13 experiments have directly demonstrated the existence of alternative stable states while 8 showed the absence of ASS in other cases. 14 experiments did not fulfil the requirements of a conclusive test, mostly because they applied a too short time scale. We found a bias towards laboratory experiments compared to field experiments in demonstrating bistability. There was no clear pattern of the distribution of ASS over categories. The absence of ASS in 38% of the tested systems indicates that ASS are just one possibility of how ecological systems can behave. The relevance of the concept of ASS for natural systems is discussed, in particular under consideration of the observed laboratory bias, perturbation frequency and variable environments. It is argued, that even for a permanently transient system, alternative attractors may still be of relevance.

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Since its introduction into ecology, the theory of alternative stable states (hereafter ASS; Lewontin 1969, Holling 1973, May 1977) has become an influential concept in ecology. It has evoked a lot of attention by

both theoreticians and empiricists and stimulated numerous research activities. In a nutshell, ASS predicts that ecological systems may exist potentially indefinitely in contrasting states under the same external

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environmental conditions. The concept of ASS and its important implications for basic and applied ecology are nowadays widely recognised among ecologists. This recognition has been facilitated by results from mathematical models (May 1977, Tilman 1982, Harrison 1986, Holt and Polis 1997, Chase 1999a, Diehl and Feißel 2000) and simulations (Dublin et al. 1990, Wilson et al. 1999, Wearing et al. 2004) demonstrating the potential of populations, communities and ecosystems to exhibit ASS under biologically relevant conditions. Moreover, a constantly mounting literature gives empirical support from a wide range of natural systems like lakes, woodlands and oceans (Scheffer et al. 2001, Resilience and SFI 2004), marine communities (Petraitis and Dudgeon 2004), ponds (Cottenie et al. 2001), forests (McCune and Allen 1985) and rivers (Dent et al. 2002) indicating that ASS can be of significance in the real world. However, those empirical findings stem predominantly from non-manipulative approaches which offer only indirect evidence that remains open for alternative explanations. Manipulation experiments offer direct evidence for the presence or absence of ASS in a system, but they are rarely conducted and sometimes even ambiguous in design and interpretations.

Our intention with this review is therefore to critically analyse the experimental evidence for ASS, to evaluate different experimental approaches with respect to practical short-comings and interpretation risks, and to evaluate the circumstances under which ASS are more likely to occur. First, we asked whether ASS have been shown to occur more frequently in laboratory than in field studies as it may be easier to find ASS under controlled and constant laboratory conditions. Second, ASS may be more likely in certain habitats. Knowlton (1992), for example, suggested that the conditions for ASS are more readily fulfilled in marine than in other habitats. Third, the likelihood for ASS may depend on organism group. Fourth, we ask if ASS occur more frequently in certain food web configurations and population interactions. Finally, we discuss the relevance of the concept of ASS to real systems with special consideration of perturbation frequency and changing environmental conditions.

The concept of ASS: definitions and implications

Formally a system exhibits ASS when its state variable responds to environmental change by a backwards folding curve (May 1977). In the following, we define an ecological system as any laboratory or natural population, community or ecosystem. The environment of a system is defined as that set of external parameters, which do influence the system but are not, in turn, affected by it. If a factor is dynamically coupled to the

system, it is not external but rather part of the system (Peterson 1984, Scheffer and Carpenter 2003). Still, if the rate of change of a coupled factor is very slow compared with the state variable, it can be regarded as constant and thus external. Also, a weakly coupled variable which is more directly controlled by other extrinsic factors than by the state variable can be used as a surrogate driving parameter. Because of the backward fold, two stable states overlap, separated by an unstable one over a given range of environmental parameters (Fig. 1). Thus, in an identical environment, the system can nonetheless be in either one of two contrasting stable states. The parameter values where stable and unstable states merge bound the region of bistability and act as thresholds for abrupt transitions between states. Reverse transitions occur at different parameter values resulting in the discontinuous response curve. This system behaviour is termed a hysteresis effect. State transitions can also occur when environmental parameters stay constant by direct perturbations of the state variable if the system is forced into the alternative basin of attraction, whose boundary is formed by the unstable state. The basin of attraction is the region of all initial values of the state variable from which any trajectory approaches the appropriate state. This implies divergence of systems depending on initial conditions. The distance between the stable and the unstable state, the resilience, measures the magnitude of perturbations from which recovery is no longer possible (Holling 1973, Carpenter et al. 2001). When a system is described by more than one state variable, the concept discussed here applies in a more general way. Especially, the unstable state becomes now a curve or manifold in phase space instead of being an

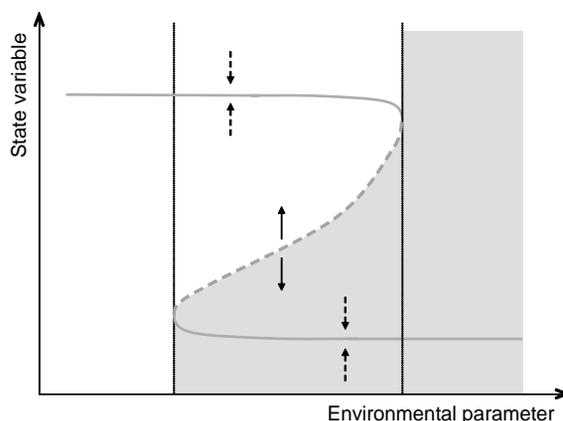


Fig. 1. The discontinuous response of a hysteresis-driven system, described by its state variable, to changes in its environment: the stable states are given by solid lines and the boundary of the basins of attraction (unstable state) by the dashed line. The region of bistability is marked by those parameter values (dotted) where unstable and stable states merge. The light-grey shaded area shows the basin of attraction of the lower stable state. Positive feedbacks are indicated by solid arrows, negative feedbacks by dashed arrows.

unstable equilibrium. Hysteresis is the resultant of the integration of positive and negative feedbacks between a state variable and its rate of change. Positive feedbacks amplify small deviations, destabilise the system globally and establish the unstable state (DeAngelis et al. 1986, Cinquin and Demongeot 2002). Negative feedbacks counteract deviations and stabilise the system locally, establishing the stable states. In ecological systems that can be considered as being driven by population processes, positive density dependence is the most common, if not exclusive positive feedback (Berryman 2002). It often comes about in the form of an Allee effect, i.e. populations are suffering from decreased or even negative population growth rates at low densities (Allee 1931, Stephens and Sutherland 1999, Stephens et al. 1999), but positive density dependence can also act at intermediate densities (Berryman 2002). Population regulation via negative density dependence constitutes the negative feedback (Turchin 1999, Berryman 2002).

Limitations of non-manipulative approaches, positive feedback demonstrations and short term experiments

Hysteresis-driven systems are predicted to show (1) abrupt state transitions over time, (2) sharp spatial boundaries between contrasting sites, (3) bimodal state variable frequency distribution or (4) dual response to driving parameters. Such behaviour can be revealed by non-manipulative empirical approaches including time series analyses, between-site comparisons and separate regression analyses, respectively (Adema et al. 2002, Scheffer and Carpenter 2003). However, while results based on these approaches may be in line with predictions and support the theory of ASS, they do not rule out alternative, often more parsimonious, explanations like an abrupt, but still continuous, response to driving parameters or cycles with a long periodicity. For example, the often cited regime shifts in the northern Pacific (Hare and Mantua 2000, Scheffer et al. 2001) are rather part of regular long-periodic dynamics when looking at longer time series (Chavez et al. 2003). A further ambiguity of non-manipulative approaches arises from their difficulty in distinguishing between system variables and environmental parameters. This can lead to misinterpretation of contrasting states as alternatively stable. Experimental demonstrations of positive feedbacks have also been used to argue for ASS (Barkai and McQuaid 1988, Hanski et al. 1995, Kuussaari et al. 1998, van de Koppel et al. 2001, Adema and Grootjans 2003, Konar and Estes 2003). However, as long as mainly interactions between subsystems are tested and integration into the whole system is ignored, it is impossible to make a statement on the overall dynamical outcome as

the net effect of all positive and negative feedbacks may still be negative. For example, the demonstration of Allee effects for only some aspects of a populations' demography is not sufficient to prove the existence of ASS, since for this it has to be evident at the total population level (Stephens et al. 1999). Also other studies used short term experiments to look for what Petraitis and Latham (1999) called the "origin" of ASS, i.e. if the necessary conditions for their occurrence are given in a particular system (Augustine et al. 1998, Boughton 1999, Petraitis and Dudgeon 1999, Sandilands et al. 2000). However, short term experiments give no information on the long term perspective of a system.

Due to the inherent difficulties of non-manipulative studies or tests for positive feedbacks and "origins" of ASS, Peterson (1984) concluded, that "... only by experiments could one convincingly demonstrate multiple stable states". Conclusive experimental approaches (Fig. 2) involve (1) the existence of different parameter thresholds for back- and forward shifts (test for discontinuity), (2) state transitions after perturbations (test for non-recovery), and (3) sensitivity of the stable end state to initial conditions (test for divergence; Scheffer and Carpenter 2003). In addition, we consider a fourth approach, even if it is not strictly spoken a manipulation experiment. Since which of the possible states in hysteresis-driven systems is realised is strongly influenced by stochastic events, random divergence or unexpected transitions to contrasting states of replicates of identically treated experimental units would also provide strong evidence for ASS (test for random divergence). This approach differs from time series observations by its control over external parameters to rule out continuous shifts and by replication of experimental units which overcomes the often anecdotal character of shifts or diverging trajectories.

Review criteria and study classification categories

We searched the reference databases Web-of-Science (years 1986–2004) and Biological Abstracts (years 1980–2004) incorporating all sources. In addition, we checked the Resilience Alliance Online Database on thresholds and alternate states (Resilience and SFI 2004). We further used citations in the extensive literature on ASS, perturbations, management strategies and restoration ecology. This review contains studies that could be assigned to any of the four experimental approaches discussed in the previous section. We included several studies, which did not explicitly state to test for ASS but nonetheless followed any of these approaches. Experiments designed to test for the origin of ASS or positive feedbacks were neglected. For each reported contrasting state, we assessed its alternative

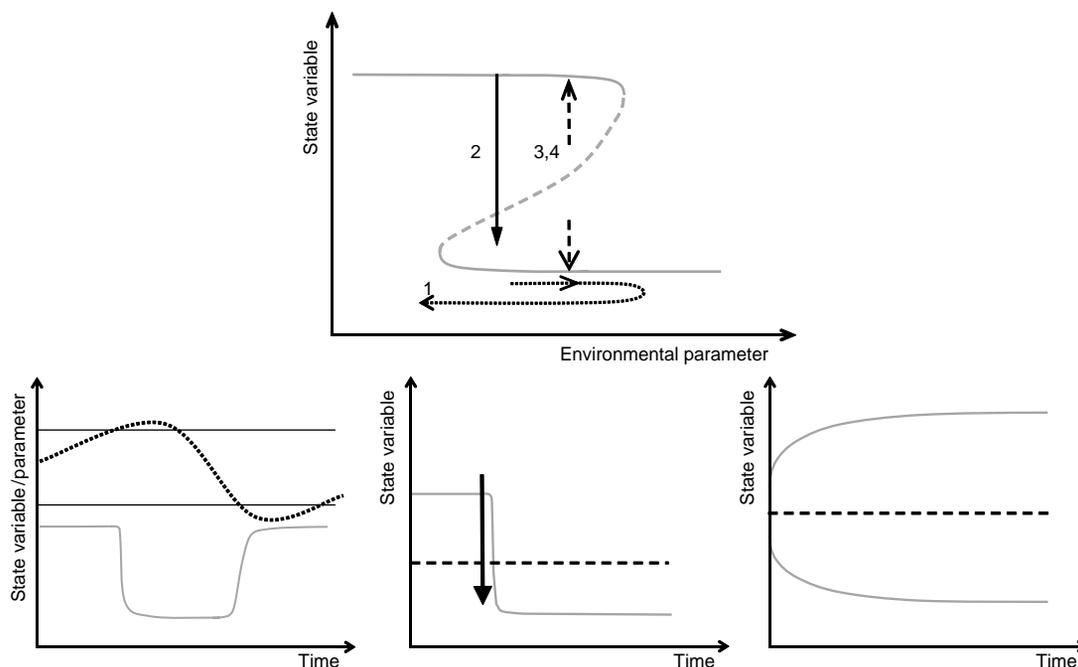


Fig. 2. The experimental approaches and their outcome. Upper panel: the four experimental approaches applicable to test for ASS. The stable states are given by solid lines and the unstable state by the dashed line. The dotted, bended arrow indicates the test for discontinuity (1); the solid arrow indicates the test for non-recovery (2), while the dashed arrows indicate the tests for divergence (3) and random divergence (4). Lower panel: the predicted outcome of the four experimental tests in the presence of ASS. Left, test for discontinuity: reverse transitions of the state variable (thick, solid, grey line) occur at different parameter thresholds (thin, solid, black lines), when the parameter (dotted line) is varied and crosses the thresholds. Middle, test for non-recovery: transitions occur, when a perturbation (arrow) forces the state variable (solid, grey line) over the basin of attraction boundary (dashed). Right, test for (random) divergence: different initial values of the state variable (solid, grey line) lead to different stable states, when situated in different basins of attraction (separated by unstable state – dashed, black line).

character and its stability. Contrasting states were alternative if they occur for identical environmental parameters (Connell and Sousa 1983). In cases where organisms modify the physical variables of their habitat, positive feedback experiments were needed in addition to clarify cause and consequence (see discussion between Peterson 1984 and Sousa and Connell 1985). Ecological stability can be concluded, if a state exhibits self-maintenance in time and space over at least one complete turnover, i.e. if it stays quantitatively and qualitatively unchanged despite that all its initially resident individuals have replaced themselves (Connell and Sousa 1983). This includes also non-fixed point dynamics like stable limit cycles or even chaotic behaviour. To obtain the minimum turnover time of a tested system, we scaled the unperturbed census time after manipulation (Grover and Lawton 1994) to the life span of the longest living species involved. A value of 1 and larger indicates a complete turnover of individuals. For random divergence studies, either each by chance arisen stable state had to last one complete turnover in a given replicate, or its capacity to do so had to be observed in a reference replicate. Only occasionally were life span estimates given by authors. For some of the organisms, data could be found in the literature. In all other cases,

we based estimates of life spans on general values for taxonomic or functional groups of species. Since life span depends on a number of external (temperature, productivity, predation pressure) and internal (mating and reproduction history, diet, genetic background) factors, the given values should be just interpreted as approximations. Data time series or statements in the text were checked for indications of ongoing change. Methodological shortcomings in the design were addressed as well as potential alternative explanations for the given results. We also looked for additional support for the presumably ASS from other empirical studies or simulation models. If contrasting alternative states lasted for one or more complete turnover, the existence of ASS was concluded. Otherwise the opposite was inferred as was done if convergence or recovery occurred before the minimum turnover time elapsed. Studies with a too short census time or inconsistencies in design were categorised as non-appropriate tests for ASS.

In addition to assigning studies to experimental approaches, we also classified them according to 4 further categories: (1) laboratory or field system where we defined field studies as those conducted under uncontrolled climate conditions including field mesocosms. (2) Habitat (marine, freshwater or terrestrial)

where “marine” is defined as below supratidal zones and “freshwater” includes bottle experiments with aqueous protists growth media. (3) Organism groups that were commonly used in experiments and regarded as ecologically relevant, where we considered the longest living species in the experiment. (4) Theoretical framework based on kind, number and form of the equations which would be used to describe the system’s food web structure, its species interactions and other ecological processes mathematically.

Considering theoretical frameworks, ASS can be found in single-species exploitation (1-dimensional consumer-resource) models (Noy-Meir 1975) where the consumer is independent of the resource in its numerical response and hence treated as an external parameter as well as in two – or more – species (≥ 2 -dimensional consumer–resource) models where interacting populations are dynamically coupled (May 1977, Harrison 1986, Knowlton 1992). In food webs with more than two populations and to even higher extend in size- or stage-structured models, a number of indirect trophic interactions create horizontal and vertical heterogeneity in food web structure (Persson 1999) with the potential for bistability. ASS can here be due to intraguild predation (Holt and Polis 1997, Diehl and Feiel 2000), apparent competition (Vayenas and Pavlou 1999), life history omnivory (Mylus et al. 2001), prey size refugia (Chase 1999a, De Roos and Persson 2002) and cannibalism (reviewed by Claessen et al. 2004). ASS were also found in models of exploitative competition systems as in the classic Lotka–Volterra case III with stronger interspecific than intraspecific competition (Begon et al. 1996) or as one potential outcome of Tilman’s (1982) mechanistic theory. With higher numbers of competitors, alternative stable communities can even occur in case of higher competition between conspecific individuals than between individuals of different species (Van Nes and Scheffer 2004).

Finally, ASS can be found in the theoretical framework of community assembly (defined here as the establishment of local communities from a regional species pool by consecutive invasions and extinctions) integrating over all trophic interactions and food web structures (Law and Morton 1993). Initial differences in presence/absence of species due to different invasion sequences or rates determine the future assembly path of the community by creating transient communities which are invadable by only some of the species remaining in the regional pool. Different assembly pathways can then lead to alternative stable communities in terms of species composition and relative densities (Drake 1990, Law and Morton 1993, Samuels and Drake 1997, but see Morton et al. 1996). Stability requires here that such a community is simultaneously persistent and resists all further invasions by non-residents (criterion of permanence). Persistent but invadable (non-permanent) communities

are dispersal-limited and thus not stable. Law and Morton (1993) found theoretically that systems with larger regional species pools or higher complexity have more alternative stable local communities probably because priority effects are then more likely. We consider community assembly as the relevant theoretical framework behind an experiment if invasion rate and/or sequence were manipulated. In contrast, initialisation of an experiment with all presumably resident species already present at different density ratios or manipulating density ratio by perturbations rather test for the potential of a certain food web structure and interaction process to create ASS. No general theoretical framework exists for whole ecosystems due to their inherent complexity. Instead specific models as for shallow lakes (Scheffer et al. 1993, Carpenter 2003) or savannah grass lands (van de Koppel et al. 1997) have been presented.

Studies according to system, habitat, organism and theoretical framework

We reviewed 35 experiments. 14 studies were not appropriate tests for ASS since they were performed on too short temporal scales or showed other major inconsistencies in design or interpretation. Of the remaining 21 experiments, 13 (62%) found evidence for ASS while 8 (38%) demonstrated the absence of ASS.

Seven of the positive studies were non-ambiguous, while six others showed only minor inconsistencies in methods or results. We still consider them as positive because of additional support from other studies of the particular system and their usually long time scales with several turnovers. Eight of the positive experiments showed alternative stable equilibria while for the remaining five at least one stable state was cyclic (for further results and details of the review process, Appendix 1).

ASS were more frequently found in laboratory than in field systems despite that both were studied rather equally frequently. Ten out of 12 conclusive laboratory experiments demonstrated bistability, while this was only true for three out of nine field experiments (Table 1). While ASS could be demonstrated in both freshwater and terrestrial habitats, none were found in marine habitats which actually all were benthic communities dominated by sessile organisms. With the exception of higher plants and macrophytes, studies using organisms with long life spans and slow reproduction (mussels and other sessile animals, fish) did not find ASS, while studies with small, short-living and fast reproducing organisms (unicellular or metazoan plankton, insects) did so (Table 1). This can be due to a sampling bias as most studies used organisms from the latter group and/or to the fact that the former group was predominantly used in field studies (below). ASS were found for all theoretical frameworks except for whole ecosystems.

Table 1. The distribution of 35 experimental tests for ASS and their results over the four categories system, habitat, organism group and theoretical framework (bold numbers). Positive =ASS present, negative =ASS absent, not appropriate =less than 1 whole turnover of the system or other inconsistencies. Numbers in square brackets give the study identities according to Appendix 1.

		Positive	Negative	Not appropriate	Total
System	laboratory	10 [1, 11, 20, 21, 22, 24, 27, 31, 34, 35]	2 [26, 33]	4 [25, 28, 29, 30]	16
	field ^a	3 [14, 17, 32]	6 [3, 6, 10, 12, 16, 18]	10 [2, 4, 5, 7, 8, 9, 13, 15, 19, 23]	19
Habitat	marine ^b	–	3 [3, 6, 18]	3 [4, 5, 13]	6
	freshwater ^c	8 [1, 11, 20, 21, 27, 32, 34, 35]	4 [10, 16, 26, 33]	7 [2, 9, 19, 25, 28, 29, 30]	19
Organism group	terrestrial	5 [14, 17, 22, 24, 31]	1 [12]	4 [7, 8, 15, 23]	10
	plants+macrophytes	3 [14, 17, 34]	3 [6, 12, 16]	3 [2, 8, 15]	9
	unicellular organisms ^d	4 [1, 11, 27, 35]	1 [33]	2 [25, 30]	7
	zooplankton	2 [20, 21]	1 [26]	3 [19, 28, 29]	6
	insects	4 [22, 24, 31, 32]	–	1 [23]	5
	sessile animals	–	2 [3, 18]	3 [4, 5, 13]	5
	vertebrates	–	1 [10]	2 [7, 9]	3
Theoretical framework	1-dim.	1 [14]	1 [12]	1 [8]	3
	competition	2 [24, 34]	3 [6, 16, 26]	3 [2, 13, 15]	8
	≥ 2-dim. ^{e,f}	7 [1, 11, 17, 20, 21, 22, 32]	1 [3]	3 [4, 5, 7]	11
	community assembly	3 [27, 31, 35]	2 [18, 33]	6 [19, 23, 25, 28, 29, 30]	11
	whole ecosystem	–	1 [10]	1 [9]	2

a) including mesocosms [2, 16, 32].

b) all marine systems are either benthic or intertidal communities dominated by sessile animals or macrophytes.

c) including bottle experiments with aqueous media [1, 11, 25, 27, 29, 30, 33, 34].

d) one with unicellular algae [27], the rest with heterotrophic protists.

e) seven cases with size-structure [3, 4, 5, 20, 21, 22, 32].

f) three cases with chemostat conditions [1, 11, 22].

Studies performed on this latter scale were exclusively shallow lake manipulations. Overall, the experiments clearly provided direct evidence that ecological systems can exist in ASS. However, there is the same clear evidence for their absence in other cases which leads us to the not surprising conclusion that bistability is a possible scenario but still only one among others. Gradual and single-threshold responses (Scheffer et al. 2001) should not be neglected. Since no clear distribution pattern over categories was observed, no a priori decision rules or probability estimations for the occurrence of ASS could be deduced. For a given system, ASS will always have to be confirmed by experiments.

There are several different explanations for the apparent bias towards laboratory studies in demonstrating ASS. First, differences in time scales between field and laboratory systems may have led to this bias. However, as the frequency of conclusive studies is similar for both systems (12:9, Table 1), we consider this explanation as less likely. Second, systems dominated by small, short-living, and fast-reproducing organisms that were almost exclusively used in the laboratory experiments may more likely exhibit ASS compared to systems with long-living, slow reproducing organisms. This explanation does, however, not explain the occurrence of ASS in higher plant or macrophyte communities and is in opposition to findings which indicate the

presence of ASS in forests (McCune and Allen 1985), coral reefs (Hughes 1994) and savannahs (Dublin et al. 1990). Third, there may be a laboratory artefact. Laboratory systems are often artificial assemblages of populations which do not have to behave as natural systems. Further, the preclusion of potentially confounding factors as stochasticity and environmental variance which may prevent the establishment of ASS in natural systems may make it easier to detect ASS in the laboratory. However, lack of experimental support can as well be due to methodological difficulties (below) which may be more influential in the field. The predominant usage of long-living animals in field studies respectively short-living species in laboratory studies is consistent with both the second and the third view but we see no reasons, why the biology of long-living organisms per se should prevent ASS.

ASS are still often perceived as contrasting equilibrium values where a system exhibits fix-point stability in each of its states (Beisner et al. 2003). However, given that intrinsically fluctuating populations are common in field and laboratory systems (Murdoch et al. 2002), and that structurally different alternative attractors can be found in models (De Roos and Persson 2003, Wearing et al. 2004), it is not surprising that ASS can also contrast in the type of their intrinsic dynamics. ASS were, for example, demonstrated as cycles contrasting in amplitude or periodicity (McCauley et al. 1999, Henson

et al. 2002) or as cycles opposed to an equilibrium dynamic (Zamamiri et al. 2001). The potential for non-fix point dynamics is important in studies of ASS as non-fix-point systems may be more sensitive to transitions due to perturbations or environmental changes when their fluctuating trajectories come close to the boundary of the basins of attraction.

Studies according to experimental approaches

(1) In the test for discontinuity the relevant parameter is systematically varied in both directions, either stepwise or uniformly. To avoid that transients are mistaken as stable, enough time has to be given to the system to adjust to the new condition before the next step is performed, respectively, the rate of change of the parameter has to be much lower than that of the state variable. Variation is performed until backward and forward state transitions have been observed at different parameter values. To obtain a complete hysteresis pattern, thresholds must not only be reached but actually crossed to observe a discontinuous shift as the rate of change directly at these bifurcation points is zero (Wissel 1984). However, if reverse crossing of only one threshold does not result in a concomitant backward transition, discontinuity can be safely concluded. Variation of the parameter in separate experimental units can not reveal discontinuity. Due to the time-intensive procedure, the test for discontinuity was conclusively performed only once and then with baker's yeast (Table 2, Zamamiri et al. 2001).

(2) For tests for non-recovery it should be noted that the concept of resilience requires an at least noticeable effect of the perturbation applied (see discussion between Connell and Sousa 1983 and Sutherland 1990). Fifteen such tests were found, of which three demonstrated ASS, five their absence and seven were inappropriate tests (Table 2). The precise perturbation depends strongly on the theoretical framework.

In 1-dimensional exploitation systems, over-consumption by too high consumer density can be considered as a perturbation. Then it is of interest whether the system remains in the state induced by the over-consumption or returns to the original state when the consumer is

excluded. Appropriate experiments were exclusively carried out in terrestrial grazing systems with externally controlled herbivores, where ASS were due to a saturated functional response of herbivores or to vegetation exerting a positive feedback on its growth (Noy-Meir 1975) via soil quality, water content or erosion rate (Wilson and Agnew 1992, Srivastava and Jefferies 1996, van de Koppel et al. 1997, Rietkert and van de Koppel 1997). Such positive density dependence is probably the cause behind the bistability of arctic salt marshes subjected to heavy grazing by geese (Srivastava and Jefferies 1996, Handa et al. 2002).

In 2- or more-dimensional exploitation systems, the density ratio of consumer and resource can be varied by perturbations. The perturbation most commonly applied was consumer removal (Paine 1976, Paine et al. 1985, Schmitz 2004). We are not aware of any manipulations of prey density or consumer addition. When consumer return does not lead to the recovery of the previous state, the presence of ASS can be concluded. In cases of size-dependent interactions, size structure of a system may be an important feature of the state, as in Paine's experiments (Paine 1976, Paine et al. 1985). After consumer removal, the consumer-induced recruitment bottleneck for larger prey size classes broke down as reflected in the bimodal size distribution. Since larger size classes will not be replaced after the consumer returned, such population structure is transient. A community without consumers should not be regarded as stable as long as no intrinsic barrier against its (re-) invasion in form of an Allee effect is demonstrated (Connell and Sousa 1983). Depending on the precise mechanisms working in a system, other manipulations can be used as perturbations (McCauley et al. 1999, Zamamiri et al. 2001).

In competition systems, recovery potential can be tested for by manipulating competitors' density ratios (Wright and Chambers 2002, Morris et al. 2003a), or, alternatively, by clearing the experimental unit of all competing populations (Kennelly 1987, Bertness et al. 2002). For the latter approach, the spatial scale of the perturbation should be varied, since recovery or its failure can depend on the size of the clearing (Petraitis and Latham 1999, see also Petraitis and Dudgeon 2004 for detailed suggestions on appropriate experimental designs).

Table 2. The distribution of experimental tests for ASS over the four experimental approaches and their results (bold numbers). Positive = ASS present, negative = ASS absent, not appropriate = less than 1 whole turnover of the system or other inconsistencies. Numbers in square brackets give the study identities according to appendix.

		Positive	Negative	Not appropriate	Total
Experimental approach	discontinuity	1 [1]	–	1 [2]	2
	non-recovery	3 [11, 14, 17]	5 [3, 6, 10, 12, 16]	7 [4, 5, 7, 8, 9, 13, 15]	15
	divergence	6 [24, 27, 31, 32, 34, 35]	2 [26, 33]	5 [23, 25, 28, 29, 30]	13
	random divergence	3 [20, 21, 22]	1 [18]	1 [19]	5

(3) The test for divergence was used in 13 experiments, six of them found evidence for the presence of ASS, two for their absence, whereas five experiments were not appropriate in design (Table 2). The precise manipulation depends again on the theoretical framework. If one is interested in the question whether an ecological interaction process leads to ASS, experimental units are to set up with all interacting populations initially present in different density ratios. Chase (2003a) demonstrated that predation and prey-size refugia were responsible for density-ratio dependent divergence, while Scheffer et al. (2003) did this for competitive exclusion among floating and submerged macrophytes.

For community assembly, the initial differences supposed to lead to ASS are usually created by different sequences or rates of subsequential invasions. Note that each species has to have the chance to invade at least once. However, since the succession stage can be of crucial importance for a successful colonisation and the consequential state transition (Lawler 1993), an assembly graph mapping as performed by Warren et al. (2003) may be more appropriate. Here, each independently arising, presumably stable sub-community is tested by each non-resident species. This design creates huge logistic problems with increasing species number, but allows the assessment of a state's permanence and reduces the risk of interpreting invadable sub-communities as alternatively stable. The conclusive community assembly experiments did not support the hypothesis of larger regional pools making ASS more likely. Warren et al. (2003), for example, used seven species and found no ASS, while Drake (1991) and Sait et al. (2000) found some with only three species each.

(4) Experiments on treatment-independent random divergence have a low explanatory power with respect to the underlying mechanisms that make interpretations more difficult. For example, Jenkins and Buikema's (1998) contrasting communities can not be regarded as permanent, since reciprocal invasions were not controllable. Additional experiments on the mechanisms can be helpful here (McCauley et al. 1999). Further, a too high process variance due to stochasticity may lead to too frequent transitions or high degree of divergence. Consequentially, basins of attraction can not be distinguished from each other (Carpenter 2003) and the system will be in a permanently transient state. Laboratory experiments with a thorough statistical–mathematical analysis may be more conclusive here as, for example, done by Henson et al. (2002) for the *Tribolium* system. We found five studies that applied this approach, of which three demonstrated the presence of ASS, one their absence and one was a non-appropriate test (Table 2). The positive ones were actually all laboratory studies (McCauley et al. 1999, Nelson et al. 2001, Henson et al. 2002).

General methodological problems in demonstrating ASS

Perturbation experiments as well as tests for divergence will only reveal ASS if they are conducted in the parameter range of bistability. In mathematical models, ASS are often prevalent at intermediate levels of environmental driving parameters such as productivity (Chase 1999a,b, Diehl and Feißel 2000) or external mortality (De Roos and Persson 2002). Correspondingly, Chase (2003a) only found predator–prey density ratio-dependent divergence at intermediate productivity and Bertness et al. (2002) proposed by verbal arguing that contrasting rocky intertidal communities may present ASS only at intermediate wave action.

Divergence of replicates to fluctuating trajectories could also be due to chaotic behaviour of the system, but those trajectories would rather be idiosyncratic than exhibiting a consistent pattern between treatments as was the case for all replicated divergence experiments resulting in alternative non-fix-point dynamics (McCauley et al. 1999, Sait et al. 2000). Another way to rule out chaos is by checking parameterised mathematical models of the system (Sait et al. 2000, Henson et al. 2002). We therefore believe that rather alternative attractors than chaos explains the observed dynamical differences in the mentioned studies.

Perturbations may not be strong enough to initiate state transitions. This explanation is unlikely to be relevant to the experiments considered above, because applied perturbations were usually absolute in consumer or competitor removal, exclusion or space clearing. Different experimental initial conditions may also still occur in the same basin of attraction, so that ASS can not be detected. In systems with more complex food web structure and interaction patterns, the basin of attraction may be complex as well and quite distinct initial conditions may still lead to convergence. However, among the studies considered above, more complex systems in terms of theoretical framework did not have more negative findings than less complex ones, suggesting that system complexity did not play an important role.

The relevance of ASS: permanent transients and temporal heterogeneity

A more quantitative question deals with the relevance of ASS and the frequency of their occurrence in the real world. The observed laboratory bias may lead to some concern about this. If the bias is just a systematic error because of larger difficulties in detecting ASS in field experiments, the real world application of the theory is still possible. If, however, the bias arises from environmental variability, the concept would be somehow

limited in its generality. An essential factor for the occurrence of ASS is the time a system is given before the next perturbation or change in environmental parameters, a discussion closely related to debates on equilibrium vs non-equilibrium theory (Chesson and Case 1986, DeAngelis and Waterhouse 1987). Systems with high perturbation frequencies or quickly changing driving parameters (i.e. the ratio to the turnover time under unperturbed conditions is less than one) will never reach their presumable stable end states regardless of how many there might be. Robinson and Edgemon (1988) proposed that ASS may be more common under low invasion rates, while open, dispersal-driven communities will rather exhibit permanent transient dynamics. In benthic, sessile communities, spatial and temporal heterogeneity in natural disturbance patterns may explain local community states that differ in which competitor is present, while the endpoint in absence of disturbances would be competitive exclusion at the regional scale (Kennelly 1987). Under highly variable environmental conditions, those transient states can be more relevant than the asymptotic behaviour of the system in understanding its dynamical pattern. This was demonstrated by the studies on ASS with a “too short” time scale, where past perturbation events or initial differences led to alternative communities, which are nonetheless rather snapshots in time and represent transient dynamics instead of stable end states. To understand a recent, transient state, history and stochasticity has to be taken into account as is necessary for bistable systems (Drake et al. 1994, Hastings 2004), but their implications for the system are totally different. As neither discontinuous threshold responses to environmental change, risks for unfavourable state transitions or divergent development trajectories occur historical and stochastic effects are reversible and will influence the system only for the limited time period of the transient, even if this time period can be long in absolute time.

However, even if a system is permanently transient, ASS may still be important in shaping it. Depending on in which basin of attraction the system is situated, the direction of ongoing changes may be opposed, or, if the alternative attractors are structurally different, the dynamics of the transients may differ. Further, the existence of alternative attractors definitely leads to hysteresis, but not necessarily to a truly bistable system. If a fast variable is internally coupled to a slow variable and responds discontinuously to it, relaxation oscillations or slow-fast cycles may occur under some conditions (May 1977, Rinaldi and Scheffer 2000). Such behaviour can e.g. describe dynamics like the regular spruce-budworm outbreak in boreal forests (Ludwig et al. 1978) or may be behind the oscillatory behaviour of the North Pacific reported by Chavez et al. (2003). Temporal heterogeneity may also be essential in systems where the fast variable shows no hysteresis to the slow

variable but to other parameters. While transient in terms of its structural dominating long-living species as for example grasslands (Valone et al. 2002), subcommunities with much shorter turnover times may exist at one of their alternative quasi-stable states, but only as long as the slow transient lasts.

Concluding remarks

While it is evident that ecological systems may exhibit alternative stable states ASS should not be taken as a rule. Rather, each particular system has to be experimentally analysed again for its potential for bistability and the burden of proof is carried by each scientist investigating a given system. However, the results from indirect approaches may be seen in a new light, especially since for natural systems with their usually large scales often only non-manipulative or short-term studies are applicable. There is no reason to assume, that such systems should be less susceptible to ASS than others. In highly variable environments, transient dynamics may be more important, however, also in permanently transient systems bistability may still be a factor worth considering. In a world experiencing dramatic anthropogenic caused changes in environmental conditions and severe perturbations, the presence of alternative stable states may have serious, unexpected consequences. Further research should therefore focus on the conditions for, the relevance of, and the specific mechanisms behind alternative stable states in ecological systems.

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Table 1A. The list of reviewed experimental studies testing for ASS. ++ = ASS present; + = ASS present, with smaller inconsistencies/alternative explanations (see column “notes”) but further support; – = ASS absent; – – = study is considered inappropriate for testing for ASS; n.c. = turn-over not computable

#	System [theoretical framework]	Experimental approach/ treatment	Organism group	Potential ASS	Interpretation	Spatial scale	Census time ^a	Life span	Turn-over ^e	Notes (inconsistencies/ alternatives)	Further support	Result ^f	Reference
1	single species lab culture ^b [2-dim.]	discontinuity/ chemostat dilution rate variation	<i>Saccharomyces cerevisiae</i>	equilibrium vs cyclic dynamic	discontinuous shift between contrasting dynamics	11	50 h	10 h (turnover of chemostat)	5	upper threshold not crossed, but no backward transition at value for forward transition	test for non-recovery (same ref., see exp. 10)	+	Zamamiri et al. 2001
2	shallow lake mesocosms [competition]	discontinuity/ variation of nutrient level	<i>Vallisneria americana</i> , <i>Azolla pinnata</i> , phytoplankton	<i>V. americana</i> vs <i>A. pinnata</i> / phytoplankton dominated community	state transition at increased nutrient levels	ca 3000 l	4 months	>3 months for <i>V. americana</i> (Blanch et al. 1998)	≤1	nutrient level was varied in separate mesocosms, no detection of discontinuity possible		– –	Morris et al. 2003b
3	natural rocky intertidal community ^c [2-dim., size-structured]	non-recovery/ consumer (starfish) removal	starfish (<i>Heliaster helianthus</i>), mussels (<i>Perumytilus</i>) and barnacles	high vs low mussel/ barnacle ground cover	recovery of original state	63 m ²	3 ² / ₃ years	2 decades ^d	<1			–	Paine et al. 1985
4	natural rocky intertidal community ^c [2-dim., size-structured]	non-recovery/ consumer (starfish) and macroalgae removal	starfish (<i>Stichaster australis</i>), macroalgae (<i>Durvillaea antarctica</i>) and mussel (<i>Perna canaliculus</i>)	mussel vs macroalgae domination	no recovery of original state	25 m ²	13 years	2 decades ^d	<1	ongoing lateral encroaching of <i>D. antarctica</i> on mussel bed		– –	Paine et al. 1985
5	natural rocky intertidal community ^c [2-dim., size-structured]	non-recovery/ consumer (starfish) removal	starfish (Piaster ochraceus) and mussel (Mytilius californianus)	high vs low mussel ground cover	no recovery of original state	20.3 m ²	15 years	at least 7–20 years for <i>M. californianus</i> (Suchanek 1981)	≈1	mussel population is over-aged and lateral shrinking		– –	Paine 1976/Paine et al. 1985
6	natural sub-littoral community ^c [competition]	non-recovery/ clearing of turf algae and kelp	dictyolenian turf algae assemblages and kelp (<i>Ecklonia radiata</i>)	turf algae vs kelp domination	recovery of both original states	2 m ²	6 months	years to decades ^d	<1	non-equilibrium competition system		–	Kennelly 1987
7	natural semi-arid grass land [2-dim.]	non-recovery/ exclusion of predators	red fox, feral cats and rabbit	low vs high rabbit densities	non-recovery of low-rabbit-densities	70–90 km ²	5 month	rabbits: 31.7 month (von Holst et al. 1999)	<1			– –	Pech et al. 1992

#	System [theoretical framework]	Experimental approach/ treatment	Organism group	Potential ASS	Interpretation	Spatial scale	Census time ^a	Life span	Turn-over ^e	Notes (inconsistencies/ alternatives)	Further support	Result ^f	Reference
8	natural grass land community [1-dim.]	non-recovery/ exclusion of grazers (sheep)	<i>Festuca</i> , short grasses, dwarf shrubs	dense, <i>Festuca</i> dominated grass land vs dwarf shrub dominated vegetation	no recovery of <i>Festuca</i> grass land	1.5 ha	9 years	several decades ^d (Valone et al. 2002)	<1			--	Gabriel et al. 1998
9	shallow lake [whole ecosystem]	non-recovery/ fish mass removal	planktivorous fish (<i>Rutilus rutilus</i> , <i>Osmerus eperlanus</i>)	occurrence vs non-occurrence of cyanobacteria blooms	no recovery of original state	whole lake (110 km ²)	3 years	10 years	0.33			--	Horpilla et al. 1998
10	small shallow lakes [whole ecosystem]	non-recovery/ fish mass removal	whole aquatic food-web (planktivorous fish to phytoplankton)	macrophytes-dominated clear water vs phytoplankton-dominated turbid water state	dependent on lake: total or partial recovery of turbid state	whole lakes	4–8 years	several years ^d	≤1	even the most stable lake switched finally back to turbid conditions (van Donk and Gulati 1995)		–	Meijer et al. 1999
11	single species lab culture [2-dim.] ^b	non-recovery/ addition of non-synchronous cells	<i>Saccharomyces cerevisiae</i>	equilibrium vs cyclic dynamic	no recovery of original state	11	80 h	6.67 h (turnover of chemostat)	12		test for discontinuity (same ref., see exp. 1)	++	Zamamiri et al. 2001
12	natural grass land community [1-dim.]	non-recovery/ exclusion of grazers (cattle) for 20 and 39 years	woody shrubs, perennial grasses	grass vs shrub land	recovery to grass land after 39, but not after 20 years	9.3 ha resp. 20 ha	39 resp. 20 years	ca 4 decades (a posteriori)	1 resp. 0.5			–	Valone et al. 2002
13	natural rocky intertidal community ^c [competition]	non-recovery/ clearings of mussel and kelp beds	mussel, barnacles and kelp (<i>Ascophyllum nodosum</i>)	mussel vs kelp domination	no recovery of each original state	1 m ² resp. 9 m ²	2.5 years	2 decades ^d	<1	contrasting states explained by environmental differences in water movement		--	Bertness et al. 2002
14	natural supratidal arctic salt marsh community [1-dim.]	non-recovery/ exclusion of grazers (geese)	graminoid grasses, dicotyledonous herbs and forbs	non-vegetated vs vegetated state	no recovery of vegetation	25 m ²	13 years	several years ^d	>1		positive feedback (Srivastava and Jefferies 1996), simulation model (Walker et al. 2003)	++	Handa et al. 2002
15	natural riparian vegetation [competition]	non-recovery/ burning of <i>Artemisia</i> and seeding grasses/ forbes	sagebrush (<i>Artemisia</i>), perennial and annual grasses and forbes	<i>Artemisia</i> -domination vs grass/forbes meadows	no recovery of <i>Artemisia</i> state	740–900 m ²	3 years	several years/ decades	<1			--	Wright and Chambers 2002

Appendix (Continued)

#	System [theoretical framework]	Experimental approach/treatment	Organism group	Potential ASS	Interpretation	Spatial scale	Census time ^a	Life span	Turn-over ^e	Notes (inconsistencies/alternatives)	Further support	Result ^f	Reference
16	shallow lake mesocosms [competition]	non-recovery/removal of <i>V. americana</i>	<i>Vallisneria americana</i> , <i>Azolla pinnata</i> , phytoplankton	<i>V. americana</i> vs <i>A. pinnata</i> /phytoplankton dominated community	recovery of <i>V. americana</i> state	ca 3000 l	4 months	>3 months for <i>V. americana</i> (Blanch et al. 1998)	≤1			–	Morris et al. 2003a
17	natural old-field community [3-level-food web predator-mediated competition]	non-recovery/exclusion of top predator	spider (<i>Pisaurina mira</i>), grasshopper (<i>Melanoplus femurrubrum</i>), grass (<i>Poa pratensis</i>) and herb (<i>Solidago rugosa</i>)	competitive dominance of <i>S. rugosa</i> vs high-diversity community	non-recovery of high-diversity community after a predator exclusion of ≥2 years	4 m ²	2–4 years	arthropods: univoltine plants: biennial and perennial	≈1	recovery after a perturbation of 1 year	dual response of diversity to driving parameter (same ref.)	++	Schmitz 2004
18	natural marine fouling community ^c [community assembly]	random divergence/colonisation of empty submerged plates	hydroids, tunicates, bryozoans, sponges, barnacles	contrasting communities in species composition and relative densities	random divergence to contrasting communities	0.23 m ²	8 years of observation	days to years ^d , depending on organism group	>1	the contrasting communities did not persist over one turnover		–	Sutherland 1974/1981
19	natural freshwater zooplankton community [community assembly]	random divergence/colonisation of newly constructed ponds	zooplankton species of several taxa (copepods, cladocerans, rotifers, <i>Chaoborus</i>)	contrasting communities in species composition and relative densities	random divergence to contrasting communities on the scale of species and populations	840 m ³	1 year of observation after filling	days to months ^d , depending on organism (ca 1 year for <i>Chaoborus</i>)	≈1	invadability of each pond community is not tested, high process variance		– –	Jenkins and Buikema 1998
20	2-species lab culture [2-dim., stage-structured]	random divergence/ randomly arising differences	<i>Daphnia pulex</i> and unicellular algae	single-generation vs predator–prey cycles	random divergence to contrasting dynamics 20 l		ca 90 days	<i>D. pulex</i> : mean 38 days, max 54 days (Dudycha and Tessier 1999)	>1		perturbation by replacing sexual reproducing females by asexual reproducing ones (same ref.)	++	McCauley et al. 1999
21	2-species lab culture [2-dim., stage-structured]	random divergence/ randomly arising differences	<i>Daphnia pulex</i> and unicellular algae	low grazer/high algae vs high grazer/low algae density ratio	random divergence to contrasting consumer-resource density ratios	80 l	120 respectively 100 days	<i>D. pulex</i> : mean 38 days, max 54 days (Dudycha and Tessier 1999)	≈2			++	Nelson et al. 2001
22	single-species lab culture ^b [2-dim., stage-structured]	random divergence/ randomly arising differences	<i>Trilobium castaneum</i>	in their periodicity contrasting cycles	random divergence to contrasting dynamics	237 ml	12–20 weeks	ca 10 weeks for larvae (Kostyukovsky et al. 2000)	≈1		simulation model (Henson et al. 2002)	++	Jillson 1980, cited by Henson et al. 2002

Appendix (Continued)

#	System [theoretical framework]	Experimental approach/treatment	Organism group	Potential ASS	Interpretation	Spatial scale	Census time ^a	Life span	Turn-over ^e	Notes (inconsistencies/alternatives)	Further support	Result ^f	Reference
23	natural mangrove ant community [community assembly]	divergence/alternating invasion sequence of both species	<i>Crematogaster ashmeadii</i> and <i>Xenomyrmex floridanus</i>	exclusive presence of only one species	divergence to states with exclusive presence of only one species	whole mangrove islands (5.09 m ³) 27 weeks	7 years for queens of <i>C. ashmeadii</i> (Tschinkel 2002)		<1			- -	Cole 1983
24	multi-species lab culture [competition]	divergence/initialisation with different relative densities	10 different <i>Drosophila</i> species	contrasting communities in species composition and relative densities	divergence to two contrasting communities	355 ml	35 days	<i>D. melanogaster</i> in average 37 days (Izmaylov and Obukhova 2003)	≈1	35 days is the very minimum life span for <i>D. melanogaster</i> , other species may live longer	competition experiment (same ref.)	+	Gilpin et al. 1986
25	multi-species lab culture [community assembly]	divergence/invasion sequence and rate	ciliates, 1 rotifer, unicellular algae	contrasting communities in species composition and relative densities	divergence to two contrasting communities	300 ml	no time after manipulation	several days ^d (for some rotifers Kirk 2001)	n.c.	introductions occurred over whole run time of the experiment		- -	Robinson and Dickerson 1987
26	multi-species lab culture [competition]	divergence/initialisation of microcosms with different relative densities	natural zooplankton and phytoplankton inoculate	contrasting communities in species composition and relative densities	convergence to one community	8 or 12 l	ca 60 days (until convergence of phytoplankton was achieved)	several weeks for crustaceans and copepods ^d days for rotifers ^d	≈1			-	Sommer 1991
27	3-species lab culture [community assembly]	divergence/invasion sequence	<i>Scenedesmus</i> , <i>Selenestrum</i> , <i>Ankistrodesmus</i>	contrasting communities in species composition and relative densities	divergence into contrasting communities	250 ml	50 days	several days ^d	»1	the time series show still some trend of ongoing change		+	Drake 1991
28	multi-species lab culture [community assembly]	divergence/invasion sequence	unicellular algae and zooplankton species	contrasting communities in species composition and relative densities	divergence to contrasting communities	40 l	15 days	<i>Daphnia magna</i> : >40 days (Martínez-Jerónimo et al. 1994) <0.3				--	Drake 1991
29	multi-species lab culture [community assembly]	divergence/accidentally differing invasion sequence	unicellular algae and zooplankton species	contrasting communities in species composition and relative densities	divergence to contrasting communities	1 l	20 days	<i>Daphnia magna</i> : >40 days (Martínez-Jerónimo et al. 1994)	<0.5			--	Drake et al. 1993
30	multi-species lab culture [community assembly]	divergence/invasion sequence	bacteria, bacterivorous and predacious protozoan	contrasting communities in species composition and relative densities	divergence to contrasting communities	240 ml	36 days	several days ^d	>1	alternative community is invadable by <i>Actinosphaerium</i> at a later succession stage and thus not stable		- -	Lawler 1993

Appendix (Continued)

#	System [theoretical framework]	Experimental approach/ treatment	Organism group	Potential ASS	Interpretation	Spatial scale	Census time ^a	Life span	Turn- over ^e	Notes (inconsistencies/ alternatives)	Further support	Result ^f	Reference
31	3-species lab-culture [community assembly]	divergence/ invasion sequence	lepidopteran moth, parasitoid wasp, moth virus	communities contrasting in structure and/or dynamics	no divergence due to invasion sequence but random divergence to multi – generation cycles vs irregular fluctuations under one treatment	4.4 l	80 weeks	moth: ca 50 days (Marzban et al. 2001), wasp: ca 40 days, Ozkan and Gurkan 2002)	8	irregular fluctuations may be just a long transient, caused by the alternative invasion sequence (simulation model, same ref.)		+	Sait et al. 2000
32	pond mesocosm community [3-link-food chain with prey size refugia]	divergence/ initial density ratios of snails and insects and productivity level	herbivore snails (<i>Physella grina</i> , <i>Heliosoma trivolis</i>), insect predator (<i>Belostoma flumineum</i>), macrophytes	high snail biomass with large individuals vs low snail biomass with small individuals	divergence to contrasting community states	380 l	175 days	insect: 110-158 days (Gilg and Kruse 2003) snail (<i>Physella</i>): 163 days ^d (Crowl 1990)	>1		bimodal state frequency distribution (Chase 2003b)	++	Chase 2003a
33	multi-species lab culture [community assembly]	divergence/ invasion sequence	6 protozoans (ciliates and 1 amoebae) and bacteria	contrasting communities in species composition and relative densities	convergence to an intransitive cycle between two invadable sub-sets	70 ml	84 days	several days ^d	»1			–	Warren et al. 2003
34	2-species lab culture [competition]	divergence/ initial density ratios of competitors	submerged (<i>Elodea nuttalli</i>) and floating (<i>Lemna gibba</i>) macrophytes	submerged vs floating macrophyte dominance	divergence to contrasting states	8 l	57 days	vegetative reproduction	?	what is the life span of a vegetative growing plant?	simulation model (same ref.)	+	Scheffer et al. 2003
35	multi-species lab culture [community assembly]	divergence/ invasion sequence	4 protozoans and bacteria	contrasting communities in species composition and relative densities	divergence to contrasting community states in terms of species composition	250 ml	48 days	several days ^d	>1	not tested for permanence		+	Price and Morin 2004

a) time after manipulation has ceased, for test for random divergence, either observation period or (when possible) the maximal duration of each alternative state is reported.

b) with semi-chemostat dynamics for the resource.

c) all marine systems are either benthic or intertidal communities dominated by sessile animals or macrophytes.

d) estimated life span based on general values for taxonomical or functional species group.

e) ratio of census time: life span.

f) our interpretation.