Qualitative Analysis of a Nonautonomous Beverton-Holt Ricker Model

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Abstract. We explore a planar discrete-time model from population dynamics subject to a general aperiodic time-varying environment in order to illustrate the recent theory of nonautonomous dynamical systems. Given such a setting, the mathematical standard tools from classical dynamical systems and bifurcation theory cannot be employed, since for instance equilibria typically do not exist or eigenvalues yield no stability information. For this reason, we apply a combination of contemporary analytical and numerical techniques adequate to tackle such situations.

Key words. Nonautonomous dynamics, numerical dynamics, pullback attractor, nonautonomous bifurcation, exponential dichotomy, Bohl exponent, population models

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1. Nonautonomous models. Mathematical models to describe evolutions with discrete time-steps are formulated in terms of recursions (or difference equations)

\[ x_{n+1} = f_\lambda(x_n), \]

where \(x_n\) represents a vector containing, for instance in the life sciences, sizes or densities of populations or biochemical substances involved at time \(n \in \mathbb{Z}\). Naturally, equations (1.1) contain parameters \(\lambda\) describing the influence of the environment on the models. In population dynamics, such factors might be seasonal and governed by the weather, describe possible catastrophes (floods, storms), unspecific predators, parasites, inner or intra-specific competition, social stress or infective diseases. They might, as well, capture dosing and control strategies including harvesting, hunting or the use of pesticides.

The complexity of these influences suggests that constant parameters \(\lambda\) in (1.1) are hardly realistic. As an improvement one should better work with time-varying parameter sequences \(\lambda_n\) and thus equations of the form

\[ x_{n+1} = f_{\lambda_n}(x_n). \] (1.2)

However, the drawback and challenge of such a nonautonomous framework (1.2) is that the classical mathematical theory of dynamical systems turns out to be hardly applicable. For instance, periodic solutions of (1.1) obtained from the fixed point relation \(x = f_p(\lambda)(x), p \in \mathbb{N}\), typically fail to be periodic solutions to (1.2) (for general parameter sequences), eigenvalues are of no use for indicating stability properties, and forward limit sets or attractors are not invariant. Hence, in absence of equilibria, what should classical bifurcation theory or numerical continuation software be applied to?

For the above reasons, an extension of the conventional dynamical systems theory is required. It is based on the leitmotiv that equilibria or periodic solutions to (1.1) persist as bounded entire solutions to (1.2) under moderately sized time-varying parameter sequences. These entire solutions also reflect the particular temporal forcing, i.e. for example almost periodic (almost automorphic, asymptotically constant, etc.)

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parameter sequences \((\lambda_n)_{n \in \mathbb{Z}}\) in (1.2); thus one also speaks of nonautonomous equilibria. In this sense, for instance a bifurcation is understood as a change in the structure or attraction properties of such entire solutions. We point out that an analogous theory as presented here also exists in the setting of continuous time nonautonomous dynamical systems (cf. [3, 19, 20, 23]). Yet, for the sake of conceptual clarity we have restricted to a discrete-time set-up.

Our considerations are based on an autonomous model

\[
\begin{align*}
    x_{n+1} &= \frac{\alpha x_n}{1 + x_n + \beta y_n}, \\
y_{n+1} &= y_n e^{\gamma - \delta x_n - y_n}
\end{align*}
\]  

from [7, 21] describing the interaction between two populations by coupling a Beverton-Holt with a Ricker equation. We propose adequate notions, tools and algorithms for answering an essential question: Do both species coexist or will we observe the extinction of at least one species in the future? The system \((\Delta')\) is interesting from an ecological point of view. Indeed, according to [7] it yields a counterexample to the so-called exclusion principle indicating that one species goes extinct, provided there exists no fixed point in the interior of the first quadrant. The latter holds for general \(d\)-dimensional systems, when exclusively Beverton-Holt- resp. Ricker-type equations are present, but [7, Sect. 4] demonstrates that for certain parameter constellations coexistence is possible in form of a period-2-solution in the open first quadrant, although there is no fixed-point in \((0, \infty)^2\). Meanwhile this behavior has been observed in various other models (see [17] and the references therein).

Nevertheless, our goal is to a minor extent biologically motivated and should rather be seen as a contribution to nonautonomous and numerical dynamics. From this mathematical perspective alone, \((\Delta')\) is a rewarding prototype example featuring dynamical behavior of different complexity, since it links the fully understood and dynamically well-behaved Beverton-Holt model \(x_{n+1} = \frac{\alpha x_n}{1 + x_n}\) with the possibly chaotic Ricker difference equation \(y_{n+1} = y_n e^{\gamma - y_n}\) (cf. [25]).

In this paper, we extend the above autonomous set-up and study \((\Delta')\) in an environment with bounded but otherwise arbitrary temporal fluctuations in the parameters \(\alpha, \beta, \gamma, \delta\). This requires various recent techniques from nonautonomous dynamics (cf. [20, 26]) in order to obtain information on the forward, as well as the pullback dynamics and the corresponding attractors. Changes in them are caused by multiple nonautonomous bifurcation scenarios (see [23, 31, 12, 27]), among which we particularly address counterparts to transcritical and flip (period doubling) bifurcations. The associate stability transitions are described using Bohl exponents which are boundary points of the dichotomy (also known as Sacker-Sell) spectrum (see [33] and [2, 1, 14]). Gaps in the dichotomy spectrum in turn give rise to invariant manifolds and we particularly perform a nonautonomous center manifold reduction (cf. [30]).

In this endeavor it turns out at an early stage that up-to-date numerical techniques are indispensable, when quantitative information on the dichotomy spectrum [13, 14] or the continuation of bounded entire solutions [11, 15] is required. Also explicit perturbation bounds for the persistence of hyperbolicity under nonautonomous forcing are given in a representative special case. In conclusion, only a combination of analytical and numerical methods yields a necessary insight into the long-term behavior of our in fact merely 2-dimensional, but nonautonomous dynamical system.

The structure of the paper is as follows. First we introduce a two-dimensional system, by coupling the Beverton-Holt with a Ricker equation. For each model,
we separately investigate its nonautonomous dynamics, attractors and bifurcations, illustrating in this way techniques suitable for time-varying problems. We then have all tools at hand for analyzing coexistence of both species in the coupled system. The final two sections are devoted to stability properties of the extinction, as well as coexistence solutions, and the bifurcations destabilizing them.

For the reader’s convenience, we summarized some basic, as well as required new results on nonautonomous dynamics, as well as more technical proofs in the appendix. Moreover, we refer to the monographs [3, 20, 26], the survey [18] and to [19] focussing on the life sciences. Finally, while our approach and the scope of this paper is strictly deterministic, let us point out that [4], [20, pp. 233ff, Chapt. 14] or [18, 19] illuminate related ideas from Random Dynamical Systems.

2. Preliminaries and the model. Throughout the paper, let us suppose that $I$ denotes a discrete interval unbounded above, i.e. the intersection of a real interval with the integers $\mathbb{Z}$. For a sequence $(a_n)_{n \in I}$ we briefly write $a_I$. The symbol $\ell^\infty$ denotes the space of bounded, and $\ell^1$ (resp. $\ell^0$) of absolutely summable sequences (resp. those with limit 0). Moreover, we abbreviate the nonnegative half-axis $\mathbb{R}_+ := [0, \infty)$.

Initial point is a general planar Beverton-Holt Ricker model

$$\begin{align*}
    v_{n+1} &= \frac{\alpha_n v_n}{\alpha_n + \beta_n^{1} v_n + \gamma_n^{1} w_n}, \\
    w_{n+1} &= w_n e^{\alpha_n^{2} - \beta_n^{2} v_n - \gamma_n^{2} w_n},
\end{align*}$$

in discrete time $n \in I$ and with parameter sequences $\alpha, \alpha_1, \beta_1, \gamma_1, i = 1, 2$. Related autonomous models, where both components are of Beverton-Holt- or of Ricker-type, have been suggested in [5]. In combining these two kinds of nonlinearities, we are able to study Beverton-Holt and Ricker behavior, as well as their interaction, in a single model. However, this type of problem has also been investigated in [7, 17] with a focus on biological and ecological implications. Our approach thus has more than just a didactical motivation.

First, we get rid of several parameters and simplify this model to its canonical form. By means of the abbreviations $x_n := \frac{\beta_1}{\alpha_n} v_n$, $y_n := \gamma_n^{2} w_n$ the reduced model is

$$\begin{pmatrix}
    x_{n+1} \\
    y_{n+1}
\end{pmatrix} = F_n(x_n, y_n), \quad F_n(x, y) := \begin{pmatrix}
    \frac{a_n x}{1 + x + b_n y} \\
    \frac{c_n e^{d_n x} - d_n x - y}{y}
\end{pmatrix} \quad (\Delta)$$

with the right-hand side $F_n : \mathbb{R}_+^2 \to \mathbb{R}_+^2$, $n \in I$, and parameter sequences

$$\begin{align*}
    a_n := & \frac{\alpha_n^{1} \beta_n^{1}}{\alpha_n + \beta_n^{1} \gamma_n^{1}}, \\
    b_n := & \frac{\gamma_n^{1}}{\alpha_n \gamma_n^{1}}, \\
    c_n := & \alpha_n^{2} + \ln \left( \frac{\gamma_n^{1} + 1}{\gamma_n^{1} - 2} \right), \\
    d_n := & \frac{\alpha_n \beta_n^{2}}{\beta_n^{1}}.
\end{align*}$$

Referring to this simplification, we can exclusively consider $(\Delta)$ with the right-hand side $F_n$ from now on. In addition, let us impose the global assumption throughout the paper that the real sequences $a_1$, $b_i$, $c_i$, $d_i$ in $(\Delta)$ are bounded; furthermore $a_3$, $b_i$, $d_i$ are supposed to have positive values, while $c_i$ can be nonnegative. Note that these conditions constrain the original parameters: Beyond their boundedness they ought to stay away from 0 uniformly in $n$. Moreover, the nonnegativity of $c_n$ requires
drastic decreases of $\gamma^2$ in forward time to be excluded, i.e. $\frac{\gamma^2}{\gamma_{n+1}} \leq e^{\alpha_n}$, $n \in \mathbb{I}$, must hold.

A solution $(\xi, \eta)$ of $(\Delta)$ is a sequence satisfying $(\xi_{n+1}, \eta_{n+1}) = F_n(\xi_n, \eta_n)$. Given an initial time $t_0 \in \mathbb{I}$ and initial states $\bar{x}, \bar{y} \geq 0$, we denote the forward solution to $(\Delta)$ satisfying the initial condition $x_{t_0} = \bar{x}, y_{t_0} = \bar{y}$ by $\varphi(\cdot; t_0, \bar{x}, \bar{y})$ and its components by $\varphi_1, \varphi_2$. Further basics from nonautonomous dynamics are summarized in Appendix A.

We start with general remarks on the stability of solutions to nonautonomous difference equations. For a solution $(\xi, \eta)$ to $(\Delta)$, the variational equation reads as

$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = F'_n(\xi_n, \eta_n) \begin{pmatrix} x_n \\ y_n \end{pmatrix}$$

with the coefficient matrix

$$F'_n(\xi, \eta) = \begin{pmatrix} \frac{a_n(1+b_n \eta)}{(1+\xi+b_n \eta)^2} & -\frac{a_n b_n \xi}{(1+\xi+b_n \eta)^2} \\ -d_n \eta e^{c_n - d_n \xi} - d_n \xi - \eta (1 - \eta) \end{pmatrix}$$

for all $n \in \mathbb{I}, \xi, \eta \geq 0$.

Since we are interested in a robust analysis it is preferable to deal with uniform stability properties of solutions $(\xi, \eta)$ to $(\Delta)$. They are determined by the dichotomy spectrum $\Sigma(\xi, \eta)$ (for this, see Appendix B.2) of $(V)$, which indicates uniform asymptotic stability of a solution $(\xi, \eta)$, i.e. the fact that $(\xi, \eta)$ is uniformly attractive

$$\exists \rho > 0 : \forall \varepsilon > 0 : \exists N \in \mathbb{N}_0 : (\bar{x}, \bar{y}) \in B_\rho(\xi_{n_0}, \eta_{n_0}) \Rightarrow \varphi(n; n_0, \bar{x}, \bar{y}) \in B_\varepsilon(\xi_n, \eta_n)$$

for all $n_0 \in \mathbb{I}$, $n \geq n_0 + N$, as well as uniformly stable

$$\forall \varepsilon > 0 : \exists \delta > 0 : \forall n_0 \in \mathbb{I} : (\bar{x}, \bar{y}) \in B_\delta(\xi_{n_0}, \eta_{n_0}) \Rightarrow \varphi(n; n_0, \bar{x}, \bar{y}) \in B_\varepsilon(\xi_n, \eta_n)$$

for all $n \geq n_0$.

**Theorem 2.1.**

(a) If $\Sigma(\xi, \eta) \subseteq [0, 1)$, then $(\xi, \eta)$ is uniformly asymptotically stable.

(b) If there exists a spectral interval $\sigma^+ \subseteq \Sigma(\xi, \eta)$ with $\min \sigma^+ > 1$, then $(\xi, \eta)$ is unstable. Moreover, in case $\mathbb{I} = \mathbb{Z}$ there exists an unstable fiber bundle, i.e. the nonautonomous counterpart to an unstable manifold.

**Proof.** See [27, Props. 3.9 and 3.10].

For analogy reasons, a solution $(\xi, \eta)$ to $(\Delta)$ is called a (nonautonomous)

- **sink,** if $\max \Sigma(\xi, \eta) < 1$,

- **saddle,** if $1 \in \mathbb{Z}$ and there exist two nonempty disjoint $\sigma_1, \sigma_2 \subseteq (0, \infty)$ with $\Sigma(\xi, \eta) = \sigma_1 \cup \sigma_2$, $\max \sigma_1 < 1 < \min \sigma_2$,

- **source,** if $1 < \min \Sigma(\xi, \eta)$.

Returning to the concrete planar system $(\Delta)$, it has the trivial equilibrium $(0, 0)$ and both coordinate axes are forward invariant. Hence, in order to understand $(\Delta)$ we initially investigate its behavior restricted to the $x$- and $y$-axes.

Restricted to the $x$-axis, $(\Delta)$ is a scalar nonautonomous Beverton-Holt equation

$$x_{n+1} = f_n(x_n), \quad f_n(x) := \frac{a_n x}{1 + x}.$$  \hspace{1cm} (BH)

while the restriction to the $y$-axis results in a nonautonomous Ricker equation

$$y_{n+1} = g_n(y_n), \quad g_n(y) := y e^{c_n - y}.$$  \hspace{1cm} (R)
Given these scalar systems, we illustrate basic nonautonomous tools for analyzing their
dynamics. First we note that their right-hand sides have at 0 the Taylor expansions
\[ f_n(x) = a_n \sum_{i=0}^{\infty} (-1)^i x^{i+1}, \quad g_n(y) = e^{c_n} \sum_{i=0}^{\infty} \frac{(-1)^i y^{i+1}}{i!} \]
with convergence radii 1 resp. \( \infty \); see Fig. 2.1.

Fig. 2.1. Right-hand sides of the Beverton-Holt model (BH) for \( a_n = 1 \) (black), and the Ricker
model (R) for \( c_n = 0 \) (red).

The function \( f_n: \mathbb{R}_+ \to \mathbb{R}_+ \) is monotone increasing with limit \( a_n > 0 \), whereas
\( g_n: \mathbb{R}_+ \to \mathbb{R}_+ \) is increasing for \( y < 1 \) with maximum \( e^{c_n} \) at \( y = 1 \) and monotone
decreasing to 0 for \( y > 1 \). Using their common properties, we immediately find
invariant and pullback absorbing sets (see Appendix A for the required terminology):

**Theorem 2.2 (pullback attractor).** Let \( I = \mathbb{Z} \) and \( h_n: \mathbb{R}_+ \to \mathbb{R}_+ \), \( n \in \mathbb{Z} \), be
continuous. If \( r \in \mathbb{R}_+ \) is a bounded sequence such that \( 0 \leq h_n(z) \leq r_n \) for all \( n \in \mathbb{Z} \), \( z \geq 0 \), then the nonautonomous set \( Z := \{(n, z) \in \mathbb{Z} \times \mathbb{R}_+ : 0 \leq z \leq r_{n-1}\} \) is forward
invariant and pullback absorbing w.r.t. the scalar difference equation
\[ z_{n+1} = h_n(z_n). \]

Furthermore, the so-called pullback attractor
\[ Z^* := \{ z_{\mathbb{Z}} \in \ell^\infty : z_{n+1} = h_n(z_n) \text{ on } \mathbb{Z} \} \subseteq Z \]
is compact, invariant, connected and pullback attracts all bounded subsets of \( \mathbb{Z} \times \mathbb{R}_+ \).

**Proof.** Since \( h_n([0, r]) \subseteq [0, r] \) holds true for all \( n \in \mathbb{Z} \) it follows that the nonautonomous set \( Z \) is forward invariant and pullback absorbing.

The \( \omega \)-limit set \( \omega_Z \) of the absorbing set \( Z \) is invariant, pullback attracting and satisfies the inclusion \( \omega_Z \subseteq Z \) by [26, p. 19, Thm. 1.3.9]. Furthermore, [26, p. 14, Thm. 1.2.25] guarantees compactness and [26, p. 20, Cor. 1.3.11] its connectedness. Finally, the dynamical characterization [26, p. 17, Thm. 1.3.4] implies \( Z^* = \omega_Z \).

**3. Nonautonomous Beverton-Holt model.** Let us first consider the dynamics of the nonautonomous Beverton-Holt equation (BH) in detail (cf. Fig. 3.1). Given
an initial pair \((n_0, \bar{x}) \in I \times \mathbb{R}_+ \), we denote its solution satisfying the initial condition
\( x_{n_0} = \bar{x} \) by \( x(\cdot; n_0, \bar{x}) \) and obtain the following properties:

- The nonautonomous set \( I \times \{0\} \) is invariant, while \( \{(n, x) \in I \times \mathbb{R}_+ : x \leq a_{n-1}\} \)
and \( \{(n, x) \in I \times \mathbb{R}_+ : 0 < x \leq a_{n-1}\} \) are forward invariant w.r.t. (BH).

- Due to the monotonicity of each \( f_n \), one has the comparison principle
\[ 0 \leq \bar{x}_1 < \bar{x}_2 \Rightarrow x(n; \bar{n}, \bar{x}_1) < x(n; \bar{n}, \bar{x}_2) \quad \text{for all } \bar{n} \leq n. \]

In particular, the Beverton-Holt equation (BH) is order-preserving.
• If \( I = \mathbb{Z} \), then Thm. 2.2 applies with \( r_n = a_n \) and the pullback absorbing set
\[
X := \{(n, x) \in \mathbb{Z} \times \mathbb{R}^+: 0 \leq x \leq a_{n-1}\}
\]
yielding the pullback attractor \( X_a^* := \{x \in \ell^\infty : x_{n+1} = \frac{a_n x_n}{1+x_n} \text{ on } \mathbb{Z}\} \).

3.1. Pullback attractor of (BH). In the autonomous Beverton-Holt equation
\[
x_{n+1} = f(x_n), \quad f(x) := \frac{\alpha x}{1+x} \quad \text{(BH')}
\]
with the right-hand side \( f : \mathbb{R}^+ \to \mathbb{R}^+ \) and a parameter \( \alpha > 0 \), the trivial solution transcritically bifurcates into the equilibrium \( \alpha - 1 \), as \( \alpha \) increases through the critical value 1. For \( \alpha = 1 \) it follows from [6, p. 478, Thm. A.3] that 0 is still asymptotically stable. Thus, its pullback attractor becomes
\[
X_\alpha^* = \begin{cases} 
\mathbb{Z} \times \{0\}, & \alpha \in (0, 1], \\
\mathbb{Z} \times [0, \alpha - 1], & \alpha > 1
\end{cases}
\]
and for \( \alpha > 1 \) every solution starting in the open interval \((0, \alpha - 1)\) is a strictly increasing heteroclinic connection between the fixed points 0 and \( \alpha - 1 \).

Our next goal are similar information on the structure of the above nonautonomous set \( X_a^* \) for arbitrary time-varying sequences \( a_i \). Here, it is helpful to introduce
\[
\Phi_a(n, m) := \begin{cases} 
a_{n-1} \cdots a_m, & m < n, \\
1, & n = m, \\
a_{n-1} \cdots a_{m-1}, & n < m
\end{cases}
\]
and that the solutions of the Beverton-Holt equation (BH) are explicit:

**Lemma 3.1.** The Beverton-Holt equation (BH) has the explicit solution
\[
x(n; n_0, \bar{x}) = \begin{cases} 
\frac{\bar{x} \Phi_a(n, n_0)}{1 + \bar{x} \sum_{i=n_0}^{n-1} \Phi_a(i, n_0)}, & n_0 \leq n, \bar{x} \geq 0, \\
\frac{\bar{x} \Phi_a(n, n_0)}{1 - \bar{x} \sum_{i=n}^{n_0-1} \Phi_a(i, n_0)}, & n < n_0
\end{cases}
\]
and \( \bar{x} \geq 0 \) satisfying \( \bar{x} \sum_{i=n}^{n_0-1} \Phi_a(i, n_0) < 1 \).
Proof. Let \( \bar{x} \geq 0 \). It holds that \( x(n_0; n_0, \bar{x}) = \bar{x} \) and moreover we get
\[
x(n + 1; n_0, \bar{x}) = \frac{\bar{x} \prod_{i=n_0}^{n} a_i}{1 + \bar{x} \sum_{i=n_0}^{n-1} a_j} = \frac{a_\bar{x} \Phi_a(n, n_0)}{1 + \bar{x} \sum_{j=n_0}^{n-1} a_j + \bar{x} \Phi_a(n, n_0)}
\]
(3.3)
\[
\frac{a_\bar{x} x(n; n_0, \bar{x})}{1 + x(n; n_0, \bar{x})} \quad \text{for all} \ n_0 \leq n.
\]
In order to obtain the relation for times \( n < n_0 \) one has to solve
\[
\bar{x} = x(n; n_0, x(n_0; n, \bar{x})) = x(n; n_0, \xi) \quad \text{for all} \ n_0 < n
\]
w.r.t. the variable \( \xi \) and arrives at the second formula given in (3.3).

A particularly important solution of (BH) results in the pullback limit \( n_0 \to -\infty \).

**Lemma 3.2.** For \( \mathbb{I} = \mathbb{Z} \) the Bevorton-Holt equation (BH) has the entire solution
\[
\xi^*_n = \frac{1}{\sum_{i=-\infty}^{n-1} \Phi_a(i, n)} \quad \text{for all} \ n \in \mathbb{Z}
\]
and the following holds: If there exists an \( n \in \mathbb{Z} \) such that
(a) \( \prod_{i=-\infty}^{n-1} a_i = \infty \), then the solution \( \xi^*_n \) is pullback attracting in \( \mathbb{Z} \times (0, \infty) \).
(b) \( \prod_{i=-\infty}^{n-1} a_i = 0 \) or
\[
0 < \inf_{i < n} \Phi_a(n, i) \leq \sup_{i < m \leq n} \Phi_a(m, i) < \infty,
\]
(3.4)
then the zero solution is pullback attracting in \( \mathbb{Z} \times \mathbb{R}_+ \).

**Proof.** (a) For \( \bar{x} > 0 \) we have the limit relation
\[
\lim_{n_0 \to -\infty} \frac{x(n; n_0, \bar{x})}{1 + x \sum_{i=n_0}^{n-1} \Phi_a(i, n)} = \xi^*_n \quad \text{for all} \ n \in \mathbb{Z}
\]
which, together with Lemma 3.1 and \( \prod_{i=-\infty}^{n-1} a_i = \infty \), follows for \( n_0 \leq n \) from
\[
x(n; n_0, \bar{x}) = \frac{x \Phi_a(n, n_0)}{1 + x \sum_{i=n_0}^{n-1} \Phi_a(i, n)} = \frac{1}{\frac{x \Phi_a(n, n_0)}{1 + x \sum_{i=n_0}^{n-1} \Phi_a(i, n)} + \sum_{i=n_0}^{n-1} \Phi_a(i, n)}
\]
(3.3)
by passing over to the limit \( n_0 \to -\infty \).
(b) Similarly to (a), the condition \( \prod_{i=-\infty}^{n-1} a_i = 0 \) yields \( \lim_{n_0 \to -\infty} x(n; n_0, \bar{x}) = 0 \) for all \( \bar{x} \geq 0 \). Under the assumption (3.4) we abbreviate
\[
a_- := \inf_{i < n} \Phi_a(n, i), \quad a_+ := \sup_{i < m \leq n} \Phi_a(m, i)
\]
and deduce
\[
0 \leq x(n; n_0, \bar{x}) \leq \frac{a_+ \bar{x}}{1 + \bar{x} \sum_{i=n_0}^{n-1} \Phi_a(i, n)} \to 0.
\]
Being a pullback solution, Thm. A.1 ensures that \( \xi^*_n \) solves (BH).

**Remark 3.3** (sufficient conditions). (1) Lemma 3.2(a) occurs for sequences \( a_\mathbb{Z} \) satisfying \( \overline{\beta}(a_\mathbb{Z}) > 1 \), where \( \overline{\beta} \) denotes the lower Bohl exponent, cf. Appendix B.1.
(2) Otherwise, for coefficient sequences \( a_\mathbb{Z} \) with upper Bohl exponent \( \overline{\beta}(a_\mathbb{Z}) < 1 \), Lemma 3.2(b) applies. Subexponential pullback convergence to 0 occurs under (3.4).
After these preparations we are in a position to characterize the set $X^*_a$:

**Theorem 3.4** (pullback attractor of \( (BH) \)). For \( I = \mathbb{Z} \) the pullback attractor of the Beverton-Holt equation \( (BH) \) is given by

\[
X^*_a = \begin{cases} 
\mathbb{Z} \times \{0\}, & \prod_{i=-\infty}^{n-1} a_i = 0 \text{ or } (3.4), \\
\{(n,x) : 0 \leq x \leq \xi^*_a\}, & \prod_{i=-\infty}^{n-1} a_i = \infty.
\end{cases}
\]

**Remark 3.5.** (1) In the autonomous case \( 0 < a_n \equiv \alpha \), condition \( \prod_{i=-\infty}^{n-1} a_i = 0 \) is equivalent to \( 0 < \alpha < 1 \) and thus, the fixed point \( 0 \) is asymptotically stable. In the center case \( (3.4) \) we get \( \alpha = 1 \) and \( 0 \) is still attracting but only with a polynomial rate of attraction. Finally, we conclude from \( \prod_{i=-\infty}^{n-1} a_i = \infty \) that \( \alpha > 1 \) and \( 0 \) is unstable.

(2) If one restricts to initial values \( x > 0 \) the entire solution \( \xi_n^* \) becomes pullback attracting in the sense that \( \omega_B = \xi_n^* \) holds for all bounded \( B \subseteq \mathbb{Z} \times (0,\infty) \).

**Proof.** Under \( \prod_{i=-\infty}^{n-1} a_i = 0 \) or \( (3.4) \) the assertion follows immediately from Lemma 3.2(b). In case \( \prod_{i=-\infty}^{n-1} a_i = \infty \) we can apply Thm. A.3 and its Cor. A.4 with the bounded sequences \( x_n := 0 \), \( x_n^+ := a_n \) and the nonautonomous set \( X \). It obviously holds that \( \xi^*_n = x^*_n = 0 \) and one shows

\[
\xi^*_n = \lim_{k \to -\infty} x(n;k,a_k) = \xi^*_n \quad \text{for all } n \in \mathbb{Z}
\]
as in the proof of Lemma 3.2.

We next illustrate that Thm. 3.4 captures the autonomous situation as well.

**Example 3.6** (attractor change in \( (BH') \)). For \( a_n \equiv \alpha \) it is \( \Phi_a(n,n_0) = \alpha^{n-n_0} \) and thus the pullback attractor \( X^*_a \) precisely changes at \( \alpha = 1 \) (cf. \( (3.1) \)). In particular,

\[
\xi^*_n = \frac{1}{\sum_{i=-\infty}^{n-1} \prod_{j=i}^{n-1} \frac{1}{\alpha^j}} = \alpha - 1 \quad \text{for all } n \in \mathbb{Z}, \alpha > 1
\]

and accordingly the entire solution \( \xi_n^* \) degenerates to the fixed point \( \alpha - 1 \).

In addition, the explicit representation \( (3.3) \) shows that structural assumptions (periodicity, almost periodicity, asymptotic constancy) on the coefficient sequence \( a_Z \) carry over to the entire solution \( \xi_n^* \) and hence the pullback attractor \( X^*_a \).

While the nonhyperbolic case \( \alpha = 1 \) was easily settled in the autonomous situation, the following example shows that for corresponding critical Bohl exponents

\[
\beta(a_Z) = \overline{\beta}(a_Z) = 1
\]

a distinction between the attractors \( X^*_a \) is more subtle in a time-variant setting:

**Example 3.7.** Let \( p \in \mathbb{R} \) and consider coefficient sequences

\[
a_j := \begin{cases} 
\frac{|j-1|^p}{j}, & j < 0, \\
1, & j \geq 0
\end{cases}
\]

with the limit behavior

\[
\prod_{j=1}^{n-1} a_j = \prod_{j=1}^{n-1} \frac{|j-1|^p}{j} = \begin{cases} 
\frac{|i-1|^p}{\min\{n,-1\}} & i \to \infty \\
1 & p = 0,
\end{cases}
\]

\[
\begin{cases}
0, & p < 0, \\
1, & p = 0,
\end{cases}
\]

\[
\begin{cases}
\infty, & p > 0
\end{cases}
\]
and Bohl exponents fulfilling (3.5). In case \( p < 0 \) we derive from Lemma 3.2(b) that the trivial solution is pullback attracting. Nonetheless, from the explicit expression
\[
\xi^*_n = \frac{1}{\sum_{i=-\infty}^{n-1} \pm i} \quad \text{for all } n < 0
\]
we observe that \( \xi^*_n \) degenerates to the trivial solution for all \( p \leq 1 \). However, for exponents \( p > 1 \) the nontrivial entire solution \( \xi^*_n \) becomes pullback attracting.

The change of the pullback attractors from Thm. 3.4 is understood as bifurcation in (BH). Indeed, one can illustrate the different approaches to a nonautonomous transcritical bifurcation from [23, 31] in the parameter-dependent Beverton-Holt model
\[
x_{n+1} = \frac{a_n(\lambda)x_n}{1 + x_n} \quad \text{(BH)}
\]

3.2. Transcritical bifurcation.

3.2.1. The case \( a_n(\lambda) = \lambda^{p_{n+1}/p_n} \). We choose the parameter sequence
\[
a_n(\lambda) = \lambda^{p_{n+1}/p_n}, \quad \text{where } 0 < p_- \leq p_n \leq p_+ < \infty \text{ for all } n \in \mathbb{Z}, \quad (3.6)
\]
which is mathematically motivated. In case \( \lambda = 1 \), the parameter sequence \( a(1) \) has the critical upper and lower Bohl exponent 1. Let us next discuss the precise nature of the occurring bifurcation w.r.t. the parameter \( \lambda \).

Assuming (3.6), the entire solution introduced in Lemma 3.2 simplifies to
\[
\xi^*_n(\lambda) = \frac{\lambda^np_n}{\sum_{i=-\infty}^{n-1} \lambda^i p_i}.
\]

A plot of this solution for different parameter sequences \( p_n \) is given in Fig. 3.2. It clearly illustrates that the attractivity of the trivial solution gets transferred to a nontrivial constant, periodic, asymptotically constant resp. entire solution of (BH) as \( \lambda \) passes through the critical value 1, if the parameter sequence \( (p_n)_{n \in \mathbb{Z}} \) has the corresponding time-dependence. Note that the heteroclinic choice of \( (p_n)_{n \in \mathbb{Z}} \) in Fig. 3.2(c) leads to \( a_n(\lambda) = \lambda \) for \( n \neq 19 \) and \( a_{19} = 3\lambda \), which explains the homoclinic behavior of the solution \( \xi^*(\lambda) \).

In [12], the model function
\[
x_{n+1} = h_n(x_n, \lambda), \quad \text{where } h_n(x, \lambda) = \frac{\lambda x}{1 + \frac{p_n}{p_{n+1}} x}, \quad 0 < p_- \leq p_n \leq p_+ < \infty
\]
is introduced that undergoes a nonautonomous transcritical bifurcation at \( \lambda = 1 \), as defined in [23] and [31]. Via the kinematic transformation \( T_n(x) = \frac{\lambda x}{1 + \frac{p_n}{p_{n+1}} x} \) we get
\[
T_{n+1} \circ h_n \circ T_n^{-1}(x) = \frac{\lambda^{p_{n+1}/p_n} x}{1 + x},
\]
which is our Beverton-Holt model (BH) with \( a_n(\lambda) = \lambda^{p_{n+1}/p_n} \). Due to this topological equivalence, (BH) also exhibits a transcritical bifurcation at \( \lambda = 1 \).

In the nonhyperbolic case \( \lambda = 1 \) one obtains
\[
\prod_{i=-\infty}^{0} a_i(1) = \prod_{i=-\infty}^{0} \frac{p_{i+1}}{p_i} \in (0, \infty),
\]
and by Lemma 3.2(b), all solutions of \((BH_\lambda)\) pullback converge to 0. Thus, the trivial solution is pullback attractive for all parameters \(0 < \lambda \leq 1\).

![Fig. 3.2. Nonautonomous transcritical bifurcation for the Beverton-Holt equation \((BH_\lambda)\) with (a) \(p_n \equiv 1\), (b) \(p_n = 1 + \frac{1}{2} \sin \frac{\pi n}{5}\), (c) \(p_n = \frac{1}{2} (n < 20)\) and \(p_n = \frac{3}{2} (n \geq 20)\), (d) \(p_n = 1 + \frac{1}{2} r_n\) with randomly chosen \(r_n \in [-1, 1]\).]

**3.2.2. The case** \(a_n(\lambda) = 1 + \lambda \alpha_n\). We deal with sequences \(a_n := 1 + \lambda \alpha_n\) and a bounded \(\alpha_I\). For \(\lambda = 0\) equation \((BH_\lambda)\) becomes autonomous and the unique equilibrium 0 is globally asymptotically stable. Provided the sequence is uniformly positive (or negative) it is possible to verify a transcritical bifurcation as understood in [31]. This means that attraction and repulsion radii of the trivial solution to \((BH_\lambda)\) decay to 0 as \(\lambda \to 0\).

**3.3. Forward behavior.** Since pullback attractors essentially capture the dynamical behavior in the past of a difference equation (cf. [18, pp. 59ff, Subsect. 4.5] and Ex. 3.12 below), we separately address the forward dynamics of \((BH)\). First, one recaptures the feature that all forward solutions to the autonomous problem \((BH')\) converge to the trivial solution for parameters \(\alpha \in (0, 1]\). Second, it is worth to point out that already the stability of the linearization \(x_{n+1} = a_n x_n\) implies an attractive zero solution to \((BH)\):

**Proposition 3.8.** If \(\Phi_{a}(\cdot, n_0) \in \ell^\infty\) for a \(n_0 \in I\), then \(\lim_{n \to \infty} x(n; \bar{n}, \bar{x}) = 0\) for all \(\bar{n} \in I, \bar{x} \geq 0\).

Note that the above assertion holds for a Bohl exponent \(\overline{\beta}(a_1) < 1\), whereas \(\beta(a_2) > 1\) enforces the trivial solution of \((BH)\) to be unstable (cf. Thm. 2.1(b)).

**Proof.** Let \(\bar{n} \in I\). Due to the inclusion \(\ell^1 \subseteq \ell_0\) one has the decomposition

\[\ell^\infty = \ell_0 \cup (\ell^\infty \setminus \ell_0) = \ell_0 \cup (\ell^\infty \setminus \ell^1)\]
and therefore it suffices to consider the following two cases:

(I) $\Phi_a(\cdot, n_0) \in \mathcal{E}_0$: Thanks to the elementary estimate $f_a(x) = \frac{a_n x}{1 + x} \leq a_n x$ for all $n \in \mathbb{N}$ and $x \geq 0$, mathematical induction implies the inequalities

$$0 \leq x(n; \bar{x}, \bar{n}) \leq \bar{x} \Phi_a(n, \bar{n}) = \bar{x} \Phi_a(n_0, \bar{n}) \Phi_a(n, n_0) \quad \text{for all } \bar{n} \leq n, \bar{x} \geq 0$$

and the claim follows in the limit $n \to \infty$.

(II) $\Phi_a(\cdot, n_0) \in \mathcal{E}^\infty \setminus \mathcal{E}^1$: Here we can deduce

$$0 \leq x(n; \bar{x}, \bar{n}) \leq \frac{\bar{x} \Phi_a(n_0, \bar{n}) \sup_{\bar{k} \leq n} \Phi_a(\bar{k}, n_0)}{1 + \bar{x} \sum_{i=n_0}^{n-1} \Phi_a(i, \bar{n})} \to 0$$

and consequently obtain the assertion. \(\Box\)

The assumption of Prop. 3.8 ensures that all forward solutions to (BH) converge towards the trivial solution. An alternative summability condition — always fulfilled in the hyperbolic autonomous case $\alpha \neq 1$ (see Ex. 3.11) — that forward solutions approach each other is given in

**Proposition 3.9.** If $\lim_{n \to \infty} \left( \sum_{j=n_0}^{n-1} \Phi_a(j, n) \right) \sum_{i=n_0}^{n-1} \Phi_a(i, n_0) = \infty$ holds for some $n_0 \in \mathbb{N}$, then

$$\lim_{n \to \infty} (x(n; n_0, \bar{x}_1) - x(n; n_0, \bar{x}_2)) = 0 \quad \text{for all } 0 < \bar{x}_1, \bar{x}_2.$$  \hspace{1cm} (3.8)

**Proof.** For $\bar{x}_1 = \bar{x}_2$ there is nothing to prove. Given reals $0 < \bar{x}_2 < \bar{x}_1$ the explicit representation from Lemma 3.1 yields

$$0 \leq x(n; n_0, \bar{x}_1) - x(n; n_0, \bar{x}_2) = \frac{\bar{x}_1 \Phi_a(n, n_0)}{1 + \bar{x}_1 \sum_{i=n_0}^{n-1} \Phi_a(i, n_0)} - \frac{\bar{x}_2 \Phi_a(n, n_0)}{1 + \bar{x}_2 \sum_{i=n_0}^{n-1} \Phi_a(i, n_0)}$$

$$= \frac{(\bar{x}_1 - \bar{x}_2) \Phi_a(n, n_0)}{\left(1 + \bar{x}_1 \sum_{i=n_0}^{n-1} \Phi_a(i, n_0)\right) \left(1 + \bar{x}_2 \sum_{i=n_0}^{n-1} \Phi_a(i, n_0)\right)} \to 0, \quad n \to \infty$$

by the assumed divergence condition. Interchanging $\bar{x}_1$ and $\bar{x}_2$ in the above estimate finally yields the claim for $0 < \bar{x}_1 \leq \bar{x}_2$, as well. \(\Box\)

In the autonomous case (BH') and for $\alpha > 1$ all nontrivial solutions converge to the fixed point $\alpha - 1$ in forward time. This behavior persists for the nonautonomous Beverton-Holt equation (BH) with $\alpha - 1$ replaced by the entire solution $\xi^*_\alpha$.

**Corollary 3.10.** If $\mathbb{I} = \mathbb{Z}$ and the limit relations

$$\lim_{j \to -\infty} \Phi_a(n_0, j) = \infty, \quad \lim_{n \to \infty} \left( \sum_{j=n_0}^{n-1} \Phi_a(j, n) \right) \sum_{i=n_0}^{n-1} \Phi_a(i, n_0) = \infty$$

hold for some $n_0 \in \mathbb{Z}$, then $\lim_{n \to -\infty} (x(n; n_0, \bar{x}) - \xi^*_\alpha) = 0$ for all $\bar{x} > 0$.

**Proof.** Set $\bar{x}_1 := \bar{x}$ and $\bar{x}_2 := \xi^*_{n_0}$ in (3.8) and use Lemma 3.2. \(\Box\)

For autonomous equations forward and pullback asymptotics coincide:
Example 3.11 (autonomous situation). Suppose that $a_n \equiv \alpha$ on $\mathbb{Z}$ holds with some $\alpha > 0$. In case $\alpha = 1$ the asymptotic equivalence (and convergence to 0) follows from Prop. 3.8. On the other hand, for $\alpha \neq 1$, one gets $\Phi_a(n,j) = \alpha^{n-j}$ and

$$
\left( \sum_{j=n_0}^{n-1} \Phi_a(j,n) \right) \sum_{i=n_0}^{n-1} \Phi_a(i,n_0) = \frac{1 - \alpha^{n_0-n} \alpha^{n-n_0} - 1}{\alpha - 1} = \frac{\alpha^{n-n_0} + \alpha^{n_0-n} - 2}{(\alpha - 1)^2} \xrightarrow{n \to \infty} \infty.
$$

Hence, in case $\alpha \in [0,1)$ all solutions converge to 0 in forward time. However, for $\alpha > 1$ the above Cor. 3.10 applies and yields forward convergence to the nontrivial fixed point $\alpha - 1$. In conclusion, the behavior from (3.1) occurs.

To illustrate that forward and pullback behavior of a nonautonomous equation (BH) can be different in general, we consider

Example 3.12. Take a bounded sequence $p_Z$ as in (3.6), choose a fixed $\alpha_- \in (0,1)$ and consider $\lambda > 0$ as bifurcation parameter. We define the sequence

$$
a_n(\lambda) := \frac{p_{n+1}}{p_n} \begin{cases}
\lambda, & n \geq 0, \\
\alpha_-, & n < 0
\end{cases} \quad \text{for all } n \in \mathbb{Z}
$$

in (BH$_\lambda$) and an easy computation implies

$$
\Phi_a(n,m) = \frac{p_n}{p_m} \begin{cases}
\lambda^{n-m}, & 0 \leq m \leq n, \\
\lambda^n \alpha_-^m, & m > 0 \leq n, \\
\alpha_-^{n-m}, & m \leq n < 0.
\end{cases}
$$

The boundedness of $p_Z$ and the choice of $\alpha_- \in (0,1)$ yields $\lim_{m \to -\infty} \Phi_a(n,m) = 0$ and by Thm. 3.4 the Beverton-Holt equation (BH$_\lambda$) has the pullback attractor $\mathbb{Z} \times \{0\}$ for all $\lambda > 0$. Yet, solutions starting in $\bar{x} > 0$ converge towards the entire solution $\xi_n^*(\lambda)$ in forward time, which needs not to be the trivial one.

3.4. Summary. For the time-variant Beverton-Holt model, we discussed survival versus extinction and bifurcations between these states. More precisely, when dealing with nonautonomous problems, equilibria (fixed points) are replaced by specific bounded entire solutions reflecting the characteristic temporal driving (e.g. periodic, almost periodic or random, see Fig. 3.2 and [28]). In particular for the Beverton-Holt equation (BH), its strictly increasing right-hand side guarantees relatively simple dynamics and even explicit solutions can be computed. This enables us to obtain the pullback attractor (see App. A.1 and [3, 18, 19, 20, 26]), as an object capturing the global dynamics. Its definition via initial times tending to $-\infty$ might not be intuitive at first glance, but its dynamical properties (invariant, compact, attracting) legitimately generalize global attractors. Bifurcations in an aperiodic setting can be understood both as a (topological) change of the pullback attractor, as well as a stability exchange from the trivial to an entire bounded solution (cf. [12, 23, 27, 31]). Eventually, since forward and pullback behavior of a time-dependent equation might be different, pullback attractors do not necessarily describe the forward behavior (see Ex. 3.12 and [18, pp. 59ff, Subsect. 4.5]).
4. Nonautonomous Ricker model. We focus on a nonautonomous Ricker equation \( (R) \) with right-hand side \( g_n : \mathbb{R}_+ \to \mathbb{R}_+ \) (cf. Fig. 4.1) for bounded sequences \( c_n \) in \( \mathbb{R}_+ \). Given pairs \((n_0, \bar{y})\) \( \in \mathbb{I} \times \mathbb{R}_+ \), let us write \( y(\cdot; n_0, \bar{y}) \) for the general solution to \( (R) \) and obtain

- The nonautonomous set \( \mathbb{I} \times \{0\} \) is invariant, while \( \mathbb{I} \times \mathbb{R}_+ \) and \( \mathbb{I} \times (0, \infty) \) are forward invariant w.r.t. \( (R) \).
- All forward solutions are bounded, i.e. it is
  \[
  0 < y(n; n_0, \bar{y}) \leq \frac{e^{c_n - 1}}{e} \quad \text{for all } n > n_0, \bar{y} > 0, \tag{4.1}
  \]
  while backward solutions to initial values \( \bar{y} > \frac{e^{c_n}}{e} \) do not exist.
- Comparing the Beverton-Holt and Ricker model for \( a_n = e^{c_n} \), we immediately see that (cf. Fig. 2.1)
  \[
  0 < y(n; n_0, \bar{y}) \leq x(n; n_0, \bar{y}) \tag{3.3}
  \]
  \[
  \text{and one particularly has the estimate }
  0 < y(n; n_0, \bar{y}) \leq \bar{y} \prod_{j=n_0}^{n-1} e^{c_j} \quad \text{for all } n \geq n_0, \bar{y} > 0. \tag{4.2}
  \]

As for the Beverton-Holt equation \( \text{(BH)} \) we obtain for \( \mathbb{I} = \mathbb{Z} \) from Thm. 2.2:

- The nonautonomous set \( \mathcal{Y} := \left\{ (n, y) \in \mathbb{Z} \times \mathbb{R} : 0 \leq y \leq \frac{e^{c_n - 1}}{e} \right\} \) is forward invariant and pullback absorbing w.r.t. \( (R) \).
- The set \( \mathcal{Y}_n^{+} \) of all bounded entire solutions to \( (R) \) is invariant, compact, connected, it pullback attracts bounded subsets of \( \mathbb{Z} \times \mathbb{R}_+ \), and satisfies \( \mathcal{Y}_n^{+} \subseteq \mathcal{Y} \).

Nevertheless, since \( (R) \) fails to be order-preserving in general (see Fig. 4.1) the dynamics inside of \( \mathcal{Y}_n^{+} \) might be chaotic (cf. [25]).

### 4.1. Pullback attractor of \( (R) \)

For the autonomous Ricker equation

\[
y_{n+1} = g(y_n), \quad g(y) := ye^{c_n-y} \tag{R'}
\]
with the right-hand side \( g : \mathbb{R}_+ \to [0, e^{\gamma-1}] \) the nontrivial equilibrium \( \gamma \) is asymptotically stable for \( \gamma \in (0, 2) \). Then one observes a flip bifurcation into a 2-periodic orbit, as \( \gamma \) crosses the critical value 2. For \( \gamma = 2 \) the right-hand side \( g \) of (R') has a negative Schwarzian \( Sg(2) = -1 \) and [6, p. 479, Thm. A.4] implies that \( \gamma = 2 \) is still an asymptotically stable fixed point of (R'). Moreover, as \( \gamma \) increases through 1, monotonicity of the solutions is lost. We observe that the pullback attractor is

\[
\mathcal{Y}^*_\gamma = \begin{cases} 
Z \times [0, \gamma], & \gamma \in (0, 1], \\
Z \times [0, \frac{c^\gamma}{e}], & \gamma > 1
\end{cases}
\]

and at least for \( \gamma \leq 1 \) every solution starting in \( (0, \gamma) \) is a strictly increasing heteroclinic connection between the fixed points 0 and \( \gamma \).

We now approach the corresponding nonautonomous problem:

**Lemma 4.1.** If \( \sup_{n \in \mathbb{N}} c_n \leq 1 \), then the Ricker equation (R) is order preserving on the forward invariant set \( \mathbb{I} \times [0, 1] \) and its forward solutions satisfy

\[
y_1 < y_2 \Rightarrow y(n; n_0, \tilde{y}_1) < y(n; n_0, \tilde{y}_2) \quad \text{for all } n_0 \leq n, \tilde{y}_1, \tilde{y}_2 \in [0, 1].
\]

**Proof.** Due to \( c_n \leq 1 \) one has \( e^{c_n-1} \leq 1 \) for all \( n \in \mathbb{I} \) and (4.1) implies that the set \( \mathbb{I} \times [0, 1] \) is forward invariant w.r.t. (R). Moreover, \( g_{n, [0,1]} \) is strictly increasing and consequently the forward solutions are order-preserving.

**Theorem 4.2.** Let \( \mathbb{I} = \mathbb{Z} \). The pullback attractor of the Ricker equation (R) is

\[
\mathcal{Y}^*_c = \begin{cases} 
\{(n, y) : 0 \leq y \leq \eta^*_n\}, & \sup_{n \in \mathbb{Z}} c_n \leq 1, \\
\{(n, y) : 0 \leq y \leq e^{c_n-1} - \epsilon\}, & 1 \leq \inf_{n \in \mathbb{Z}} c_n
\end{cases}
\]

with the pullback solution \( \eta^*_n \) given by

\[
\eta^*_n := \lim_{k \to -\infty} y(n; k, 1) \quad \text{for all } n \in \mathbb{Z}.
\]

**Proof.** (I) First, we note that \( c_n \leq 1 \) implies the inclusion \( \mathcal{Y} \subseteq \mathbb{Z} \times [0, 1] \) and Lemma 4.1 guarantees that also \( \mathbb{Z} \times [0, 1] \) is forward invariant and pullback absorbing. Moreover, the dynamical characterization of the pullback attractor as the set consisting of all bounded entire solutions implies \( \mathcal{Y}^*_c = \omega_{\mathcal{Y}} = \omega_{\mathbb{Z} \times [0, 1]} \). Finally, because (R) is order preserving in \( \mathbb{Z} \times [0, 1] \), the claim results from Cor. A.4.

(II) In the complementary situation \( c_n \geq 1 \) for all \( n \in \mathbb{Z} \), the pullback absorbing set \( \mathcal{Y} \) turns out to be invariant. Hence, Cor. A.2 implies the claim.

Although for time-varying coefficients \( c_n \) no nontrivial equilibrium of (R) exists, Thm. 4.2 shows that \( \mathcal{Y}^*_c \) has a similar structure as in the autonomous situation, namely

\[
\mathcal{Y}^*_c = \{(n, y) : 0 \leq y \leq \eta^*_n\}
\]

with an entire bounded solution \( \eta^*_n \) to (R) — at least in case \( c_n \leq 1 \). Let us next show that the pullback solution \( \eta^*_n \) from (4.3) remains well-defined for a larger parameter regime, without essentially weakening its attraction properties.

This requires to introduce the Lambert-W-function \( W : [-e^{-1}, \infty) \to [-1, \infty) \), i.e. the inverse of \( x \mapsto xe^x \) restricted to \( [-1, \infty) \).

**Lemma 4.3.** If the sequence \( c_1 \) satisfies (cf. Fig. 4.2 (left))

\[
\tilde{y} := 1 - W(e^{-1}) \leq \min \left\{ c_n, g_n \left( \frac{e^{c_n-1}}{e} \right) \right\} \quad \text{for all } n \in \mathbb{I},
\]

then...
then the following holds true:

(a) \( (R) \) possesses a forward invariant nonautonomous set

\[
\tilde{Y}_c := \left\{ (n, y) : \tilde{y} \leq y \leq \max \left\{ 1, \frac{e^{c_n - 1}}{e} \right\} \right\}
\]

(b) For all \( \bar{n} \in \mathbb{I} \) and \( \bar{y}_1, \bar{y}_2 \in \tilde{Y}_c(\bar{n}) \) one has

\[
|y(n; \bar{n}, \bar{y}_1) - y(n; \bar{n}, \bar{y}_2)| \leq \left( \prod_{j=\bar{n}}^{n-1} e^{c_j-2} \right) |\bar{y}_1 - \bar{y}_2| \quad \text{for all } n \leq \bar{n}.
\]

For a proof we refer to Appendix C.

For a proof we refer to Appendix C.

Having Lemma 4.3 at hand, the uniform bounds on \( c_Z \) in Thm. 4.2 can be weakened for the price of a smaller domain of attraction.

**Proposition 4.4.** Let \( \mathbb{I} = \mathbb{Z} \). If \( c_Z \) satisfies (4.4) and \( \prod_{j=-\infty}^{n_0-1} e^{c_j-2} = 0 \) holds for some \( n_0 \in \mathbb{Z} \), then the pullback solution \( \eta_Z^* \) given in (4.3) solves \( (R) \) and pullback attracts the nonautonomous set \( \tilde{Y}_c \).

**Proof.** For each fixed \( n \in \mathbb{Z} \) our assumptions combined with

\[
|y(n; k_1, 1) - y(n; k_2, 1)| = |y(n; k_1, 1) - y(n; k_1, y(k_1; k_2, 1))| 
\]

(4.5)

\[
\leq \left( \prod_{j=k_1}^{n-1} e^{c_j-2} \right) |1 - y(k_1; k_2, 1)|
\]

for all \( k_2 \leq k_1 \leq n \) (resp. an analogous estimate for \( k_1 \leq k_2 \leq n \)) readily yield that \((y(n; k, 1))_{k \leq n}\) is a Cauchy sequence in the complete space \( \tilde{Y}_c(n) \) and thus convergent. Hence, by Thm. A.1 the sequence \( \eta_Z^* \) solves \( (R) \). Moreover, (4.5) also implies that \( \tilde{Y}_c \) is pullback attracted by \( \eta_Z^* \).

In Fig. 4.3 we depicted the absorbing set \( \tilde{Y}_c \) and the entire bounded solution \( \eta_Z^* \) for different sequences \( c_Z \) fulfilling the assumptions of Prop. 4.4. Again it is indicated that structural properties of \( c_Z \) (constancy, periodicity, etc.) get transferred to the absorbing set and the pullback solution \( \eta_Z^* \).
Fig. 4.3. The pullback absorbing sets $\tilde{Y}_c$ (blue shaded) containing the entire solutions $y_{n}^c$ (red dots) for sequences $c_n \equiv \frac{3}{2}$ (top left); $c_n = \frac{3}{2} + \frac{1}{2} \sin \frac{\pi n}{5}$ (10-periodic, top right); $c_n = 2$ ($n < 20$) and $c_n = 1$ ($n \geq 20$, bottom left); $c_n = \frac{3}{2} + \frac{1}{2}r_n$ ($r_n \in [-1,1]$ randomly chosen, bottom right).

For 200 starting points $y_{0}^i$, $i = 1, \ldots, 200$, we computed the maximal distance between corresponding forward orbits $e_n := \max_{i,j=1,\ldots,200} |y(n,0,y_{0}^i) - y(n,0,y_{0}^j)|$ in Fig. 4.4. In addition, parameter sequences are considered that (on purpose) do not satisfy the assumptions of Lemma 4.3. The convergence of these solutions towards each other in case (b) and (c) indicates that (4.4) might be of technical nature.

Another possibility to obtain entire solutions to (R) in the pullback attractor $Y^c_*$ follows from a perturbation argument: For $\gamma \neq 2$ the nontrivial equilibrium $\gamma$ of the autonomous equation $(R')$ persists as an entire bounded solution to (R) locally. Quantitatively one has
Theorem 4.5. Suppose that $I = \mathbb{Z}$, $\gamma \neq 2$ and choose $\nu \in (0, 1)$. If $\varepsilon, \rho > 0$ fulfill
\[
\frac{2e^\gamma}{|\gamma - 2|} e^{2\rho} - \frac{1}{\rho} \left( \rho + \frac{\varepsilon}{2} \right) \leq \nu, \quad \frac{2\rho}{|\gamma - 2|} (1 + e^{\gamma + \rho}) \leq \varepsilon(1 - \nu),
\]
then for every parameter sequence $c \in \mathbb{Z}$ satisfying $\sup_{n \in \mathbb{Z}} |c_n - \gamma| < \rho$ there exists a unique bounded solution $\eta$ of $(R)$ such that $\sup_{n \in \mathbb{Z}} |\eta_n - \gamma| < \varepsilon$.

The interested reader will find a proof in Appendix C.

4.2. Flip bifurcation. Standard results (cf. [32, p. 244, Thm. 3.1]) guarantee a flip bifurcation for the autonomous equation $(R')$, i.e. the nontrivial equilibrium $\gamma$ bifurcates into an asymptotically stable 2-periodic solution for parameters $\gamma > 2$.

To obtain an impression of the behavior in the critical and nonhyperbolic situation $\gamma = 2$, we now investigate the autonomous $(R')$ under time-varying perturbations
\[y_{n+1} = y_ne^{c_n(\gamma)} - y_n\]
and suppose the parameter sequence is given as
\[c_n(\gamma) := \gamma + \varepsilon \gamma_n \quad \text{for all } n \in I,
\]
with a bounded sequence $\gamma_n$ and a real $\varepsilon \geq 0$. Even in this perturbed autonomous situation the basic problem arises that established nonautonomous bifurcation results (cf., e.g., [23, 31]) require a whole family (parametrized by $\gamma$) of bounded entire solutions $\eta(\gamma)$ along which the bifurcation occurs with $\varepsilon = 0$ and $\eta(0) = \gamma$.

Numerically, we can approximate such bounded solutions $\eta(\gamma)$ by solving the $(n_+ - n_- + 1)$-dimensional nonlinear boundary value problem
\[
F\begin{pmatrix}
y_{n_-} \\
\vdots \\
y_{n_+}
\end{pmatrix} := \begin{pmatrix}
y_{n_-+1} - y_{n_-} e^{c_{n_-}(\gamma)} - y_{n_-} \\
\vdots \\
y_{n_+} - y_{n_+1} e^{c_{n_+1}(\gamma)} - y_{n_+1} - b(y_{n_-}, y_{n_+})
\end{pmatrix} = 0,
\]
with periodic boundary operator $b(y_{n_-}, y_{n_+}) := y_{n_+} - y_{n_-}$. For this task, we apply Newton’s method and note that the derivative $F'$ has a sparse structure, which allows efficient computations. Assuming hyperbolicity (i.e. an exponential dichotomy of the variational equation) it turns out that approximation errors decay exponentially fast towards the midpoint of the finite interval, see [15].

With $\gamma_n \in [-1, 1]$ chosen randomly, let us illustrate the accordingly computed bounded trajectories $\eta(\gamma)_1$ in Fig. 4.5 for $\varepsilon = 0$ (left, autonomous case) and $\varepsilon = 0.02$ (right). The dichotomy spectrum of the corresponding linearization
\[y_{n+1} = (1 - \eta_n(\gamma)) e^{c_n(\gamma)} - \eta_n(\gamma) y_n\]
is illustrated in Fig. 4.6.
2-periodic solutions

\[
\begin{align*}
\text{Fig. 4.5. Bounded trajectories of the Ricker model (R_{\gamma}) for } & \epsilon = 0 \text{ (left) and } \epsilon = 0.02 \text{ (right).} \\
\text{Fig. 4.6. Dichotomy spectrum for the gray trajectories from Fig. 4.5 for parameters } & \epsilon = 0 \text{ (left) and } \epsilon = 0.02 \text{ (right).}
\end{align*}
\]

Thus, we observe that the autonomous flip bifurcation in (R') at \( \gamma = 2 \) turns into a “nonautonomous flip bifurcation” in (R_{\gamma}) given perturbation strengths \( \epsilon > 0 \).

**Remark 4.6 (nonautonomous flip bifurcation).** Once a reference solution branch \( \eta(\gamma) \) is known in a neighborhood of \( \gamma = 2 \), a nonautonomous flip bifurcation can be approached analytically as follows: As in the autonomous situation, where a period doubling means a pitchfork bifurcation in the second iterate of (R'), one introduces the equation of perturbed motion

\[
y_{n+1} = (y_n + \eta_n(\gamma))e^{c_n(\gamma)} - y_n - \eta_n(\gamma) =: \hat{g}_n(y_n, \gamma)
\]

and applies nonautonomous bifurcation criteria from [23, 31] to the difference equation

\[
y_{n+1} = G_n(y_n, \gamma), \quad G_n(y, \gamma) := \hat{g}_{n+1}(\hat{g}_n(y, \gamma), \gamma)
\]

near \( \gamma = 2 \). Due to the tedious computations we skip the details here.

Before addressing forward convergence of solutions, let us illustrate that the trivial solution to (R) can be both pullback attracting and unstable simultaneously:

**Example 4.7.** Let \( I = \mathbb{Z} \). For the sequence

\[
c_j := \begin{cases} 
\ln \frac{j+1}{j}, & j < -1, \\
\ln 2, & j \geq -1
\end{cases}
\]

of positive coefficients, we obtain from (4.2) the limit relation

\[
0 < y(n; n_0, \bar{y}) \leq \bar{y} \prod_{j=n_0}^{n-1} e^{c_j} = \frac{n}{n_0} \rightarrow 0 \quad \text{for all } n < -1, \ \bar{y} > 0
\]

and therefore it is \( Y^* = \mathbb{Z} \times \{0\} \). However, due to \( \beta(e^{\hat{g}_n}) = \beta(e^{\hat{g}_n}) = 2 \) our Thm. 2.1(b) implies that 0 is unstable.
4.3. **Forward behavior.** Concerning the forward dynamics of the Ricker equation (R), Thm. 2.1(b) implies that the trivial solution is unstable, provided \( \beta(e^c) > 1 \).

One readily deduces a criterion for asymptotic equivalence of all forward solutions.

**Proposition 4.8.** Under the assumptions
\[
\liminf_{n \to \infty} c_n > 0, \quad \limsup_{n \to \infty} c_n < \ln 2 + 1 \approx 1.30
\]

all nontrivial forward solutions to (R) fulfill
\[
\lim_{n \to \infty} \left( y(n; \bar{n}, \bar{y}_2) - y(n; \bar{n}, \bar{y}_1) \right) = 0 \quad \text{for all } \bar{n} \in \mathbb{I}, \bar{y}_1, \bar{y}_2 > 0.
\]

**Proof.** The right-hand side \( g_n \) of (R) is strictly increasing in \([0, 1]\) and strictly decreasing on \([1, \infty)\). At \( y = 1 \) it achieves its global maximum \( e^{c_n-1} \).

(I) Thanks to \( c_* := \liminf_{n \to \infty} c_n > 0 \) we can choose
\[
\eta \in \left(0, \min\{c_*, 2e^{-2}\}\right)
\]
and get an \( N_1 \in \mathbb{I} \) such that \( c_n \geq \eta \) for all \( n \geq N_1 \). This implies \( g_n(\eta) = \eta e^{c_n-\eta} \geq \eta \), as well as \( \eta \leq \eta e^{c_n} \leq 2e^{c_n-2} = g_n(2) \leq g_n(2-\eta) \), since \( g_n \) decreases on the closed interval \([1, 2]\). Due to \( c_* := \limsup_{n \to \infty} c_n < \ln 2 + 1 \) we can furthermore choose \( \eta > 0 \) so small that \( c_n < \ln(2 - \eta) + 1 \) holds for almost all \( n \in \mathbb{I} \), say for every \( n \geq N_2 \). Consequently, it is \( g_n(y) \leq e^{c_n-1} < 2 - \eta \) for all \( y \geq 0 \) and we arrive at the inclusion
\[
g_n([\eta, 2 - \eta]) \subseteq [\eta, 2 - \eta] \quad \text{for all } n \geq \max\{N_1, N_2\}.
\]

(II) For every \( y \in [\eta, 2 - \eta] \) we obtain
\[
\left| \frac{g'(y)}{g_n(y)} \right| = \left| \frac{1 - y}{y} \right| = \frac{|1 - y|}{y} \leq \frac{|1 - \eta|}{\eta} \quad \text{for all } y \in [\eta, 2 - \eta]
\]
and according to [22, Lemma 2.1] the mappings \( g_n \) are \([1 - \eta]\)-cave functions. Now because of the estimate \(|1 - \eta| < 1\) we obtain from [22, Thm. 3.2(ii)] that
\[
\lim_{n \to \infty} |y(n; \bar{n}, \bar{y}_1) - y(n; \bar{n}, \bar{y}_2)| = 0 \quad \text{for all } \bar{n} \geq \max\{N_1, N_2\}
\]
and \( \bar{y}_1, \bar{y}_2 \in [\eta, 2 - \eta] \). Since the Ricker equation (R) is permanent (cf. [34]), every forward solution to (R) eventually enters an interval \([\eta, 2 - \eta]\) with sufficiently small \( \eta > 0 \). Hence, the above limit relation even holds for all \( \bar{n} \in \mathbb{I} \) and \( \bar{y}_1, \bar{y}_2 > 0 \).

An alternative condition on \( c_\circ \) for asymptotic equivalence of all solutions is

**Proposition 4.9.** If \( c_\circ \) satisfies (4.4) and \( \prod_{j=n_0}^{\infty} e^{c_j-2} = 0 \) for some \( n_0 \in \mathbb{I} \), then
\[
\lim_{n \to \infty} \left( y(n; \bar{n}, \bar{y}_1) - y(n; \bar{n}, \bar{y}_2) \right) = 0 \quad \text{for all } \bar{n} \in \mathbb{I}, \bar{y}_1, \bar{y}_2 > 0.
\]

**Remark 4.10.** The limit relation \( \prod_{j=n_0}^{\infty} e^{c_j-2} = 0 \) always holds in the setting of Prop. 4.8. Indeed, even if \( c_* := \limsup_{n \to \infty} c_n < 2 \), then there exists a \( N \in \mathbb{I} \) such that \( c_n < \frac{e^{c_*-2}}{2} < 2 \) for all \( n \geq N \) and consequently \( \prod_{j=n_0}^{\infty} e^{c_j-2} = 0 \).

**Proof.** Since \( \prod_{j=n_0}^{\infty} e^{c_j-2} = 0 \) implies \( \prod_{j=n}^{\infty} e^{c_j-2} = 0 \) for all \( \bar{n} \in \mathbb{I} \), it suffices to restrict to initial times \( \bar{n} = n_0 \). Then, in case \( \bar{y}_1, \bar{y}_2 \in \mathbb{Y}(n_0) \) the proof follows immediately from Lemma 4.3(b).
Let \( \tilde{y}_1, \tilde{y}_2 > 0 \). If the parameter sequence \( c_l \) satisfies \( \lim_{n \to \infty} c_n = \tilde{y} \), then both solutions converge towards the asymptotic fixed point \( \tilde{y} \). Otherwise, there is an \( N(\tilde{y}_1, \tilde{y}_2) \in I \) such that \( y(n; n_0, \tilde{y}_1), y(n; n_0, \tilde{y}_2) \in \bar{\mathcal{Y}}_c(n_0) \) for all \( n \geq N(\tilde{y}_1, \tilde{y}_2) \) and the claim follows from Lemma 4.3(b).

Corollary 4.11. Let \( I = \mathbb{Z} \). If the sequence \( c_Z \) satisfies (4.4) and
\[
\prod_{j=-\infty}^{n_0-1} e^{c_{\tilde{y}}-2} = \prod_{j=n_0}^{\infty} e^{c_{\tilde{y}}-2} = 0 \quad \text{for some} \ n_0 \in \mathbb{Z},
\]
then one has the limit relation \( \lim_{n \to \infty} (y(n; n_0, \tilde{y}) - \eta_{n_0}^c) = 0 \) for all \( \tilde{y} \in \bar{\mathcal{Y}}_c(n_0) \).

Proof. Set \( \tilde{y}_1 := \tilde{y} \) and \( \tilde{y}_2 := \eta_{n_0}^c \) in (4.5).

4.4. Summary. For the Ricker model we found criteria on the environment (i.e. the parameters) to prevent extinction. Due to more complicated and for some parameters chaotic dynamics even in the autonomous case, our understanding of the Ricker equation (R) is less complete and partially based on numerical tools. Yet, we describe the pullback attractor under uniform conditions on the coefficients \( c_Z \) yielding monotonicity. Without them we can establish a pullback attracting solution \( \eta_{n_0}^c \) ad hoc and compute its domain of attraction (cf. Fig. 4.3) under further (technical) assumptions. In Thm. 4.5 explicit estimates for the robustness of the autonomous behavior under temporal fluctuations are given. A bifurcation analysis in the nonautonomous model requires the computation of entire solutions, replacing fixed points from the autonomous world. The latter are approximated numerically (see [11, 15]), and Fig. 4.5 indicates persistence of a flip bifurcation under moderately fluctuating parameters. Summability conditions on \( c_Z \) also imply forward convergence towards \( \eta_{n_0}^c \).

5. Global Dynamics. In this section, we tackle the planar system \((\Delta)\) to obtain information on its global dynamics. Above all, the first (and biologically relevant) quadrant \( \mathbb{R}_+^2 \) is forward invariant w.r.t. \((\Delta)\), i.e. each mapping \( F_n : \mathbb{R}_+^2 \to \mathbb{R}_+^2 \), \( n \in \mathbb{I} \), is well-defined. As above, \( \varphi = (\varphi_1, \varphi_2) \) is the general solution of \((\Delta)\).

5.1. Pullback attractor. Lemma 5.1. For \( \mathbb{I} = \mathbb{Z} \) the nonautonomous set
\[
\mathcal{A} := \{(n, x, y) \in \mathbb{R}^2 : 0 \leq x \leq a_{n-1}, 0 \leq y \leq \frac{e^{c_n-1}}{e}\}
\]
is forward invariant and pullback absorbing w.r.t. \((\Delta)\).

Proof. For arbitrary reals \( x, y \geq 0 \) one has
\[
0 \leq \frac{a_n x}{1 + x + b_n y} \leq \frac{a_n x}{1 + x} \leq a_n, \quad 0 \leq ye^{c_n-a_n x-y} \leq ye^{c_n-y} \leq \frac{e^{c_n}}{e}
\]
and thus the right-hand side of \((\Delta)\) satisfies \( F_n(\mathbb{R}_+^2) \subseteq \mathcal{A}(n+1) \) for \( n \in \mathbb{I} \). By means of (5.1), induction yields \( \varphi(n; n_0, \mathbb{R}_+^2) \subseteq \mathcal{A}(n) \) for \( n_0 < n \) and \( \mathcal{A} \) is pullback absorbing. In particular, \( F_n(\mathcal{A}(n)) \subseteq \mathcal{A}(n+1) \) and consequently \( \mathcal{A} \) is also forward invariant.

Theorem 5.2 (pullback attractor for \((\Delta)\)). If \( \mathbb{I} = \mathbb{Z} \), then the set \( \mathcal{A}^\star \) of all bounded entire solutions to \((\Delta)\) is invariant, compact, connected, it pullback attracts every bounded nonautonomous subset of \( \mathbb{Z} \times \mathbb{R}_+^2 \) and satisfies \( \mathcal{A}^\star \subseteq \mathcal{A} \).

Proof. On the basis of Lemma 5.1 the proof follows along the lines of Thm. 2.2 applying the corresponding results from [26].

Since both coordinate axes are forward invariant w.r.t. \((\Delta)\), the nonautonomous set \( \mathcal{A}^\star \) contains the pullback attractors \( \mathcal{X}_d^\star \) of (BH) and \( \mathcal{Y}_c^\star \) of (R) in the sense that
\[
\mathcal{X}_d^\star \times \{0\} \subseteq \mathcal{A}^\star, \quad \{0\} \times \mathcal{Y}_c^\star \subseteq \mathcal{A}^\star
\]
and also $\mathbb{Z} \times \{(0,0)\} \subseteq \mathcal{A}^*$.

**Lemma 5.3.** For all $\xi, \eta \geq 0$ one has the estimates

\begin{align*}
0 \leq \varphi_1(n; n_0, \xi, \eta) \leq x(n; n_0, \xi) & \quad \text{for all } n_0 \leq n, \\
0 \leq \varphi_2(n; n_0, \xi, \eta) \leq \frac{\epsilon_n}{\epsilon} & \quad \text{for all } n_0 < n.
\end{align*}

**Proof.** The second estimate is essentially a consequence of the forward invariance of $\mathcal{A}$ shown in Lemma 5.1. The first estimate follows by induction: It obviously holds for $n = n_0$. Concerning the induction step $n \rightarrow n + 1$ one has

\[
0 \leq \varphi_1(n + 1; n_0, \xi, \eta) = \frac{a_n \varphi_1(n; n_0, \xi, \eta)}{1 + \varphi_1(n; n_0, \xi, \eta) + b_n \varphi_2(n; n_0, \xi, \eta)} \leq f_n(\varphi_1(n; n_0, \xi, \eta)) \leq f_n(x(n; n_0, \xi)) = x(n + 1; n_0, \xi),
\]

since $f_n$ is strictly increasing, and this completes the proof. \[\blacksquare\]

Our following result is a criterion ensuring that the pullback behavior of the planar difference equation $(\Delta)$ is dominated by the Ricker dynamics of $(R)$:

**Theorem 5.4.** Let $\mathbb{I} = \mathbb{Z}$. If $\prod_{j=-\infty}^{n_0-1} a_j = 0$ for a $n_0 \in \mathbb{Z}$, then $\mathcal{A}^* = \{0\} \times \mathcal{Y}^*_c$.

**Proof.** The set $\{0\} \times \mathcal{Y}^*_c$ is closed and a combination of Lemma 5.3 with (3.7) shows that $\{0\} \times \mathcal{Y}^*_c$ is pullback attracting. Then [26, p. 19, Thm. 1.3.9(b)] implies $\mathcal{A}^* \subseteq \{0\} \times \mathcal{Y}^*_c$ and the claim follows together with (5.2). \[\blacksquare\]

**Lemma 5.5.** Let $\mathbb{I} = \mathbb{Z}$. If $\sup_{n \in \mathbb{Z}} c_n \leq 1$, then $(\Delta)$ is order-preserving (w.r.t. the south-east cone $C := \mathbb{R}^+_c \times (-\infty, 0 \right) \mathbb{Z}$) on the forward invariant and pullback absorbing set $\mathcal{A}_0 := \{(n, x, y) \in \mathbb{Z} \times \mathbb{R}^+_c : x \leq a_{n-1}, y \leq 1\}$.

**Remark 5.6.** In the terminology of [33], Lemma 5.5 shows that $(\Delta)$ is competitive on $\mathcal{A}_0$.

**Proof.** The estimates (5.1) imply that $\mathcal{A}_0$ is forward invariant and as a superset of $\mathcal{A}$, by Lemma 5.1 also pullback absorbing. Thus, $(\Delta)$ defines a difference equation in the nonautonomous set $\mathcal{A}_0$. With arbitrary pairs $(x, y) \in C$ we derive

\[
F^\nu_n(\xi, \eta) \left(\begin{array}{c} x \\ y \end{array}\right) = \left(\begin{array}{c}
-\frac{a_n b_n \xi}{(1 + \xi + b_n \eta)} \\
-\frac{a_n b_n \eta - d_n e_n^\nu_a - d_n \xi - n}{(1 + \xi + b_n \eta)}
\end{array}\right) \left(\begin{array}{c} x \\ y \end{array}\right) \in C
\]

for all $n \in \mathbb{I}$ and $\xi \geq 0, \eta \in [0, 1]$. Therefore, the derivative $F^\nu_n(\xi, \eta)$ is positive (w.r.t. the cone $C$) and the criterion [10, Lemma 2.2] ensures that $F^\nu_n|_{\mathcal{A}_0(n)}$ is order-preserving. \[\blacksquare\]

**Theorem 5.7.** Let $\mathbb{I} = \mathbb{Z}$. If $\sup_{n \in \mathbb{Z}} c_n \leq 1$, then the pullback attractor of $(\Delta)$ fulfills

\[
\mathcal{A}^* \subseteq \left\{(n, \xi, \eta) \in \mathbb{Z} \times \mathbb{R}^+_c : \xi \leq \lim_{k \to -\infty} x(n; k, a_{k-1}), \eta \leq \lim_{k \to -\infty} y(n; k, \frac{e^{k-1}}{\epsilon})\right\}.
\]

**Proof.** We use the terminology from the above proof of Lemma 5.5, where the south-east cone $C$ induces a partial ordering

\[
(x_1, y_1) \preceq (x_2, y_2) \iff x_1 \leq y_1 \text{ and } y_2 \leq y_1
\]
on $\mathbb{R}^2$. Let us apply Thm. A.3 to the sequences $(x_n, y_n) := (0, \frac{\epsilon_n}{\epsilon})$ and $(x_n^+, y_n^+) := (a_{n-1}, 0)$ satisfying $(x_n^+, y_n^+) \preceq (x_n, y_n)$ for all $n \in \mathbb{Z}$. The resulting set $\mathcal{A}_0$ is forward invariant and consequently Thm. A.3 yields the entire solutions

\[
\xi_n := \lim_{k \to -\infty} \varphi(n; k, (0, \frac{\epsilon_{k-1}}{\epsilon})) = \left(\lim_{k \to -\infty} \varphi(n; k, \frac{\epsilon_{k-1}}{\epsilon})\right),
\]

and the claim follows together with (5.2). \[\blacksquare\]
Lemma 4.3 allows the inclusion \( k \) w.r.t. (BH) and hence \( \lim_{n \to \infty} x(n; k, a_{k-1}) \) from Cor. A.4 we deduce the claimed inclusion
\[
\mathcal{A}^* \subseteq \left\{ (n, x, y) \in \mathbb{Z} \times \mathbb{R}^2_+ : \zeta_n^* \leq (x, y) \leq \zeta_n^+ \right\}
\]
and the proof is completed. \( \square \)

**Corollary 5.8.** If \( \prod_{j=-\infty}^{a_j} = \infty \) for a \( n_0 \in \mathbb{Z} \) and \( cz \) satisfies (4.4), then
\[
\mathcal{A}^* \subseteq \left\{ (n, x, y) \in \mathbb{Z} \times \mathbb{R}^2_+ : x \leq \zeta_n^*, y \leq \eta_n^* \right\}.
\]

**Proof.** On the one hand, by Lemma 3.2(a) we see that \( \zeta_n^* \) is pullback attracting w.r.t. (BH) and hence \( \lim_{k \to -\infty} x(n; k, a_{k-1}) = \zeta_n^* \) holds true for every \( n \in \mathbb{Z} \). On the other hand, because of \( c_n \leq 1 \) one has \( \prod_{j=-\infty}^{a_j} e^{-j} = 0 \) and the set \( \mathcal{Y}_e \) from Lemma 4.3 allows the inclusion \( (n, \frac{c^{n-1}}{e}) \in \mathcal{Y}_e \). By Prop. 4.4, in particular the sequence \( (n, \frac{c^{n-1}}{e}) \) is pullback attracted to \( \eta_n^* \) and thus \( \lim_{k \to -\infty} y(n; k, \frac{c_{n-1}}{e}) = \eta_n^* \) is satisfied for all \( n \in \mathbb{Z} \). \( \square \)

**5.2. Forward behavior.** Since the right-hand side of (\( \Delta \)) is globally bounded, we obtain that all its forward solutions are bounded and immediately contained in the invariant rectangle (cf. (5.1))
\[
[0, \sup_{n \in I} a_n] \times [0, e^{\sup_{n \in I} c_n - 1}].
\]

The subsequent results illustrate the role of the parameter \( a_I \) in the extinction of one species \( x \) or \( y \). Indeed, a Beverton-Holt equation (BH) with an attractive trivial solution (see Prop. 3.8) guarantees an asymptotically vanishing population \( x \) for (\( \Delta \)):

**Theorem 5.9 (extinction of \( x \)).** If \( \Phi_n(\cdot, n_0) \in \ell^\infty \) for a \( n_0 \in I \), then
\[
\lim_{n \to \infty} \text{dist} (\varphi(n; n_0, \bar{x}, \bar{y}), \emptyset \times \mathbb{R}_+) = 0 \quad \text{for all } \bar{x}, \bar{y} \geq 0.
\]

**Proof.** Thanks to Prop. 3.8 and Lemma 5.3 one has
\[
0 \leq \text{dist} (\varphi(n; n_0, \bar{x}, \bar{y}), \emptyset \times \mathbb{R}_+) = \varphi_1(n; n_0, \bar{x}, \bar{y}) \leq x(n; n_0, \bar{x}) \to 0 \quad \text{as } n \to \infty
\]
and therefore the claim. \( \square \)

On the other hand, sufficiently large values of \( a_I \) in comparison to \( c_I \) (cf. (5.4) for a concretization) yield to extinction of the \( y \)-species in the full equation (\( \Delta \)):

**Theorem 5.10 (extinction of \( y \)).** If there exists an \( s > 0 \) such that
\[
\limsup_{n \to \infty} e^{c_n} \max \left\{ \frac{1}{a_n^*} s, \left( \frac{1}{a_n^*} s \right)^{d_n^*} \right\} < 1,
\]
then \( \lim_{n \to \infty} \text{dist} (\varphi(n; n_0, \bar{x}, \bar{y}), \mathbb{R}_+ \times \emptyset) = 0 \) for all \( \bar{x}, \bar{y} > 0 \).
A proof is given in Appendix C.
Remark 5.11. If the sequence $b_1$ is eventually constant to a value $\beta > 0$, one can choose $s := \beta^{-1}$ and the condition (5.4) becomes

$$\limsup_{n \to \infty} \frac{e^{cn} a_s^n}{e^{c_n}} e^{d_n - \beta} < 1.$$  

For $b_1$ being eventually equal to $\delta > 0$, the choice $s := \delta$ allows to simplify (5.4) to

$$\limsup_{n \to \infty} \frac{e^{cn}}{e^{d_n} - \delta} < 1;$$

this is based on the fact that the functions $s \mapsto (sb_n)^s e^{b_n - s}$ and $s \mapsto (\frac{c_n}{n})^s e^{d_n - s}$ attain their global minimum 1 on $(0, \infty)$ for $s = b_n^{-1}$ resp. $s = d_n$.

5.3. Summary. After analyzing the dynamics of the two species separately, we continued by studying the complete interaction. A rough global analysis of the full nonautonomous system ($\Delta$) can be done analytically; it is dissipative and hence yields a pullback attractor. A partial insight into its structure is possible under a smallness condition on $n$, where the Ricker dynamics dominates and the $x$-population gets extinct, or a uniform bound on $c$, where monotonicity arguments apply. Under ambient assumptions the pullback attractor can be bounded inside a "nonautonomous rectangle" given by the previous reference solutions $\xi^*$ and $\eta^*$. Regarding forward convergence, conditions for the extinction of each species are given, where the $y$-variable situation requires a nonautonomous version of LaSalle's invariance principle.

6. Nonautonomous equilibria and stability. Our next objective is a more detailed understanding of the dynamics in the pullback attractor $A^*$ for ($\Delta$). The starting point for our investigations are the equilibria of the autonomous system ($\Delta'$) and their stability, especially with regard to their persistence when passing over to the full nonautonomous problem ($\Delta$). Since the corresponding linearizations are time-variant, it is well-known (cf., e.g., [6, p. 190, Ex. 4.17]) that eigenvalues in general do not yield stability information. Hence, the appropriate tools for stability investigations are the dichotomy spectrum and Bohl exponents (cf. [1, 14]); for readers unfamiliar with this concept, we have summarized some essential aspects in Appendix B. When dealing with Bohl exponents let us implicitly assume that the associated sequences have bounded inverses (cf. (B.1)).

We start our analysis with the trivial equilibrium and continue with increasingly more involved cases.

6.1. The trivial equilibrium. The trivial equilibrium $(0, 0)$ of ($\Delta$) exists for all parameter constellations and yields the linearization

$$F'_n(0, 0) = \begin{pmatrix} a_n & 0 \\ 0 & e^{c_n} \end{pmatrix}$$

in the variational equation ($V$). Since all $F'_n(0, 0)$ are diagonal, the dichotomy spectrum is the union of the spectra for the diagonal elements (cf. Prop. B.5), i.e.

$$\Sigma(0, 0) = [\beta(a_1), \beta(a_1)] \cup [\beta(c_1), \beta(c_1)].$$

Due to $1 \leq \beta(c_1)$ this offers the following possibilities for the local asymptotics of ($\Delta$) near the origin, i.e. the stability properties of the trivial solution (cf. Thm. 2.1):
In the Beverton-Holt-stable case $\beta(a_1) < 1 < \beta(e^{\alpha})$ it is unstable, despite the $x$-axis as stable direction. For $I = \mathbb{Z}$ the $y$-axis becomes the unstable fiber bundle and the origin is a saddle.

Finally, for $\min\{\beta(a_1), \beta(e^{\alpha})\} > 1$ it is unstable in form of a source.

### 6.2. The Beverton-Holt equilibrium

For a constant sequence $a_n \equiv \alpha > 0$ the difference equation $(\Delta)$ has the so-called Beverton-Holt equilibrium $(\alpha - 1, 0)$, which is only present for values $\alpha \geq 1$. The linearization

$$F_n^\alpha(\alpha - 1, 0) = \begin{pmatrix} \frac{1}{\alpha} & \frac{1 - \alpha b_n}{e^{\alpha n} - (\alpha - 1)d_n} \\ 0 & \end{pmatrix} \quad \text{for all } n \in I$$

is upper-triangular and yields the dichotomy spectrum

$$\Sigma(\alpha - 1, 0) = \begin{cases} \{ \frac{1}{\alpha} \} \cup [\beta(e^{\alpha - (\alpha - 1)d_1}), \overline{\beta}(e^{\alpha - (\alpha - 1)d_1})], & \alpha > 1, \\ \{ 1 \} \cup [\beta(e^\alpha), \overline{\beta}(e^\alpha)], & \alpha = 1. \end{cases}$$

On a semiaxis $I$ this holds due to Prop. B.5(a), because here the dichotomy spectrum is determined by the corresponding diagonal system, as well as for $I = \mathbb{Z}$, since one spectral interval is a singleton and therefore Prop. B.6(b) applies.

See Fig. 6.1 (left) for a visualization of $\Sigma(\alpha - 1, 0)$ for different $\alpha$: An intersection of the green and red shapes with a horizontal line indicates the spectrum $\Sigma(\alpha - 1, 0)$ for a particular value of $\alpha$. The red curve illustrates the singleton spectral interval $\{ \frac{1}{\alpha} \}$, while the green shape represents the interval $[\beta(e^{\alpha - (\alpha - 1)d_1}), \overline{\beta}(e^{\alpha - (\alpha - 1)d_1})]$.

![Fig. 6.1. The dashed vertical line indicates the stability boundary:](image)

**Left:** Dichotomy spectrum $\Sigma(\alpha - 1, 0)$ for $a_n \equiv \alpha \in [1.2]$ with $c_n := 1$ ($n \geq 0$), $c_n := 0.5$ ($n < 0$) and $b_n := 2 + \sin n$. It indicates uniform asymptotic stability for $\alpha > 1.5$.

**Right:** Dichotomy spectrum $\Sigma(\xi I, 0)$ for $d_n \equiv \delta$ in $[0.3]$ with $a_n := 2$ ($n \geq 0$), $a_n := 1.5$ ($n < 0$), $c_n := 1$ ($n \geq 0$), $c_n := 0.5$ ($n < 0$). It indicates uniform asymptotic stability for $\delta > 1$.

This allows the following choices determining the asymptotic behavior near the equilibrium $(\alpha - 1, 0)$ for varying $\alpha > 1$ (note $\frac{1}{\alpha} \in (0, 1)$):

- If $\beta(e^{\alpha - (\alpha - 1)d_1}) < 1$, then $(\alpha - 1, 0)$ is a uniformly asymptotically stable sink and the nonautonomous set $\mathbb{Z} \times \{ (\alpha - 1, 0) \}$ is a local pullback attractor for $(\Delta)$; a sufficient condition for this behavior is $\overline{\beta}(e^{\alpha}) < (\alpha - 1)\overline{\beta}(e^d)$. Hence, an unstable behavior is enforced by choosing the coupling sequence $c_1$ larger.

- If $1 < \beta(e^{\alpha - (\alpha - 1)d_1})$, then $(\alpha - 1, 0)$ becomes unstable with the $y$-axis as unstable direction, and for $I = \mathbb{Z}$ even a saddle. Due to Prop. B.1 a sufficient condition for this behavior is $(\alpha - 1)\overline{\beta}(e^d) < \beta(e^\alpha)$.

For time-varying coefficients $a_1$, the planar system $(\Delta)$ does not have an equilibrium on the $x$-axis anymore. Nonetheless, on the whole integer axis $I = \mathbb{Z}$ we
know from Sect. 3 that the Beverton-Holt equilibrium \((\alpha - 1, 0)\) persists as the entire bounded solution \((\xi, 0)\) given in Lemma 3.2. Stability of the corresponding entire solution \((\xi, 0)\) can be obtained from the variational equation (cf. (V))

\[
\begin{pmatrix}
x_{n+1} \\
y_{n+1}
\end{pmatrix} = F'_{n}(\xi, 0) \begin{pmatrix} x_n \\ y_n \end{pmatrix}, \quad F'_{n}(\xi, 0) = \begin{pmatrix} \frac{\alpha \xi}{1+\xi^2} & -\frac{\alpha \xi}{1+\xi^2} \\ \frac{\alpha \xi}{1+\xi^2} & \frac{\alpha \xi}{1+\xi^2} \end{pmatrix},
\]

(6.1)

where the dichotomy spectrum fulfills (cf. Prop. B.5 and Prop. B.6(b))

\[
\Sigma(\xi, 0) = \sigma_1 \cup \sigma_2, \quad \sigma_1 \cap \sigma_2 \text{ has no interior points},
\]

\[
\subseteq \sigma_1 \cup \sigma_2, \quad \text{otherwise}
\]

with the spectral intervals

\[
\sigma_1 := \left[ \beta \left( \frac{\alpha \xi}{(1+\xi^2)^2} \right), \beta \left( \frac{\alpha \xi}{(1+\xi^2)^2} \right) \right], \quad \sigma_2 := \left[ \beta \left( e^{-\xi} \right), \beta \left( e^{-\xi} \right) \right].
\]

Keeping the parameter sequence \(dz\) constant to the value \(\delta > 0\), Fig. 6.1 (right) visualizes \(\Sigma(\xi, 0)\) for different values of \(\delta\). The spectral intervals \(\sigma_1\) are in red, while \(\sigma_2\) are marked in green for varying \(\delta\).

Depending on the location of \(\sigma_1, \sigma_2 \subseteq (0, \infty)\) we also illustrated the stability properties of the Beverton-Holt solution \((\xi, 0)\) in Fig. 6.2. In particular, under the condition \(\max \Sigma(\xi, 0) < 1\) (this corresponds to Fig. 6.2(h1)) the nonautonomous set

\[
\{(n, \xi, 0) \in \mathbb{R} \times \mathbb{R}^2 : n \in \mathbb{Z}\}
\]

is a local pullback attractor of the planar equation \((\Delta)\), whereas \((\xi, 0)\) becomes unstable for \(\min \sigma_1 > 1\) or \(\min \sigma_2 > 1\) (see Fig. 6.2(h2) or (h3)).

More subtle are the nonhyperbolic situations described in Fig. 6.3. Provided there exists a gap between the spectral intervals \(\sigma_1\) and \(\sigma_2\) such that

\[
\max \sigma_1 < \min \sigma_2 \leq 1, \quad 1 \in \sigma_2
\]

(6.2)

(see Fig. 6.3(n1)), or with \(\sigma_1\) and \(\sigma_2\) exchanged, one can determine stability properties for \((\xi, 0)\) by means of a reduction to a center fiber bundle.

**Proposition 6.1** (reduced equation). Let \(I = \mathbb{Z}\). If

\[
\beta \left( \frac{\alpha \xi}{(1+\xi^2)^2} \right) < \beta \left( e^{-\xi} \right) \leq 1, \quad \beta \left( \frac{\alpha \xi}{(1+\xi^2)^2} \right) < \beta \left( e^{-\xi} \right)^2
\]

(6.3)
then the stability properties of the solution \((\xi_n^\ast,0)\) to the planar system \((\Delta)\) correspond to the stability of the trivial solution to the scalar equation (the reduced equation)

\[ y_{n+1} = e^{c_n - d_n \xi_n^\ast} \left( y_n - (1 + d_n t_n^\ast)g_n^2 + \frac{(1 + d_n t_n^\ast)^2 - d_n \omega_n}{2} g_n^3 + O(g_n^4) \right) \]  

(6.4)

uniformly in \(n \in \mathbb{Z}\) with

\[ t_n^\ast = -\sum_{j=-\infty}^{n-1} \frac{a_j b_j \xi_j^\ast e^{d_j \xi_j^\ast - c_j}}{(1 + \xi_j^\ast)^2} \prod_{i=j+1}^{n-1} \frac{a_i e^{d_i \xi_i^\ast - c_i}}{(1 + \xi_i^\ast)^2}, \]

\[ \omega_n = \sum_{j=-\infty}^{n-1} h_j \prod_{i=j+1}^{n-1} \frac{a_i e^{d_i \xi_i^\ast - 2c_i}}{(1 + \xi_i^\ast)^2} \]

and \(h_j := \frac{2 e^{d_j \xi_j^\ast - 2c_j} (a_j (b_j + t_j^\ast) e^{d_j \xi_j^\ast} (b_j \xi_j^\ast + t_j^\ast) + e^{d_j \xi_j^\ast + 1} (1 + \xi_j^\ast)^3 (d_j t_j^\ast + 1))}{(1 + \xi_j^\ast)^3}\).

A proof is given in Appendix C. However, note that a further analysis of the reduced equation (6.4) requires appropriate stability criteria for nonautonomous scalar difference equations with nonhyperbolic linear part.

6.3. The Ricker equilibrium. In the situation of a constant parameter sequence \(c_n \equiv \gamma\) the so-called Ricker equilibrium \((0, \gamma)\) to \((\Delta)\) is present for \(\gamma \geq 0\), yielding a variational equation \((V)\) with lower-triangular coefficient matrix

\[ F_n^\prime(0, \gamma) = \begin{pmatrix} \frac{a_n}{1 + \gamma d_n} & 0 \\ -\gamma d_n & 1 - \gamma \end{pmatrix}. \]

Reasoning as above, due to a singleton as spectral interval, the dichotomy spectrum is determined by the diagonal elements (cf. Prop. B.6 and B.1)

\[ \Sigma(0, \gamma) = \{ |1 - \gamma| \} \cup \left[ \beta \left( \frac{a_n}{1 + \gamma d_n} \right), \beta \left( \frac{a_n}{1 + \gamma d_n} \right) \right] \]

Consequently, \((0, \gamma)\) is unstable for \(\gamma > 2\) because of Thm. 2.1(b). A more detailed analysis of the Ricker equilibrium \((0, \gamma)\) reads as follows:

- For \(\gamma \in (0, 2)\) and \(\beta \left( \frac{a_n}{1 + \gamma d_n} \right) < 1\) it is a uniformly asymptotically stable sink.
- For \(\gamma \in (0, 2)\) and \(1 < \beta \left( \frac{a_n}{1 + \gamma d_n} \right)\) it is unstable and for \(\mathbb{I} = \mathbb{Z}\) even a saddle.
- If \(\gamma > 2\) and \(\beta \left( \frac{a_n}{1 + \gamma d_n} \right) < 1\), then \((0, \gamma)\) is unstable and for \(\mathbb{I} = \mathbb{Z}\) a saddle. Moreover, due to a flip bifurcation in \((R')\) at \(\gamma = 2\), there exists an asymptotically stable 2-periodic solution to \((\Delta)\) on the \(y\)-axis for small \(\gamma - 2 > 0\).
- If \(\gamma > 2\) and \(1 < \beta \left( \frac{a_n}{1 + \gamma d_n} \right)\) it is an unstable source. For \(\mathbb{I} = \mathbb{Z}\) the 2-periodic solution to \((\Delta)\) existing for small \(\gamma - 2 > 0\) becomes a saddle.

This analysis shows that a strong coupling, i.e., large values of the sequence \(b_j\) in \((\Delta)\), yield a stabilization of the Ricker equilibrium \((\gamma, 0)\). See Fig. 6.4 for an illustration of \(\Sigma(\gamma, 0)\) as a function of the parameter \(\gamma\). Here, the singleton spectral interval \(|1 - \gamma|\) is in red, while \(\left[ \beta \left( \frac{a_n}{1 + \gamma d_n} \right), \beta \left( \frac{a_n}{1 + \gamma d_n} \right) \right]\) is in green.
A NONAUTONOMOUS BEVERTON-HOLT RICKER MODEL

Fig. 6.4. Dichotomy spectrum $\Sigma(0, \gamma)$ for $c_n \equiv \gamma \in [0, 2.5]$ with $a_n := 1 + 0.5 \cos n$ and $b_n := 2$ ($n \geq 0$), $b_n := 1$ ($n < 0$). It indicates uniform asymptotic stability for $\gamma \in (0, 2)$.

For nonconstant sequences $c_n$, Sect. 4 provides conditions that the equilibrium $\gamma$ of (R') persists as the pullback solution $\eta^*_n$ for (R) given in (4.3). Hence, a similar stability analysis is possible for the solution $(0, \eta^*_n)$ to $(\Delta)$, as we have done it for the entire Beverton-Holt solution $(\xi^*_n, 0)$. In the hyperbolic case this is possible on basis of the dichotomy spectrum alone, while nonlinear effects (and thus a center-unstable fiber bundle) come into play, if a dominant spectral interval contains 1. We do not give the details.

Nonetheless, the basic difference to the above situation is that there exists no explicit expression for $\eta^*_n$ anymore. During the whole analysis one rather has to work with a numerical approximation for $\eta^*_n$.

6.4. The coexistence equilibrium. We restrict to the autonomous situation $(\Delta')$ first, where there exists a coexistence equilibrium $(\xi^*, \eta^*) := (\alpha - \beta \gamma - 1, \delta(1 - \alpha + \beta \gamma) + \gamma)$ for $\beta \delta \neq 1$. Thanks to [7, Lemma 5.1] we know that $\gamma < (\alpha - 1)\delta$ (yielding asymptotic stability of Beverton-Holt equilibrium) and $1 + \beta \gamma < \alpha$ (implying the Ricker equilibrium to be unstable) ensure that $(\xi^*, \eta^*)$ is not contained in $(0, \infty)^2$.

Due to the linearization

$$F'(\xi^*, \eta^*) = \frac{1}{1 - \beta \delta} \begin{pmatrix} \frac{\beta \gamma - \alpha \delta + 1}{\alpha} & \frac{\delta(1 - \alpha + \beta \gamma)}{\alpha} \\ \delta(\alpha \delta - \gamma - \delta) & 1 - \gamma - (1 - \alpha + \beta \delta) \end{pmatrix} \nonumber$$

nonhyperbolicity occurs in one of the three cases:

- $1$ is an eigenvalue of $F'(\xi^*, \eta^*)$. Since the remaining eigenvalue $\lambda$ fulfills
  $$\det F'(\xi^*, \eta^*) = \lambda, \quad \text{tr} F'(\xi^*, \eta^*) = 1 + \lambda,$$
  this form of nonhyperbolicity is given if and only if $\beta \gamma = \alpha - 1$ or $\alpha \delta = \gamma + \delta$, i.e. $(\xi^*, \eta^*)$ is contained in one of the coordinate axes.

- $-1$ is an eigenvalue of $F'(\xi^*, \eta^*)$. For the remaining eigenvalue $\lambda$ this means
  $$\det F'(\xi^*, \eta^*) = -\lambda, \quad \text{tr} F'(\xi^*, \eta^*) = -1 + \lambda$$
  and such a form of nonhyperbolicity occurs if and only if
  $$\alpha^2 \delta + \alpha \beta \gamma \delta - 4 \alpha \beta \delta - \alpha \gamma + 2 \alpha - \beta \gamma^2 - \beta \gamma \delta + 2 \beta \gamma - \gamma - \delta + 2 = 0.$$

- $F'(\xi^*, \eta^*)$ has a pair of complex-conjugated eigenvalues $\lambda, \bar{\lambda}$ of modulus 1. Consequently, the parameters have to satisfy
  $$1 = \det F'(\xi^*, \eta^*), \quad \text{tr} F'(\xi^*, \eta^*) = 2 \Re \lambda.$$
In the complimentary hyperbolic situation, the coexistence equilibrium \((\xi^*, \eta^*)\) of \((\Delta')\) will persist as an entire bounded solution \((\xi, \eta)(a, b, c, d)\in \mathbb{Z}\) to \((\Delta)\) satisfying
\[
\sup_{n\in \mathbb{Z}} \|(\xi, \eta)(a, b, c, d)_n - (\xi^*, \eta^*)(\alpha, \beta, \gamma, \delta)\| < \varepsilon,
\]
when the constant parameters \(\alpha, \beta, \gamma, \delta > 0\) are replaced by time-varying sequences \(a_n, b_n, c_n, d_n\) resp. \(n\in \mathbb{Z}\) (see [15, Lemma 2] or [28, Thm. 2.17] for details), if
\[
\sup_{n\in \mathbb{Z}} \max \{|a_n - \alpha|, |b_n - \beta|, |c_n - \gamma|, |d_n - \delta|\} < \rho
\]
for small \(\rho > 0\). In fact, as in Thm. 4.5 one can give an estimate for the size of \(\varepsilon, \rho > 0\). However, since this is essentially a technical extension of the proof for Thm. 4.5, we omit the details.

Finally, Fig. 6.5 illustrates the discussed equilibria in the autonomous setup (left) as well as corresponding bounded solutions for a nonautonomous choice of parameters.

Fig. 6.5. Left: Equilibria and trajectories starting nearby (in red) for \(\alpha = 1.5, \beta = 0.1, \gamma = \delta = 1\). Right: The corresponding nonautonomous diagram with randomly perturbed parameters.

The coexistence equilibrium \((\xi^*, \eta^*)\) of \((\Delta')\) is created via bifurcations from the two extinction equilibria \((\alpha - 1, 0)\) and \((0, \gamma)\). In the next section, we investigate to what extent this bifurcation scenario persists in the nonautonomous situation of \((\Delta)\).

6.5. Summary. We studied environmental conditions for extinction of one or of both species as well as for coexistence. A first attempt to understand the dynamics inside the pullback attractor of \((\Delta)\) is a local stability analysis of reference solutions, like for instance the trivial equilibrium or the extinction solutions \(\xi^*_n, \eta^*_n\) on the coordinate axes. Since the corresponding variational equations are nonautonomous, a classical eigenvalue analysis is useless. Thus, numerical methods to obtain their Bohl exponents and dichotomy spectrum are crucial (see [13, 14]). In the critical situation of a spectral interval touching or including the stability boundary \(1\), we illustrate that a center manifold reduction to a scalar difference equation (6.4) can be performed also in the nonautonomous case (see [30]). A central problem remains the coexistence equilibrium, which can be recaptured by means of numerical continuation schemes, e.g. starting with an autonomous equation and perturbing away for increasingly larger fluctuations. In Fig. 6.5 both the autonomous, as well as the numerically computed nonautonomous equilibria are given, together with heteroclinic trajectories connecting them (cf. [11, 15]).
7. Bifurcation. The above Sects. 3 and 4 provided a quite detailed insight on the dynamics of the nonautonomous Beverton-Holt equation (BH) resp. the Ricker equation (R) in terms of their attractors $\mathcal{A}^\beta_n$ and $\mathcal{Y}^\nu_c$. Thus, the uncoupled equations

\[
\begin{align*}
x_{n+1} &= \frac{a_n x_n}{1+x_n}, \\
y_{n+1} &= y_n e^{c_n - y_n}
\end{align*}
\]

simply form a product system and therefore its pullback attractor is $\mathcal{A}^* = \mathcal{A}^\beta_n \times \mathcal{Y}^\nu_c$. In particular, bifurcation phenomena in (BH) or (R) carry over to $\mathcal{A}^*$.

Another source yielding changes in the dynamics of (Δ) are the coupling sequences $b_n$ and $d_n$. For the sake of a bifurcation analysis, we restrict to the respective time-constant case $b_n \equiv \beta$ and $d_n \equiv \delta$ and interpret $\beta$ or $\gamma$ as bifurcation parameters.

7.1. Beverton-Holt entire solution. First, we investigate the behavior near the entire solution $(\xi^*_n, 0)$ to the planar difference equation

\[
\begin{align*}
x_{n+1} &= \frac{a_n x_n + b_n y_n}{1+x_n}, \\
y_{n+1} &= y_n e^{c_n - \delta x_n - y_n}
\end{align*}
\]

being a special case of (Δ) with constant coupling $d_n \equiv \delta$.

Let us interpret $\delta$ as bifurcation parameter to study the loss of stability in the Beverton-Holt solution $(\xi^*_n, 0)$ as the coupling strength $\delta$ changes. If we assume the estimate $\overline{\beta}(\frac{a_n}{1+\xi^*_n}) \leq \beta(e^{c_n-\delta^* \xi^*_n})$, then according to Prop. B.6 and following Sect. 6.2 the associate dichotomy spectrum reads as

\[
\Sigma(\xi^*_n, 0) = \left[\beta\left(\frac{a_n}{1+\xi^*_n}\right), \overline{\beta}\left(\frac{a_n}{1+\xi^*_n}\right)\right] \cup \left[\beta\left(e^{c_n-\delta^* \xi^*_n}\right), \overline{\beta}\left(e^{c_n-\delta^* \xi^*_n}\right)\right].
\]

From now on, we suppose that

\[
\overline{\beta}(\frac{a_n}{1+\xi^*_n}) < \beta\left(e^{c_n-\delta^* \xi^*_n}\right), \quad \overline{\beta}(e^{c_n-\delta^* \xi^*_n}) = 1
\]

holds for some critical value $\delta^* > 0$. A reduction to the center-unstable fiber bundle as in Sect. 6.2 yields that the bifurcation in (Δ) is determined by the scalar equation

\[
y_{n+1} = e^{c_n-\delta^* \xi^*_n} \left[(1 - (\delta - \delta^*) \xi^*_n) y_n - (1 + \delta^* \xi^*_n) y_n^2\right] + O((\delta - \delta^*)^2 y_n, (\delta - \delta^*) y_n^2, y_n^3)
\]

uniformly in $n \in \mathbb{Z}$. This indicates a transcritical bifurcation as $\delta$ decreases through the critical value $\delta^*$.

One can verify the spectral assumption (7.1) numerically with the algorithm from Appendix B.1. Let $\tau \in \{-0.05, 0.05\}^2$ be a uniformly distributed random sequence. For $n \in \mathbb{Z}$ we choose the parameters $a_n = r_n + 1.5$, $b_n = r_n + 0.1$, $c_n = r_n + 1$, $\delta = 2.5$ and obtain from our numerical experiments:

\[
\overline{\beta}(\frac{a_n}{1+\xi^*_n}) = 0.66771 < \beta(e^{c_n-\delta^* \xi^*_n}) = 0.77618, \quad \overline{\beta}(e^{c_n-\delta^* \xi^*_n}) = 0.78163.
\]

For $\delta^* = 2$ the assumptions (7.1) are approximately satisfied:

\[
\overline{\beta}(\frac{a_n}{1+\xi^*_n}) = 0.66771 < \beta(e^{c_n-\delta^* \xi^*_n}) = 0.99781, \quad \overline{\beta}(e^{c_n-\delta^* \xi^*_n}) = 1.00250.
\]

Note that neither the bounded Beverton-Holt trajectory $\xi^*_n$, nor the Ricker trajectory depend on $\delta$. For $\delta < 2$ a bounded coexistence trajectory exists, that bifurcates from
the Beverton-Holt and Ricker solution, respectively, see Fig. 7.1. The coexistence trajectory is attracting and can be computed via forward iteration, instead of solving boundary value problems as described in Section 4.2.

Fig. 7.1. Coexistence trajectories (cyan) for fixed $b_n = r_n + 0.1$ and various values of $\delta \in [0, 2]$ (left) and for fixed $\delta = 1$ and various values of $b_n = r_n + b$, $b \in [0, 1]$ (right).

7.2. Ricker equilibrium. Let us eventually investigate also the behavior of the Ricker equilibrium $(0, \gamma)$ to the planar difference equation

$$
\begin{align*}
x_{n+1} &= \frac{a_n x_n}{1 + x_n + y_n}, \\
y_{n+1} &= y_n e^{\gamma - d_n x_n - y_n},
\end{align*}
$$

(\Delta_b)

where $\gamma \in (0, 2)$ is assumed to be fixed from now on, while $\beta > 0$ will be considered as bifurcation parameter. Referring to Sect. 6.3 this yields the dichotomy spectrum

$$
\Sigma(0, \gamma) = \{|1 - \gamma|\} \cup \left[\frac{1}{1 + \gamma \beta}, \beta(aZ)\right]
$$

and the critical stability situation $\max \Sigma(0, \gamma) = 1$ precisely holds for the parameter $\beta^* = \beta(aZ) - 1/\gamma$. As $\beta$ passes through $\beta^*$ one can observe a subcritical shovel bifurcation (see [27, Thm. 3.15(a)]); this quite coarse bifurcation scenario precisely means

- For $\beta < \beta^*$ the additional assumption $\beta(aN) < 1 + \gamma \beta$ implies that $(0, \gamma)$ is asymptotically stable and, provided $\beta(aZ) = 1 + \gamma \beta^*$, embedded into a 1-parameter family of bounded entire solutions to $(\Delta_b)$.
- For $\beta = \beta^*$ the additional assumption $\beta(aN) < 1 + \gamma \beta^* = \beta(aZ)$ ensures $(0, \gamma)$ to be asymptotically stable.
- For $\beta > \beta^*$ the Ricker equilibrium is (locally) the unique bounded entire solution to $(\Delta_b)$ in a neighborhood of $(0, \gamma)$.

See Fig. 7.2 for the dichotomy spectra yielding a subcritical shovel bifurcation.

Fig. 7.2. Dichotomy spectra $\Sigma(0, \gamma)$ for $I = N$ (left), $I = Z$ (center) and $I = Z^-$ (right) for various values of $\beta \in [3, 5]$ with coefficients $a_n := 2 + \sin \ln(1 + n)$, $n > 0$ and $a_n := 5$ ($n \leq 0$), $\gamma = 0.9$, $d_n := 1 + 0.5 \sin n$ and consequently $\beta^* = \frac{40}{9}$. 
7.3. **Summary.** This section illustrated that coexistence of both species leads to extinction if the environment changes. Formally it is established that the (attractive) coexistence solution of (Δ) is created by means of a transcritical bifurcation either from the Beverton-Holt solution $\xi^*_Z$, or the Ricker solution $\eta^*_Z$ (cf. Fig. 7.1). Here, the critical bifurcation parameter has to be computed numerically. Being attractive, one conveniently obtains the coexistence solution using forward convergence, rather than solving a large boundary value problem as in the general hyperbolic situation (see [11, 15] for the general situation). The destabilization of the Ricker equilibrium can also be interpreted as a subcritical shovel bifurcation, an intrinsically nonautonomous phenomenon, where a family of bounded entire solutions collapses into an isolated equilibrium (cf. [27]).

8. **Conclusion.** We studied a two-species model from population dynamics, for which notably persistence was analyzed — first in a single species situation and then for the full system. It turned out that one has to carefully distinguish between forward and pullback dynamics. The pullback attractor could be bounded by the extinction equilibria of the decoupled system (see Thm. 5.7 and Cor. 5.8). Beyond that we were able to obtain information on the behavior inside the pullback attractor for (Δ) using a local stability analysis (even in the nonhyperbolic situation, cf. Prop. 6.1). Stability changes based on the dichotomy spectrum induced nonautonomous bifurcations. In detail, this enabled us to conclude that the coexistence equilibrium is created via nonautonomous transcritical bifurcations (see Fig. 7.1).

Let us point out that the machinery presented here is not limited to the particular model (Δ). Indeed, it applies to wide classes of nonautonomous systems and is not restricted to population dynamics. However, in contrast to a classical autonomous bifurcation analysis, where efficient numerical continuation software such as AUTO or MatCont is available, one is nowhere near this situation in a time-dependent set-up. This refers to both a numerical and an analytical level.

Yet, as punch lines one should keep in mind that

- Bounded solutions replace fixed points.
- Explicit inequalities for constant parameters are replaced by summability conditions on the parameter sequences.
- Pullback convergence requires to know the whole history of an equation.
- Stability theory is more subtle, since in the autonomous case various notions coincide. Due to its robustness, we advocate the use of uniform stability concepts and to work with the dichotomy, rather than the Lyapunov spectrum.

From a (biological) modeling perspective one might primarily be interested in forward behavior. However, it is our impression that nonautonomous dynamics unfolds its whole potential in the interplay between forward and backward resp. pullback dynamics. As a rule of thumb, here the stability boundary is "wider": Spectral intervals require whole ranges of parameter values in order to cross it, and collapsing spectral intervals on the stability boundary yield a variety of intrinsically nonautonomous bifurcation phenomena (see [18, pp. 88, Sect. 7.3]) — they are not generic though. It is decisively the full time situation, where such new phenomena occur. An interplay becomes important, when parameters are regulated from one value (yielding the past) to another (giving the future).
Appendix A. Nonautonomous discrete dynamics. Let $\mathcal{J}$ be a discrete interval unbounded below, $\mathcal{J}' := \{k \in \mathbb{J} : k + 1 \in \mathcal{J}\}$ and $\Omega \subseteq \mathbb{R}^d$. Suppose that the mapping $F_n : \Omega \rightarrow \Omega, n \in \mathcal{J}'$, is continuous. Given a pair $n_0 \in \mathcal{J}$, $\bar{x} \in \Omega$, we write $\varphi,[n_0,\bar{x})$ for the forward solution to the nonautonomous difference equation

$$x_{n+1} = F_n(x_n)$$

(A.1)

satisfying the initial condition $x_{k_0} = \bar{x}$ and denote it as general solution to (A.1). A solution to (A.1) existing on the whole discrete integer axis is called an entire solution.

A.1. Pullback attraction. First of all, one has

**Theorem A.1 (pullback solution).** Let $\bar{x}_J$ denote a sequence in $\Omega$. If the limits

$$\xi_n^* := \lim_{k \rightarrow +\infty} \varphi(n; k, \bar{x}_k)$$

exist for all $n \in \mathcal{J}$, then also this so-called pullback solution $\xi_n^*$ solves (A.1).

**Proof.** Due to the continuity of $F_n$ one has

$$\xi_{n+1}^* = \lim_{k \rightarrow +\infty} \varphi(n+1; k, \bar{x}_k) \overset{(A.1)}{=} \lim_{k \rightarrow +\infty} F_n(\varphi(n; k, \bar{x}_k))$$

$$= F_n \left( \lim_{k \rightarrow +\infty} \varphi(n; k, \bar{x}_k) \right) = F_n(\xi_n^*) \text{ for all } n \in \mathcal{J}'$$

and this completes the proof. \(\blacksquare\)

A subset $\mathcal{A} \subseteq \mathcal{J} \times \Omega$ is denoted as nonautonomous set with the $n$-fibers

$$\mathcal{A}(n) := \{x \in \Omega : (n, x) \in \mathcal{A}\} \text{ for all } n \in \mathcal{J}.$$

For the cartesian product of two nonautonomous sets $\mathcal{A}, \mathcal{B} \subseteq \mathcal{J} \times \Omega$ we define

$$\mathcal{A} \times \mathcal{B} := \{(n, x, y) \in \mathcal{J} \times \Omega^2 : (x, y) \in \mathcal{A}(n) \times \mathcal{B}(n)\}.$$

One says a nonautonomous set $\mathcal{A}$ (cf. [26]) is

- bounded, if there exists a $\rho > 0$ such that $\mathcal{A}(n) \subseteq B_\rho(0) \subseteq \mathbb{R}^d$ for all $n \in \mathcal{J}$,
- compact (resp. connected), if each fiber $\mathcal{A}(n) \subseteq \Omega, n \in \mathcal{J}$, is compact (resp. connected),
- forward invariant, if $F_n(\mathcal{A}(n)) \subseteq \mathcal{A}(n + 1)$ for all $n \in \mathcal{J}'$,
- invariant, if $F_n(\mathcal{A}(n)) = \mathcal{A}(n + 1)$ for all $n \in \mathcal{J}'$,
- pullback absorbing, if for every bounded nonautonomous set $\mathcal{B}$ there is a $K \in \mathbb{N}_0$ such that $\varphi(n; n-k, \mathcal{B}(n-k)) \subseteq \mathcal{A}(n)$ holds for all $n \in \mathcal{J}$ and $k \geq K$.

For given $\mathcal{A}$, the nonautonomous set $\omega_A$ defined by the fibers

$$\omega_A(n) := \bigcap_{m \geq 0} \bigcup_{k \geq m} \varphi(n; n-k, \mathcal{A}(k-n)) \text{ for all } n \in \mathcal{J}$$

is called the $\omega$-limit set of $\mathcal{A}$. When $\mathcal{A}$ is pullback absorbing, one denotes the nonautonomous set $\mathcal{P} := \omega_A$ as pullback attractor of (A.1).

**Corollary A.2.** If $\mathcal{A}$ is invariant, then $\omega_A = \overline{\mathcal{A}}$.

**Proof.** The invariance of $\mathcal{A}$ implies

$$\omega_A(n) = \bigcap_{m \geq 0} \bigcup_{k \geq m} \varphi(n; n-k, \mathcal{A}(k-n)) = \bigcap_{m \geq 0} \bigcup_{k \geq m} \mathcal{A}(n) = \overline{\mathcal{A}}(n) \text{ for all } n \in \mathcal{J}$$

and this finishes the proof. \(\blacksquare\)
A.2. Order-preserving difference equations. A cone $C \subseteq \mathbb{R}^d$ is a closed subset satisfying $\lambda C \subseteq C$ for $\lambda \geq 0$, $C + C \subseteq C$ and $C \cap (-C) = \{0\}$; we define the partial order

$$x \preceq y :\iff y - x \in C \text{ for all } x, y \in \mathbb{R}^d.$$  

A difference equation (A.1) is called order-preserving, if one has the implication

$$x \preceq y \implies F_n(x) \preceq F_n(y) \text{ for all } n \in \mathbb{N}, x, y \in \Omega$$

and consequently mathematical induction yields the implication

$$\bar{x} \preceq \bar{y} \implies \phi(n; n_0, \bar{x}) \preceq \phi(n; n_0, \bar{y}) \text{ for all } n_0 \leq n, x, y \in \Omega. \quad (A.2)$$

The following result is a discrete-time counterpart to [3, pp. 257–258, Lemma 9.3]:

**Theorem A.3.** Assume that (A.1) is order-preserving. If $x_l^-$, $x_l^+$ are sequences in $\Omega$ such that the nonautonomous set

$$A := \{(n, x) \in \mathbb{N} \times \Omega : x_n^− \preceq x \preceq x_n^+\}$$

is forward invariant, then there exist entire solutions $ξ_l^−, ξ_l^+$ to (A.1) being minimal resp. maximal in the following sense: Every entire solution $x_n$ of (A.1) in $A$ fulfills

$$x_n^− \preceq ξ_n^− \preceq x_n \preceq ξ_n^+ \preceq x_n^+ \text{ for all } n \in \mathbb{N}$$

and $A$ contains in particular at least one entire solution.

**Proof.** Let $n \in \mathbb{N}$ be fixed. Since the set $A$ is forward invariant one obtains

$$x_n^− \preceq \phi(n; k, x_k^+) = \phi(n; l, \phi(l; k, x_k^+)) \preceq \phi(n; l, x_l^+) \quad (A.2)$$

and thus the sequence $y_k := \phi(n; k, x_k^+)$, $k \leq n$, in $\Omega$ is decreasing and bounded below by $x_n^-$. Therefore (cones in finite-dimensional spaces are regular), it is convergent and thanks to Thm. A.1 the pullback solution $ξ_n := \lim_{k \to -\infty} \phi(n; k, x_k^+)$ solves equation (A.1) on $\mathbb{N}$. Similarly, one verifies that also the limit $ξ_n^+ := \lim_{k \to -\infty} \phi(n; k, x_k^+)$ exists and defines an entire solution to (A.1).

**Corollary A.4.** If (A.1) is order-preserving and has a bounded and pullback absorbing set $A$, then the pullback attractor $A^*$ fulfills

$$A^* \subseteq \{(n, x) \in \mathbb{N} \times \Omega : x_n^− \preceq x \preceq x_n^+\}.$$  

Moreover, equality holds in case $\{(n, x) \in \mathbb{N} \times \Omega : x_n^− \preceq x \preceq x_n^+\}$ is invariant.

**Proof.** (I) First, [26, p. 19, Thm. 1.3.9] shows that the pullback attractor $A^* = ω_A$ exists with $A^* \subseteq A$. Hence, it is bounded, [26, p. 17, Cor. 1.3.4] implies that $A^*$ consists of all bounded entire solutions to (A.1) and thus

$$A^* \subseteq \{(n, x) \in \mathbb{N} \times \Omega : x_n^− \preceq x \preceq x_n^+\} =: A_0.$$  

(II) If $A_0$ is invariant, then Cor. A.2 implies $ω_{A_0} = \overline{A_0} = A_0$ and with (I) this yields $A^* \subseteq A_0 = ω_{A_0} \subseteq ω_A = A^*$ (cf. [26, p. 9, Prop. 1.2.13(a)]), i.e. $A^* = A_0$.  


Appendix B. Nonautonomous hyperbolicity.

B.1. Bohl exponents. Let $a_{1} = (a_{n})_{n \in \mathbb{I}}$ be a real or complex sequence and suppose $\mathbb{I}$ is a discrete interval unbounded above. For simplicity we assume

$$0 < \inf_{n \in \mathbb{I}}|a_{n}| \leq \sup_{n \in \mathbb{I}}|a_{n}| < \infty$$ (B.1)

throughout. Let us define the lower resp. upper Bohl exponent of $a_{1}$ by

$$\underline{\beta}(a_{1}) := \lim_{n \to \infty} \inf_{k \in \mathbb{I}} \prod_{i=k}^{k+n-1} |a_{i}|, \quad \overline{\beta}(a_{1}) := \lim_{n \to \infty} \sup_{k \in \mathbb{I}} \prod_{i=k}^{k+n-1} |a_{i}|.$$ (B.2)

Thanks to (B.1) we know that both Bohl exponents are finite and the limits in (B.2) exist due to [2, Lemma 3.1]. Moreover, they fulfill the following elementary

**Proposition B.1.** For unbounded subintervals $J \subseteq \mathbb{I}$ it is $\overline{\beta}(a_{1}) \leq \overline{\beta}(a_{2}) \leq \underline{\beta}(a_{2}) \leq \underline{\beta}(a_{1})$ and

$$\overline{\beta}(\lambda a_{1}) = |\lambda| \overline{\beta}(a_{1}), \quad \underline{\beta}(\lambda a_{1}) = |\lambda| \underline{\beta}(a_{1}) \quad \text{for all } \lambda \in \mathbb{C}.$$ (B.3)

If the sequences $a_{1}, b_{1}$ additionally both satisfy (B.1), then the following relations hold

$$\overline{\beta}(a_{1} b_{1}) \leq \overline{\beta}(a_{1}) \overline{\beta}(b_{1}), \quad \underline{\beta}(a_{1} b_{1}) \geq \underline{\beta}(a_{1}) \underline{\beta}(b_{1}),$$

$$\overline{\beta} \left( \frac{a_{1}}{b_{1}} \right) \leq \frac{\overline{\beta}(a_{1})}{\overline{\beta}(b_{1})}, \quad \underline{\beta} \left( \frac{a_{1}}{b_{1}} \right) \geq \frac{\underline{\beta}(a_{1})}{\underline{\beta}(b_{1})}.$$ (B.4)

**Proof.**

The claimed inequality for the Bohl exponents on different intervals $\mathbb{I}$ and $\mathbb{J}$ immediately follows from elementary properties of sup and inf; so does (B.3). A proof of the remaining inequalities is left to the interested reader. □

**Example B.2.** Let $\mathbb{J} := [\kappa, \infty) \cap \mathbb{Z}$ with some $\kappa \in \mathbb{Z}$.

1. For a constant sequence $a_{n} := \alpha, \alpha \in \mathbb{C}$, all Bohl exponents coincide, i.e.,

$$\overline{\beta}(a_{1}) = \underline{\beta}(a_{1}) = \overline{\beta}(a_{2}) = \underline{\beta}(a_{2}) = |\alpha|.$$

2. Also in case of an $\omega$-periodic, $\omega \in \mathbb{N}$, sequence $a_{2}$ one deduces

$$\overline{\beta}(a_{1}) = \underline{\beta}(a_{1}) = \overline{\beta}(a_{2}) = \underline{\beta}(a_{2}) = \sqrt{|a_{\kappa} \cdots a_{\kappa+\omega-1}|}.$$

3. For a sequence $a_{n}$ satisfying $\lim_{n \to \pm \infty} a_{n} = \alpha_{\pm}$ it is

$$\overline{\beta}(a_{1}) = |\alpha_{+}|, \quad \underline{\beta}(a_{2}) = \min \{|\alpha_{-}|, |\alpha_{+}|\}, \quad \overline{\beta}(a_{2}) = \max \{|\alpha_{-}|, |\alpha_{+}|\}.$$

4. In the situation $a_{n} := 3 - \text{sgn} n + \sin \ln(1 + |n|)$ the sequence $(\sin \ln(1 + |n|))_{n \in \mathbb{I}}$ comes arbitrarily close to the values $\pm 1$ on increasingly larger intervals. Hence, it is

$$\overline{\beta}(a_{1}) = 1, \quad \underline{\beta}(a_{2}) = 3, \quad \overline{\beta}(a_{2}) = 1, \quad \underline{\beta}(a_{2}) = 5.$$

5. For a bounded sequence $c_{1}$ one has

$$\overline{\beta}(e^{c}) = \exp \left( \lim_{n \to \infty} \frac{1}{n} \inf_{k \in \mathbb{I}} \sum_{i=k}^{k+n-1} c_{i} \right), \quad \underline{\beta}(e^{c}) = \exp \left( \lim_{n \to \infty} \frac{1}{n} \sup_{k \in \mathbb{I}} \sum_{i=k}^{k+n-1} c_{i} \right).$$
Remark B.3 (computation of Bohl exponents). For the geometric means
\[ \beta_{n,k}(a_I) := \prod_{i=k}^{k+n-1} |a_i|, \]
one has \( \ln \beta_{n,k}(a_I) = \frac{1}{n} \sum_{i=k}^{k+n-1} \ln |a_i| \). We consequently find approximations of \( \ln \beta(a_I) \) and \( \ln \overline{\beta}(a_I) \) by computing
\[ \sup_{k \in I} \ln \beta_{n,k}(a_I) \quad \text{and} \quad \inf_{k \in I} \ln \beta_{n,k}(a_I) \]
for sufficiently large \( n \in \mathbb{N} \), respectively. Note the recursion
\[ \ln \beta_{n,k+1}(a_I) = \ln \beta_{n,k}(a_I) + \frac{1}{n} \ln \frac{a_{k+n}}{a_k}, \]
which allows to compute the sequence \( \beta_{n,k}(a_I) \) efficiently.

For the sequence \( a_I \) defined in Ex. B.2(4), we obtained the results from Tab. B.1 demonstrating that larger values of \( n \) for fixed \( I \) do not yield convergence (caused by the exponential increase in the “period” of the \( \sin \circ \ln \)-function). Indeed, for infinite \( I \) theoretical considerations guarantee that the approximations \( \inf_{k \in I} \beta_{n,k}(a_I) \) to \( \overline{\beta}(a_I) \) are increasing, while the approximations \( \sup_{k \in I} \beta_{n,k}(a_I) \) to \( \underline{\beta}(a_I) \) are decreasing as \( n \to \infty \). These monotonicity properties can serve as an indicator for convergence and suggest to increase both \( n \), as well as the length of \( I \) during the computation.

<table>
<thead>
<tr>
<th>( n )</th>
<th>( \beta(a_I) )</th>
<th>( \beta_{10^6}(a_I) )</th>
<th>( n )</th>
<th>( \beta(a_I) )</th>
<th>( \beta_{10^6}(a_I) )</th>
</tr>
</thead>
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<td>2.99999936133</td>
<td>10</td>
<td>1.00000000116</td>
<td>4.99999936133</td>
</tr>
<tr>
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<td>1.00000011725</td>
<td>4.99999721913</td>
</tr>
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<td>10^3</td>
<td>1.0001172586</td>
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<tr>
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<td>2.95027314483</td>
<td>10^4</td>
<td>1.00117000882</td>
<td>4.9471156401</td>
</tr>
</tbody>
</table>

Table B.1
Ex. B.2(4) with \( \mathcal{I} = [1, 10^6] \) (left) and \( \mathcal{I} = [-10^6, 10^6] \) (right).

On the other hand, for the almost periodic sequence \( a_n = \cos n \), Tab. B.2 indicates that the approximations to \( \underline{\beta}(a_I) \) actually increase, while those to \( \overline{\beta}(a_I) \) decrease to \( \frac{1}{2} \).

<table>
<thead>
<tr>
<th>( n )</th>
<th>( \beta(a_I) )</th>
<th>( \beta_{10^6}(a_I) )</th>
<th>( n )</th>
<th>( \beta(a_I) )</th>
<th>( \beta_{10^6}(a_I) )</th>
</tr>
</thead>
<tbody>
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<td>0.52837200045</td>
<td>10^4</td>
<td>0.42625376980</td>
<td>0.52837200045</td>
</tr>
<tr>
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<td>0.50335789629</td>
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<td>0.4898956683</td>
<td>0.50335789629</td>
</tr>
<tr>
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<tr>
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<td>10^5</td>
<td>0.49992964104</td>
<td>0.50021544123</td>
</tr>
</tbody>
</table>

Table B.2
\( a_n = \cos n \) with \( \mathcal{I} = [0, 10^6] \) (left) and \( \mathcal{I} = [-10^6, 10^6] \) (right).

B.2. Exponential dichotomies. Let \( A_I = (A_n)_{n \in \mathcal{I}} \) denote a bounded sequence of square matrices \( A_n \in \mathbb{R}^{d \times d} \). The associated linear difference equation
\[ x_{n+1} = A_n x_n \quad (L) \]
induces an evolution operator

\[
\Phi(n, m) := \begin{cases} A_{n-1} \cdots A_m, & m < n, \\ I, & n = m. 
\end{cases}
\]

A difference equation \((L)\) is said to possess an exponential dichotomy (ED for short, cf. [9]) on \(\mathbb{I}\), if there exists a sequence \((P_n)_{n \in \mathbb{I}}\) of projections in \(\mathbb{R}^{d \times d}\) (i.e. \(P_n = P_n^2\)) and real numbers \(\alpha \in (0, 1)\), \(K \geq 1\), such that

(a) \(P_{n+1}A_n = A_nP_n\) and \(A_n|_{N(P_n)} : N(P_n) \to N(P_{n+1})\) is invertible,

(b) \(\|\Phi(n, m)P_n\| \leq K \alpha^{n-m}\) for all \(m \leq n\),

(c) \(\|\Phi(n, m)(I - P_n)\| \leq K \alpha^{m-n}\) for all \(n \leq m\), and \(\Phi(n, m) : N(P_m) \to N(P_n)\), \(n \leq m\), being the inverse of \(\Phi(m, n)|_{N(P_n)}\).

Geometrically, an ED is a hyperbolic splitting of the extended state space \(\mathbb{I} \times \mathbb{R}^d\) for \((L)\) into a stable vector bundle \(V^s := \{(n, x) \in \mathbb{I} \times \mathbb{R}^d : x \in R(P_n)\}\) and a complementary unstable vector bundle \(V^u := \{(n, x) \in \mathbb{I} \times \mathbb{R}^d : x \in N(P_n)\}\). When restricted to the invariant set \(V^s\), a dichotomous equation \((L)\) becomes uniformly asymptotically stable.

On this basis, we define the dichotomy spectrum

\[
\Sigma(A_1) = \{ \gamma > 0 : x_{n+1} = \gamma^{-1}A_n x_n \text{ does not have an ED on } \mathbb{I} \}
\]

and the dichotomy resolvent \(\rho(A) := (0, \infty) \setminus \Sigma(A)\). Referring to [1, Spectral theorem], the dichotomy spectrum consists of up to \(d\) disjoint spectral intervals and reads as

\[
\Sigma(A_1) = \begin{cases} (0, b_1] \\ [a_1, b_1] \\ \bigcup_{i=2}^k [a_i, b_i] \end{cases}
\]

with real numbers \(0 < a_1 < b_1 < a_2 \leq \ldots \leq b_k\) for some integer \(k \leq d\). A spectral interval \((0, b_1]\) can occur, if some inverse \(A_n^{-1}\) does not exist or \(\sup_{n \in \mathbb{I}} \|A_n^{-1}\| = \infty\).

There is a close relation between the dichotomy spectrum and Bohl exponents, which we are going to explore next:

**Proposition B.4.** Given a real sequence \(a_1\) satisfying (B.1), the dichotomy spectrum of a scalar equation

\[x_{n+1} = a_n x_n\]  \hspace{1cm} (B.6)

is \(\Sigma(a_1) = [\beta(a_1), \bar{\beta}(a_1)]\) with the Bohl exponents \(\beta(a_1)\) and \(\bar{\beta}(a_1)\).

**Proof.** Above all, the evolution operator \(\Phi_a(n, m)\) of (B.6) is given by (3.2).

Hence, the scaled difference equation \(x_{n+1} = \gamma^{-1}a_n x_n\) has an ED on \(\mathbb{I}\) if and only if there exist reals \(K \geq 1\), \(\alpha \in (0, 1)\) such that

\[
\gamma^{m-n} |\Phi_a(n, m)| \leq K \alpha^{n-m}\] or \(\gamma^{n-m} |\Phi_a(m, n)| \leq K \alpha^{m-n}\) for all \(m \leq n\)

\[
\Leftrightarrow |\Phi_a(n, m)| \leq K (\alpha \gamma)^{n-m}\] or \(\frac{1}{K} \left( \frac{\alpha}{\gamma} \right)^{m-n} \leq |\Phi_a(n, m)|\) for all \(m \leq n\)

\[
\Leftrightarrow \prod_{j=k}^{k+n-1} |a_j| \leq K^\frac{1}{\alpha} \alpha \gamma\] or \(\frac{1}{K^\frac{1}{\alpha}} \leq \prod_{j=k}^{k+n-1} |a_j|\) for all \(k \in \mathbb{I}, n \geq 0\)

\[
\Leftrightarrow \sup_{k \in \mathbb{I}} \prod_{j=k}^{k+n-1} |a_j| \leq K^\frac{1}{\alpha} \alpha \gamma\] or \(\frac{1}{K^\frac{1}{\alpha}} \leq \inf_{k \in \mathbb{I}} \prod_{j=k}^{k+n-1} |a_j|\) for all \(n \geq 0\).
(I) In the limit \( n \to \infty \) this immediately implies
\[
\frac{\beta(a)}{\alpha} \leq \gamma \quad \text{or} \quad \gamma \leq \alpha\beta(a). \tag{B.7}
\]

(II) Conversely, if we choose an arbitrary \( q > 1 \), then (B.7) implies that there exists an \( N_q \in \mathbb{N} \) such that
\[
\sup_{k \in \mathbb{N}} \left( \prod_{j=k}^{k+n-1} |a_j| \right) \leq q^\frac{1}{q} \alpha \gamma \quad \text{or} \quad \frac{1}{q^\frac{1}{q} \alpha} \leq \inf_{k \in \mathbb{N}} \left( \prod_{j=k}^{k+n-1} |a_j| \right) \quad \text{for all} \ n \geq N_q
\]
and proceeding as in the chain of equivalences above, we obtain
\[
\gamma^{m-n} |\Phi_a(n, m)| \leq qa^{n-m} \quad \text{or} \quad \gamma^{n-m} |\Phi_a(m, n)| \leq qa^{n-m} \quad \text{for all} \ N_q \leq n - m.
\]

By choosing an appropriate constant \( Q \geq q \), using the boundedness assumption on \( a \) and (B.1), it is easy to see that these inequalities extend to
\[
\gamma^{m-n} |\Phi_a(n, m)| \leq Qa^{n-m} \quad \text{or} \quad \gamma^{n-m} |\Phi_a(m, n)| \leq Qa^{n-m} \quad \text{for all} \ m \leq n.
\]

(III) If we combine the steps (I) and (II), the scaled equation \( x_{n+1} = \gamma^{-1}a_n x_n \) has an ED on \( I \), if and only if (B.7) holds. The logical contraposition to this statement is that \( \gamma \in \Sigma(a) \) is equivalent to \( \gamma \in \left( \frac{\alpha\beta(a), \beta(a)}{\alpha} \right) \) for all \( \alpha \in (0, 1) \), i.e.
\[
\gamma \in \bigcap_{\alpha \in (0, 1)} \left( \frac{\alpha\beta(a), \beta(a)}{\alpha} \right) = [\beta(a), \beta(a)]
\]
and consequently the claim \( \Sigma(a) = [\beta(a), \beta(a)] \). \( \blacksquare \)

In order to meet the purposes of this paper we now restrict to two dimensions:

**Proposition B.5.** If \((L)\) has a diagonal coefficient sequence
\[
A_n = \left( \begin{array}{c} a_n \\ b_n \end{array} \right) \quad \text{for all} \ n \in \mathbb{I}
\]
with bounded diagonal sequences \( a_1, b_1 \), then

(a) \( \Sigma(A) = \Sigma(a) \cup \Sigma(b) \),

(b) \( \Sigma(A) = \left[ \beta(a), \beta(a) \right] \cup \left[ \beta(b), \beta(b) \right] \), provided \( a_1, b_1 \) satisfy (B.1).

**Proof.** We define the linear operators
\[
L_n \in L(\ell^\infty(\mathbb{R}^d)), \quad (L_n \phi)_n := \phi_{n+1} - \gamma^{-1} A_n \phi_n, \tag{B.8}
\]
\[
L_n^\alpha \in L(\ell^\infty(\mathbb{R}^d)), \quad (L_n^\alpha \phi)_n := \phi_{n+1} - \gamma^{-1} a_n \phi_n,
\]
\[
L_n^b \in L(\ell^\infty(\mathbb{R}^d)), \quad (L_n^b \phi)_n := \phi_{n+1} - \gamma^{-1} b_n \phi_n.
\]

(I) Suppose that \( \mathbb{I} \) is bounded below. Due to [16, Thm. 3.2] we obtain
\[
\gamma \not\in \Sigma(A) \Leftrightarrow L_n \text{ is onto} \Leftrightarrow \forall \psi \in \ell^\infty(\mathbb{R}^d) : \exists \phi \in \ell^\infty(\mathbb{R}^d) : L_n \phi = \psi
\]
\[
\Leftrightarrow \forall \psi \in \ell^\infty(\mathbb{R}^d) : x_{n+1} = \gamma^{-1} A_n x_n + \psi_n \text{ has a bounded solution} \ \phi
\]
\[
\Leftrightarrow \forall \psi^a, \psi^b \in \ell^\infty(\mathbb{R}) : x_{n+1} = \frac{a_n}{\gamma} x_n + \psi^a_n \text{ and } x_{n+1} = \frac{b_n}{\gamma} x_n + \psi^b_n \text{ have bounded solutions} \ \phi^a, \phi^b
\]
\[ \forall \phi^a, \phi^b \in \ell^\infty(\mathbb{R}) : \exists \gamma^a, \gamma^b \in \ell^\infty(\mathbb{R}) : L^a_\gamma \phi^a = \psi^a \text{ and } L^b_\gamma \phi^b = \psi^b \]

\[ \therefore L^a_\gamma, L^b_\gamma \text{ are onto} \]

\[ \therefore x_{n+1} = \frac{a_n}{b_n} x_n \text{ and } x_{n+1} = \frac{b_n}{a_n} x_n \text{ have an ED } \iff \gamma \notin \Sigma(a) \cup \Sigma(b), \]

yielding claim (a) in the logical contraposition. Claim (b) results using Prop. B.4.

(II) The situation \( I = \mathbb{Z} \) can be shown similarly with the characterization [9, p. 230, Thm. 7.6.5] applied to the operators \( L_\gamma \) and \( L^a_\gamma, L^b_\gamma \).

We remind the reader of the symmetric difference of two sets \( M_1, M_2 \) defined as

\[ M_1 \triangle M_2 := (M_1 \cup M_2) \setminus (M_1 \cap M_2), \]

containing all elements which are either in \( M_1 \) or in \( M_2 \). We note that the intersection of sets distributes over the symmetric difference, i.e. for arbitrary sets \( M \) one has

\[ (M_1 \triangle M_2) \cap M = (M_1 \cap M) \triangle (M_2 \cap M). \quad (B.9) \]

**Proposition B.6.** Let \( I = \mathbb{Z} \). If \((L)\) has an upper triangular coefficient sequence

\[ A_n = \begin{pmatrix} a_n & c_n \\ 0 & b_n \end{pmatrix} \quad \text{for all } n \in \mathbb{Z} \]

and \( a_z, b_z, c_z \) are bounded sequences, then the following holds true:

(a) \( \Sigma(a_z) \triangle \Sigma(b_z) \subseteq \Sigma(A_z) \subseteq \Sigma(a_z) \cup \Sigma(b_z) \).

(b) If \( \Sigma(a_z) \cap \Sigma(b_z) \) has no interior points, then \( \Sigma(A_z) = \Sigma(a_z) \cup \Sigma(b_z) \).

**Remark B.7.** (1) The same assertion holds for difference equations \((L)\) with lower triangular coefficient matrices.

(2) An alternative condition guaranteeing \( \Sigma(A_z) = \Sigma(a_z) \cup \Sigma(b_z) \) is \( 1 \notin \Sigma(\frac{az}{bz}) \) (in the upper triangular case) resp. \( 1 \notin \Sigma(\frac{bz}{az}) \) (in the lower triangular case).

*Proof.* Let us introduce a weighted shift operator \( T_A \in \mathcal{L}(\ell^\infty(\mathbb{R}^2)) \) as

\[ (T_A \phi)_n := A_{n-1} \phi_{n-1} = \begin{pmatrix} a_{n-1} \phi_{n-1}^1 + c_{n-1} \phi_{n-1}^2 \\ b_{n-1} \phi_{n-1}^2 \end{pmatrix} \quad \text{for all } n \in \mathbb{Z}. \]

If we define the bounded projection \( P \in \mathcal{L}(\ell^\infty(\mathbb{R}^2)) \), \( (P \phi)_n := \begin{pmatrix} \phi^1 \\ 0 \end{pmatrix} \) and the closed subspaces \( X := R(P), Y := N(P) \) of \( \ell^\infty(\mathbb{R}^2) \), then the following holds true

\[ (T_A P \phi)_n = \begin{pmatrix} a_{n-1} \phi_{n-1}^1 \\ 0 \end{pmatrix}, \quad (T_A (I - P) \phi)_n = \begin{pmatrix} c_{n-1} \phi_{n-1}^2 \\ b_{n-1} \phi_{n-1}^2 \end{pmatrix} \quad \text{for all } n \in \mathbb{Z}, \]

as well as \( \ell^\infty(\mathbb{R}^2) = X \oplus Y \). Furthermore, \( T_A \) can be represented as block-diagonal operator \( T_A = \begin{pmatrix} T_a & C \\ 0 & T_b \end{pmatrix} \in \mathcal{L}(X \oplus Y) \) with \( T_a \in \mathcal{L}(X), T_b \in \mathcal{L}(Y), C \in \mathcal{L}(Y, X), \)

\[ (T_a \phi)_n := a_{n-1} \phi_{n-1}, \quad (T_b \phi)_n := b_{n-1} \phi_{n-1}, \quad (C \phi)_n := c_{n-1} \phi_{n-1}. \]

(a) Due to [8, Cor. 4] one has \( \sigma(T_a) \triangle \sigma(T_b) \subseteq \sigma(T_A) \subseteq \sigma(T_a) \cup \sigma(T_b) \) and thus the first claimed inclusion follows from (B.9), if we set \( M_a := \sigma(T_a), M_b := \sigma(T_b), M := \mathbb{R}^+ \) and make use of \( \Sigma(A_z) = \sigma(T_A) \cap \mathbb{R}^+ \) and corresponding relations for \( T_a, T_b \) (cf. [29, (1.1)]). The second claimed inclusion follows directly using [29, (1.1)].

(b) Thanks to the relation \( \sigma(T_a) \cap \sigma(T_b) = \{ \lambda \in \mathbb{C} : |\lambda| \in \Sigma(a_z) \cap \Sigma(b_z) \} \) and our assumption on interior points, the intersection \( \sigma(T_a) \cap \sigma(T_b) \subseteq \mathbb{C} \) is a finite union
of circles centered around 0 (or empty) and has thus no interior points. Hence, [8, Cor. 8] ensures \( \sigma(T_{\alpha}) = \sigma(T_{\alpha}) \cup \sigma(T_{\beta}) \) and again [29, (1.1)] yields the claim. \[ \square \]

The following example ultimately illustrates that Prop. B.6(b) fails without the additional assumption on interior points:

**Example B.8.** We investigate \((L)\) on \( \mathbb{Z} \) with upper-triangular coefficients.

(1) In the situation

\[
A_n := \begin{cases} 
A^+, & n \geq 0, \\
A^-, & n < 0, 
\end{cases}
A^+ := \begin{pmatrix} 2 & 1 \\ 0 & 1/2 \end{pmatrix}, \quad A^- := \begin{pmatrix} 1/2 & 0 \\ 0 & 2 \end{pmatrix}
\]

the diagonal sequences of \( A_n \) fulfill \( \Sigma(a_\mathbb{Z}) = \Sigma(b_\mathbb{Z}) = [1/2, 2] \) (see Prop. B.4), whereas \( \Sigma(A_\mathbb{Z}) = \{1/2, 1\} \) (cf. [29, Exam. 5.5]).

(2) Prop. B.6(b) can be used to detect gaps in the dichotomy spectrum. In case

\[
A_n := \begin{cases} 
A^+, & n \geq 0, \\
A^-, & n < 0, 
\end{cases}
A^+ := \begin{pmatrix} 4 & 0 \\ 0 & 2 \end{pmatrix}, \quad A^- := \begin{pmatrix} 1 & 1 \\ 0 & 3 \end{pmatrix}
\]

the diagonal sequences of \( A_n \) imply \( \Sigma(a_\mathbb{Z}) = [1, 4], \Sigma(b_\mathbb{Z}) = [2, 3] \) (see Prop. B.4). Hence, it is \([1, 2] \cup [3, 4] \subseteq \Sigma(A_{\mathbb{Z}}) \subseteq [1, 4] \), which holds for \( \Sigma(A_{\mathbb{Z}}) = [1, 2] \cup [3, 4] \).

**Appendix C. Auxiliary proofs.** In this final appendix, we summarize the more technical proofs promised in the main text:

**C.1. Proof of Lemma 4.3.** The derivative of \( g_n \) is \( g'_n(y) = (1 - y)e^{c_n - y} \) and consequently \( |g'_n(\cdot)| \) has the global maximum \( e^{c_n} \geq 1 \) (for \( y = 0 \)) and the local maximum \( e^{c_n - 2} \) (for \( y = 2 \), cf. Fig. 4.2 (right)). Moreover, one easily sees that the equation \( |g'_n(y)| = e^{c_n - 2} \) possesses the two solutions \( \bar{y} = 1 - W(e^{-1}) \) and 2. This particularly implies

\[
\max_{y \leq \bar{y}} |g'_n(y)| = e^{c_n - 2} \quad \text{for all } n \in \mathbb{I}. \tag{C.1}
\]

(a) We show the forward invariance of \( \tilde{Y}_c \). Due to (4.4) one has \( \bar{y} \leq c_n \) and thus

\[
\bar{y} \leq g_n(\bar{y}) \quad \text{for all } n \in \mathbb{I} \tag{C.2}
\]

(cf. Fig. 4.1), yielding the inclusions

\[
g_n(\tilde{Y}_c(n)) = g_n \left( [\bar{y}, \max \left\{ 1, \frac{e^{c_n - 1}}{e} \right\}] \right)
\subseteq \left[ \min \left\{ g_n(\bar{y}), g_n \left( \max \left\{ 1, \frac{e^{c_n - 1}}{e} \right\} \right) \right\}, \max \left\{ 1, \frac{e^{c_n}}{e} \right\} \right]
\subseteq \left[ \min \left\{ g_n(\bar{y}), g_n \left( \frac{e^{c_n - 1}}{e} \right) \right\}, \max \left\{ 1, \frac{e^{c_n}}{e} \right\} \right]
\quad \left[ \min \left\{ \bar{y}, g_n \left( \frac{e^{c_n - 1}}{e} \right) \right\}, \max \left\{ 1, \frac{e^{c_n}}{e} \right\} \right]
\subseteq \left[ \bar{y}, \max \left\{ 1, \frac{e^{c_n}}{e} \right\} \right] = \tilde{Y}_c(n + 1) \quad \text{for all } n \in \mathbb{I}. \tag{C.4}
\]

(b) In order to show (4.5) we proceed by induction. The claim obviously holds for \( n = \bar{n} \). In the induction step \( n \to n + 1 \) we obtain from the mean value estimate

\[
|y(n + 1; \bar{n}, \bar{y}_1) - y(n + 1; \bar{n}, \bar{y}_2)| \overset{\text{(H)}}{=} |g_n(y(n; \bar{n}, \bar{y}_1)) - g_n(y(n; \bar{n}, \bar{y}_2))|
\]
for all $\tilde{y}_1, \tilde{y}_2 \in \tilde{Y}_c(\tilde{n})$. □

**C.2. Proof of Thm. 4.5.** We subdivide the proof into two steps:

(I) First, we introduce the functions $g, G : \mathbb{R}_+ \times \mathbb{R} \to \mathbb{R}$,

$$g(y, \gamma) := ye^{\gamma - y}, \quad G(y, \gamma) := g_y(y, \gamma) = (1 - y)e^{\gamma - y}.$$ 

The elementary estimate

$$|(n - t)e^{\gamma - t}| \leq ne^\gamma \text{ for all } t \geq 0, n \in \mathbb{N}, \gamma \in \mathbb{R} \quad (C.3)$$

yields $|G(y, \gamma)| \leq e^\gamma$ and therefore the partial derivative $g_y(\cdot, \gamma)$ is globally bounded. For all $y, \bar{y} \geq 0$ and $\gamma > 0$ the mean value theorem implies

$$|g(y, \gamma) - g(\bar{y}, \gamma)| \leq \int_0^1 |g_y(y + t(\bar{y} - y), \gamma)| \, dt \leq e^\gamma |y - \bar{y}|. \quad (C.4)$$

In addition, the derivative of $G$ reads as $G'(y, \gamma) = (y - 2, 1 - y)e^{\gamma - y}$. Choosing an arbitrary $\rho > 0$, again the mean value theorem implies

$$|g_y(y, \gamma) - g_y(\bar{y}, \hat{\gamma})| \leq \int_0^1 \left| G'(y + t(\bar{y} - y), \gamma + t(\hat{\gamma} - \gamma)) \right| \, dt$$

$$\leq \int_0^1 |y + t(\bar{y} - y) - 2| e^{\gamma + t(\gamma - \gamma) - y - t(y - \bar{y})} \, dt \leq e^\gamma \left( 2e^{\gamma - \gamma} t - 1 \right) (2|y - \bar{y}| + |\gamma - \hat{\gamma}|)$$

$$\leq e^{\gamma e^{2\rho} - 1} (2|y - \bar{y}| + |\gamma - \hat{\gamma}|) \text{ for all } y, \bar{y} \geq 0 \quad (C.5)$$

and $\gamma, \hat{\gamma} > 0$ with $|\hat{\gamma} - \gamma| < 2\rho$, since $t \mapsto e^{(\rho - \rho)\gamma}$ is strictly increasing.

(II) For fixed $\gamma > 0$ let $c_\mathbb{Z}, \tilde{c}_\mathbb{Z}$ be sequences in $(0, \infty)$ satisfying $\sup_{n \in \mathbb{Z}} |c_n - \gamma| < \rho$ and $\sup_{n \in \mathbb{Z}} |\tilde{c}_n - \gamma| < \rho$. This implies $c_n < \gamma + \rho$ and $|c_n - \tilde{c}_n| < 2\rho$ for all $n \in \mathbb{Z}$, which yields the estimates

$$|g(y, c_n) - g(\bar{y}, c_n)| \leq \omega_0(|y - \bar{y}|),$$

$$|g_y(y, c_n) - g_y(\bar{y}, \tilde{c}_n)| \leq \omega_1 \left( \sup_{n \in \mathbb{Z}} |c_n - \tilde{c}_2|, |y - \bar{y}| \right) \text{ for all } y, \bar{y} \geq 0, n \in \mathbb{Z},$$

with the real functions $\omega_0(t) := e^{t + \rho t}$ and $\omega_1(t, s) := e^{\rho e^{2\rho} - 1} \left( t + \frac{\rho}{2} \right)$. Then the claim follows from the quantitative perturbation result [28, Cor. 2.12]. □
C.3. Proof of Thm. 5.10. Following [7, Thm. 5.2] we define $V(x, y) := \frac{y}{x}$.

In order to show that $V$ is a Lyapunov function

$$
\frac{V(F_n(x, y))}{V(x, y)} = \frac{e^{c_n}}{a_n^s} v_n(x, y)
$$

for all $n \in \mathbb{I}$

with $v_n(x, y) := (1 + x + b_n y)^s e^{-d_n x - y}$ defined on $\mathbb{R}_+^2$. As in [7, Thm. 5.2] one derives

- $b_n d_n \geq 1$ implies that $v_n(x, y) \leq v_n\left(0, \frac{sb_n - 1}{d_n}\right) = (s b_n)^s e^{-s}$
- $b_n d_n \leq 1$ implies that $v_n(x, y) \leq v_n\left(x - \frac{d_n}{a_n}, 0\right) = \left(\frac{1}{a_n}\right)^s e^{d_n}$

for all $n \in \mathbb{I}$, $x, y \geq 0$. Therefore, our assumptions imply

$$
\frac{V(F_n(x, y))}{V(x, y)} \leq \frac{e^{c_n}}{a_n^s} \max \left\{ \left(\frac{sb_n}{a_n}\right)^s e^{-s}, \left(\frac{1}{a_n}\right)^s e^{d_n} \right\},
$$

thanks to (5.4) there exist $\mu \in (0, 1), N \in \mathbb{I}$ with $\frac{V(F_n(x, y))}{V(x, y)} \leq 1 - \mu$ for all $n \geq N$ and $x, y > 0$. Because of $V(F_n(x, y)) - V(x, y) \leq -\mu V(x, y) \leq 0$ for all $n \geq N, x, y > 0$

this establishes $V$ as Lyapunov function for $(\Delta)$ in the sense of [24, p. 49, Def. 7.1]. Since all solutions to $(\Delta)$ are bounded, [24, p. 50, Thm. 7.2] yields

$$
\varphi(n; n_0, \bar{x}, \bar{y}) \xrightarrow{n \to \infty} \{(x, y) \in \mathbb{R}_+^2 : V(x, y) = 0\} = \mathbb{R}_+ \times \{0\}
$$

for all $\bar{x}, \bar{y} > 0$

and the proof is complete. \[\square\]

C.4. Proof of Prop. 6.1. We finally address the nonautonomous center manifold reduction from Prop. 6.1. It relies on

**Lemma C.1.** Let $\mathbb{I} = \mathbb{Z}$. Under one of the assumptions

(i) $\beta(\frac{a_n e^{d_i \xi_n^s} e^{c_i \xi_n^s}}{(1 + \xi_n)^2}) < 1$ or

(ii) $1 < \beta(\frac{a_n e^{d_i \xi_n^s} e^{c_i \xi_n^s}}{(1 + \xi_n)^2})$

the variational equation (6.1) is kinematically similar to the diagonal system

$$
\begin{pmatrix}
  x_{n+1} \\
  y_{n+1}
\end{pmatrix} = \begin{pmatrix}
  \frac{a_n}{1 + \xi_n^2} & 0 \\
  e^{c_n - d_n \xi_n^s} & \frac{a_n}{1 + \xi_n^2}
\end{pmatrix} \begin{pmatrix}
  x_n \\
  y_n
\end{pmatrix}
$$

by means of the kinematic transformation $T_\mathbb{Z}$ with $T_n := \begin{pmatrix}
  1 & -\xi_n^s \\
  0 & 1
\end{pmatrix}$ and

$$
t_n^*: = \begin{cases}
  \sum_{j=-\infty}^{n-1} a_{j} b_{j} e^{d_{j} \xi_{j}^{s}} e^{c_{j} \xi_{j}^{s}} & \text{if (i) holds,} \\
  \sum_{j=n}^{\infty} a_{j} b_{j} e^{d_{j} \xi_{j}^{s}} e^{c_{j} \xi_{j}^{s}} & \text{if (ii) holds.}
\end{cases}
$$

**Proof.** During the present proof we abbreviate

$$
\alpha_n := \frac{a_n}{1 + \xi_n^2}, \quad \beta_n := -\frac{a_n b_n \xi_n^s}{(1 + \xi_n^2)^2}, \quad \gamma_n := e^{c_n - d_n \xi_n^s};
$$

note that these sequences, as well as $\frac{a_n b_n \xi_n^s e^{d_i \xi_n^s} e^{c_i \xi_n^s}}{(1 + \xi_n)^2} = \frac{a_n}{1 + \xi_n^2}$ are bounded. In order to determine the bounded sequence $t_n^*$ one applies the kinematic transformation $T_\mathbb{Z}$ to the variational equation (6.1) and obtains a linear difference equation

$$
\begin{pmatrix}
  x_{n+1} \\
  y_{n+1}
\end{pmatrix} = \begin{pmatrix}
  \alpha_n & \alpha_n t_n^* + \beta_n - \gamma_n t_{n+1}^* \\
  0 & \gamma_n
\end{pmatrix} \begin{pmatrix}
  x_n \\
  y_n
\end{pmatrix},
$$
To establish Prop. 6.1 we now proceed in three steps:

(I) First of all, our assumptions imply the estimate
\[
\beta \left( \frac{a_2 e^{c_2 n} - c_2}{1 + (\xi_n^*)^2} \right) \leq \frac{\beta(a_2 c_2 - c_2)}{\beta(e^{c_2 n} - d_2 \xi)} < 1
\]
and therefore we are in the situation of Lemma C.1(i). Then the difference equation of perturbed motion for \((\Delta)\) w.r.t. the solution \((\xi_n^*, 0)\) becomes
\[
\begin{cases}
x_{n+1} = F_n(x_n + \xi_n^*, y_n) - F_n(\xi_n^*, 0), \\
y_{n+1} = y_n e^{c_n - d_n(x_n + \xi_n^* + t_n^*) - y_n}
\end{cases}
\]
and applying the kinematic transformation \(T_Z\) from Lemma C.1 yields
\[
\begin{cases}
x_{n+1} = a_n \frac{x_n + (\xi_n^* - b_n n)}{(1 + x_n + b_n y_n + \xi_n^* + y_n)} - y_n t_n^* e^{c_n - d_n(x_n + \xi_n^* + t_n^*) - y_n}, \\
y_{n+1} = y_n e^{c_n - d_n(x_n + \xi_n^* + t_n^*) - y_n}.
\end{cases}
\]

(II) This planar system has the trivial solution and our assumptions guarantee the existence of a center-unstable fiber bundle \(\mathcal{W} \subseteq \mathbb{R}^2\) being an open neighborhood of \((0, 0)\), whose fibers \(\mathcal{W}(n)\) are graphs of functions \(w_n : U_0 \to \mathbb{R}\) defined on a neighborhood \(U_0 \subseteq \mathbb{R}\) of \(0\) uniformly in \(n \in \mathbb{Z}\) (see [26, p. 259, Thm. 4.6.4(b) and p. 260, Rem. 4.6.5(2)]). Due to the reduction principle [26, p. 267, Thm. 4.6.15] stability properties of \((\xi_n^*, 0)\) are determined by those of the trivial solution to
\[
y_{n+1} = y_n e^{c_n - d_n(w_n(y_n) + \xi_n^* + t_n^*) - y_n}.
\]

Now the right inequality in (6.3) guarantees that each such function \(w_n\) is of differentiability class \(C^2\). Hence, Taylor’s theorem in connection with \(w_n(0) = 0\) and the tangentiality property \(w_n'(0) = 0\) yields the representation \(w_n(y) = w_n(0) y^2 + O(y^3)\) uniformly in \(n \in \mathbb{Z}\). Given this, a Taylor expansion in the right-hand side of (C.8) implies the claimed representation (6.4), where we have abbreviated \(\omega_n := w_n'(0)\).

(III) It remains to establish the expression for the Taylor coefficient \(\omega_n\). The following argument is based on the fact that the mappings \(w_n\) defining the center-unstable fiber bundle \(\mathcal{W}\) fulfill the invariance equation (cf. [30])
\[
w_{n+1} \left( y e^{c_n - d_n(w_n(y) + \xi_n^* + t_n^*) - y} \right) = a_n \frac{w_n(y) + (t_n^* - b_n \xi_n^*) y}{(1 + \xi_n^*)^2} - y t_n^* e^{c_n - d_n(w_n(y) + \xi_n^* + t_n^*) - y} - y t_n^* e^{c_n - d_n(w_n(y) + \xi_n^* + t_n^*) - y}.
\]

for every \(y \in U_0\) and \(n \in \mathbb{Z}\). The above Taylor expansion of \(w_n\) as ansatz in the invariance equation shows that the coefficients \(\omega_n\) indeed satisfy the linear difference equation (see [30, Thm. 4.2(b)])
\[
\omega_n^* = a_n \frac{2 d_n \xi_n^* - 2 c_n}{(1 + \xi_n^*)^2} + \frac{e^{d_n \xi_n^* - 2 c_n b_n t_n^*}}{(1 + \xi_n^*)^3} + 2 e^{d_n \xi_n^* - c_n} t_n^* + 1 + d_n t_n^*,
\]
whose unique bounded solution is given by the expression stated above. \(\square\)
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