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Evolutionary literacy as a catalyst for sustainable futures: connecting biological evolution education and education for sustainability

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Abstract
In the face of growing societal, public health and environmental challenges linked to the functioning of the biosphere, strong evolutionary literacy emerges as indispensable to plan and achieve sustainable futures. However, research on evolution education has mainly focused on the content taught in classrooms, leaving its application to sustainability issues largely unexplored. Given this, in this paper, we suggest an integrated view of biological evolution education and sustainability education. For that, we argue for the pivotal role of evolutionary literacy to address diverse sustainability issues and for the development of key competencies in sustainability, namely systems thinking and anticipatory competencies. To support the implementation in classrooms, we propose educational strategies to promote evolutionary literacy, systems thinking and anticipatory competencies through socioscientific issues linked to sustainability topics. Finally, we identify future research needed at the intersection of evolution education and education for sustainability to effectively promote evolutionary literacy and the development of key competencies in sustainability. With this, we aim to contribute to further enhancing education for sustainability through the lens of evolution.

Keywords Evolutionary literacy, Education for sustainable development, Socioscientific issues, Systems thinking competency, Anticipatory competency, Key competencies for sustainability, Evolution education

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Introduction

Sustainability, as defined by Wiek et al. (2015), embodies the collective willingness and capacity of a society to sustain its viability, vitality, and integrity over extended periods while facilitating other societies in achieving or maintaining their own sustainability. Presently, we confront a range of major challenges to sustainability that are jeopardizing the existence of numerous societies and endangering the biological support systems of the planet (Folke et al. 2021; United Nations 2023, 2015). These challenges, which have recently been conceptualized as a polycrisis (Søgaard Jørgensen et al. 2024a), encompass, but are not limited to, global health crisis, biodiversity crisis, climate change-induced phenomena such as heightened global temperatures and rising sea levels, ocean acidification, increasingly frequent and severe natural disasters, depletion of natural resources, and various forms of environmental degradation (e.g., desertification, drought, land degradation, freshwater scarcity, and loss of biodiversity). These multifaceted challenges are characterized by intricate interdependencies, lack of straightforward solutions, substantial potential for global harm, and urgent imperatives (Wiek et al. 2011). Given their complex, ill-structured and controversial nature, these challenges can also be considered socioscientific issues (SSI, Zeidler et al. 2019).

To effectively address these challenges, individuals and all levels of society must possess the capacity to make informed decisions and devise innovative and effective solutions. This requires a comprehensive overhaul of education on a large scale, aimed at equipping not only sustainability professionals but also future generations of professionals across diverse domains with the requisite skills (Wiek et al. 2011). But a recent study showed that while university students value sustainability and would appreciate greater integration into their courses, they perceive it as being lacking in their curricula (Isaac et al. 2024). Education for sustainable development plays a crucial role in fostering competencies that enable effective problem-solving and task performance in addressing real-world sustainability challenges (Wiek et al. 2011). These competencies are essential for creating a fair and sustainable society and empowering current and future generations to meet their needs in a balanced and integrated way across economic, social, and environmental dimensions of sustainable development (UNESCO 2018; Wiek et al. 2015, 2011). Sustainability competencies are not limited by disciplinary boundaries or specific content knowledge (De Haan 2006). Instead, they represent overarching learning goals that are necessary for addressing the complex challenges we encounter in our daily lives (UNESCO 2018; Wiek et al. 2015). Different authors have presented varying numbers of key competencies in sustainability. Initially, Wiek et al. (2011) proposed a set of five competencies (systems-thinking, anticipatory, normative, strategic, and interpersonal competencies), introducing later a sixth competency (integrated problem-solving, Wiek et al. 2015). Building from these, (UNESCO 2018) suggests a broader range of eight competencies: systems-thinking, anticipatory, normative, strategic, collaborative, critical thinking, self-awareness, and integrated problem-solving.

By embracing a holistic approach to competency development, individuals can harness the power of evolutionary perspectives to address the multifaceted societal challenges of today (Eirdosh and Hanisch 2023; Hanisch and Eirdosh 2023). Indeed, the integration of evolutionary insights into governance and policies stands as a promising pathway towards achieving the ambitious targets set forth by the United Nations Sustainable Development Goals (SDGs, Jørgensen et al. 2019; Søgaard Jørgensen et al. 2024b). This is not limited to biological evolution, but also extends to general systems dynamics, and human cultural evolution (Richerson et al. 2024). Practices grounded in evolutionary biology hold significant promise in driving sustainable outcomes across diverse fields (Carroll et al. 2014; Jørgensen et al. 2019; Matthews et al. 2020). In fact, a deep understanding of evolutionary processes is essential for tackling several important societal issues such as biodiversity loss, climate change, public health, food security (Carroll et al. 2014), antimicrobial resistance and pandemics (Lederberg 1988). To address these complex socioscientific issues, we need citizens with a thorough understanding of biological evolution and evolutionary processes who can effectively apply this knowledge to make well-informed choices, devise solutions, and/or evaluate those by anticipating their most probable evolutionary outcomes (Fowler and Zeidler 2016). Recognising the crucial role played by evolution education for future societies and democracies, the Resolution 1580 of the Parliamentary Assembly of European Council (Parliamentary Assembly of European Council 2007) urges the teaching of evolution as a fundamental scientific theory in the school curricula. In the U.S., National Academy of Sciences (NAS) states that "few other ideas in science have had such a far-reaching impact on our thinking about ourselves and how we relate to the world" (National Academy of Sciences 1998, p. 21) and that "the teaching of evolution should be an integral part of science instruction" (National Academy of Sciences 1999, p. 2). In addition, the American Association for the Advancement of Science (2011) and the NGSS Lead States (2013), consider it a core idea for achieving biological literacy, emphasizing that it plays a vital role in facilitating the organization of biological knowledge. The U.S. National Research Council (2012) argues that evolution should be considered one of the four key concepts of biology to be explored from kindergarten onward, progressively increasing in complexity. However, despite its widespread recognition as a fundamental unifying principle in biology, evolution continues to be inadequately understood by most (Asghar et al. 2007; Athanasiou and Mavrikaki 2014; Kuschmierz et al. 2020; de Lima and Long 2023; Nehm et al. 2009) and it is even rejected by many individuals (Weisberg et al. 2018). Despite Resolution 1580 (Parliamentary Assembly of European Council 2007), a recent analysis of mandatory curricula from 18 European countries and Israel (Mavrikaki et al. 2024) reveals that these still cover, on average, fewer than half of the essential learning objectives crucial for scientific literacy in evolution (Sá-Pinto et al. 2021a; b). Furthermore, the predominant learning goals address basic knowledge of evolution and objectives concerning the mechanisms of evolution are frequently omitted or sparingly referenced. Equally important, the integration of evolution with its practical applications in daily life is notably lacking across the analyzed curricula (Mavrikaki et al. 2024). The analysis of 8 European best selling textbooks show that these educational resources reflect the same problems identified in the countries' curricula, although more evolution key concepts were explored in the textbooks than those predicted by the countries' curricula (Panayides et al. 2024).

The present situation is not in line with the results of studies that show that students can successfully learn, understand, and apply evolutionary key concepts to explain and predict biological scenarios after pedagogical interventions even at early educational levels (Brown et al. 2020; Campos and Sá-Pinto 2013; Emmons et al. 2018; Kelemen et al. 2014; Sá-Pinto et al. 2021a, b). Until recently, most studies have focused on assessing the impact of pedagogical interventions on the acquisition of evolution content knowledge rather than exploring their influence on the broader development of evolutionary literacy (as defined by Kampourakis 2022). This broader perspective is pertinent to addressing questions that students may encounter as active citizens and considers the philosophical implications of scientific knowledge on one's worldview. In fact, research suggests that even biology majors do not often use evolutionary principles to argue about complex societal challenges, such as genetic engineering issues, with consequences in their decision-making (Sadler 2005).

Despite the recognition of the importance of integrating evolutionary insights to achieve ambitious sustainability targets (Jørgensen et al. 2019; Søgaard Jørgensen et al. 2024b) and the acknowledged need to reconsider evolution education for enabling students to effectively address ongoing societal challenges (Kampourakis 2022), to the authors' knowledge, no study has yet explicitly connected biological evolution within the concept of education for sustainable development. This absence in the literature contributes to a fragmentation of knowledge, where the integration of evolution education and sustainability education remains largely unexplored. While systems thinking has some presence in this intersection, many of the other key competencies in education for sustainability may not be exactly linked with evolutionary principles. Although evolutionary literacy can contribute to the development of various sustainability competencies, systems thinking and anticipatory competencies are especially pertinent when applying evolutionary insights to real-world problems. In fact, evolutionary processes offer a crucial foundation for systems thinking, helping students grasp the complexity of biological systems and strengthen anticipatory competency by enabling students to predict how evolutionary dynamics may shape future biological and environmental challenges. In this paper, we focus on the role of biological evolution in addressing sustainability challenges (Carroll et al. 2014; Matthews et al. 2020; Jørgensen et al. 2019). While evolutionary literacy can encompass both biological and cultural evolution, our emphasis is primarily on biological evolution, particularly in the context of primary and secondary education. We recognize the relevance of cultural evolution in addressing sustainability issues (Brooks et al. 2018; Currie et al. 2024); however, this paper is limited to biological evolution, which has been underexplored in sustainability education at these educational levels. As such, we do not attempt to cover every evolutionary concept in detail but rather focus on the most fundamental and basic concepts to foster sustainability competencies in younger students. Future research should build upon this foundation, potentially integrating cultural evolutionary perspectives and more complex evolution concepts to further enrich sustainability education. Thus, in this paper, we: (1) explore the importance of evolution education in enhancing students' systems thinking and anticipatory competencies within the context of biological systems; and (2) discuss and propose teaching resources to explore evolutionary principles within the scope of sustainability issues that are promising for promoting the development of systems thinking and anticipatory competencies in students from primary to secondary school; (3) identify future work needed for evolution education to more effectively contribute to students' key competencies in sustainability.

The importance of evolution education in enhancing students' systems thinking and anticipatory competencies

Systems thinking competency

Systems thinking competency involves recognizing and understanding relationships, analyzing complex systems, understanding how systems are connected across various domains and scales, and navigating uncertainties (UNESCO 2018; Wiek et al. 2011). This competency facilitates the efficient analysis and synthesis of information (Senge 1990) and is fundamental to inform reasoning processes needed for anticipatory competence (Arnold and Wade 2015). The importance of systems thinking in education has been underscored by researchers and educators (Arnold and Wade 2015; Brandstädter et al. 2012; Plate 2010; Senge 1990), and recognized as one of the fundamental competencies that requires substantial attention in 21st-century education (National Research Council 2010).

In biology education, the development of systems thinking skills is a key learning goal since biology is considered to be the study of living systems (Momsen et al. 2022; Verhoeff et al. 2018). Living systems scale from cells' organelles and organisms to communities and ecosystems, and consist of various components that interact, share common properties and perform essential functions (Momsen et al. 2022). These functions involve the acquisition, utilization, and conversion of energy and matter, the storage, employment, and transmission of genetic information, and the reception and response to environmental cues. The importance of systems in biology is highlighted by key educational standards. Vision and Change (American Association for the Advancement of Science 2011) and the Next Generation Science Standards (NGSS Lead States 2013) both identify systems as core concepts. This emphasis is also reflected in most European national science curricula (European Commission. Education, Audiovisual and Culture Executive Agency and Eurydice 2011).

In biology, evolution is universally acknowledged as the predominant unifying theme in the field (American Association for the Advancement of Science 2011; NGSS Lead States 2013) as it serves as a fundamental link that connects various biological components and scales and affects and is affected by numerous biological processes (Momsen et al. 2022). Evolution can provide a fundamental link between biological content and emphasize the similarities in the complexity of the discipline (Tibell and Harms 2017), serving as a catalyst for inter- and intradisciplinary connections, facilitating the integration of concepts derived from diverse scientific disciplines, including biology, physics, and Earth and space sciences (National Research Council 2012), thus contributing to the understanding of complex systems. This integrative role empowers students to develop their systems thinking, acquiring a comprehensive understanding of the natural world and its countless biological systems through diverse disciplinary lenses, enabling them to effectively tackle new situations (National Research Council 2012). Evolution is an emergent process as it occurs in a given organizational level due to the behavior of agents in lower levels (Cooper 2016). In fact evolution occurs at population level causing species divergence and the emergence of higher taxonomic groups. However it results from the interactions between the individuals in their environment, which in turn are affected by processes taking place at cellular level. This feature makes evolution a very good topic to explore and link different organizational levels, allowing students to better understand the complexity of biological systems (Tibell and Harms 2017). Furthermore, understanding evolutionary processes enables and requires individuals to recognize the intricate web of relationships within ecosystems, populations, and genetic networks, from organismal interactions to feedback loops shaping population dynamics (Carroll et al. 2014; Jørgensen et al. 2019; Matthews et al. 2020; Sá-Pinto et al. 2021a, b). In fact, selective pressures in a given ecosystem result in species evolution, but this evolution will in turn change the ecological interactions and the selective pressures that affect this species (Beckerman et al. 2016). Ignoring such feedback loops and processes may seriously compromise sustainability. A good example of this is the human induced evolution in fish size and its outcomes. A decrease of the average size of individuals across generations has been reported for many marine species, caused by several human related factors including size-selective harvesting and climate change (reviewed in Audzijonyte 2013). But even small decreases of average size of certain species result in positive feedback loops that lead to higher mortality rates due to natural predation and resulting in much lower biomass and catches of these species (Audzijonyte 2013). Fisheries management plans that ignore such processes will result in unsustainable practices and overcatching. In the paper by Matthews et al. (2020), the authors also discuss how human activities affecting gene flow among populations can lead to the introduction of beneficial or deleterious alleles, impacting population adaptation and conservation efforts. These examples highlight the interplay between genetic variation, population and ecosystems dynamics, and human activities, illustrating the relevance of systems thinking in understanding the multifaceted nature of evolutionary processes and how these interact with human driven changes. This understanding fosters the development of systems thinking competency by encouraging students to analyze complex systems and to analyze how changes in one part or hierarchical level of a system can lead to cascading effects throughout the entire system. Moreover, students can develop an appreciation for the dynamic nature of biological systems and the mechanisms through which organisms adapt to environmental pressures (Carroll et al. 2014; Jørgensen et al. 2019; Matthews et al. 2020). By examining the processes of speciation, adaptation, and extinction over geological timescales, students can also develop a deep appreciation for the temporal dynamics of biological systems (Carroll et al. 2014; Jørgensen et al. 2019; Matthews et al. 2020). This long-term perspective encourages students to consider the historical context and evolutionary trajectories of complex systems. Given this, we argue that understanding evolution and how its key concepts are interconnected is essential to understanding biological systems and developing systems thinking competency. Prior research has shown that even university students have problems with systems thinking, especially when it comes to sustainability. Students struggle with understanding complex interconnections, considering long-term consequences, and integrating knowledge from diverse fields (Hiller Connell et al. 2012). Evolutionary literacy can mitigate these challenges by emphasizing the interplay between ecological interactions, population dynamics, genetic diversity, and evolutionary time scales, which help students appreciate the adaptive capacity of species, the critical role of biodiversity, and the necessity of long-term perspectives in addressing sustainability issues. However, to the best of the authors' knowledge, there are no studies that have explored how understanding evolution enables the development of systems thinking competency. Nevertheless, some research has looked at systems thinking competency development in the context of other biology-related fields (Brandstädter et al. 2012; Knippels and Waarlo 2018; Lankers et al. 2023; Reinagel and Bray Speth 2016).

Anticipatory competency

Anticipatory competency is crucial in sustainability education (Rieckmann 2012) and involves creating personal visions for the future, assessing various potential outcomes, and managing risks and changes (UNESCO 2018; Wiek et al. 2011). Building on systems thinking, this competency requires forward-thinking abilities (De Haan 2006) and empowers individuals to envision and actively shape future scenarios. Students with anticipatory competency can predict and address future challenges by developing scenarios, synthesizing solutions, and implementing proactive measures, all aimed at steering societal, economic, communal, and environmental transformations in line with the Sustainable Development Goals (Wiek et al. 2015, 2011). The limited studies on the development of anticipatory competency highlight key challenges, including a lack of awareness and traditional curricula focused on short-term outcomes (Julien et al. 2018). Withycombe (2010) also emphasizes the conceptual complexity and cultural resistance to future thinking, which contribute to hesitation in adopting this competency. Evolution literacy can help address these challenges by fostering long-term thinking and providing a clear framework for understanding complex systems and the inevitability of change.

Understanding evolution is important for understanding how species have and are adapting over time and this knowledge is also crucial for anticipating and preparing for future challenges in diverse domains and inform proactive intervention strategies, in issues as diverse as those related with resistant pathogens and pests, biodiversity conservation and human health, allowing to understand and guide interventions to address issues like obesity and diabetes, among many others (Ashley et al. 2003; Carroll et al. 2014; Cordain et al. 2005; Gaziano and Pagidipati 2013; Greene and Reid 2012; Jørgensen et al. 2019; Mace and Purvis 2008; Matthews et al. 2020; Tabashnik et al. 2014; Woodcock et al. 2011; see Sect. "Systems thinking competency" for more detailed information).

To the best of the authors knowledge, no studies have examined how knowledge of evolution promotes the development of students' anticipatory competency from the standpoint of science education and education for sustainability, although evolutionary biology has been used to inform a number of research areas pertaining to sustainable development (Hendry et al. 2011).

Contributions based on the literature to the teaching of evolution for education for sustainable development

Connecting evolution's main principles with sustainability issues

The teaching and learning of evolution faces challenges from both religious/cultural objections and the non-intuitive complexity of evolutionary concepts for students (Kampourakis 2014; Smith 2010a, 2010b). To overcome the complexity of evolutionary concepts, Tibell and Harms (2017) proposed a comprehensive two-dimensional framework comprising fundamental principles, key concepts, and threshold concepts related to evolution, specifically natural selection, in an attempt to develop a tool that could assist in addressing students' challenges in this area. Although not developed with this purpose, this instrument can be used to promote the development of systems-thinking and anticipatory competency through evolution education. However, for this purpose, it is crucial to relate these concepts and connections to real-world cases and issues. In other words, it is necessary to foster two types of literacy in students. Firstly, evolution literacy, which pertains to the comprehension of evolutionary concepts taught in academic settings, and secondly, evolutionary literacy, which encompasses the understanding of societal issues that students may encounter as active members of the community associated with evolution knowledge and the corresponding ethical issues and dilemmas (Kampourakis 2022).

There are various issues, related to sustainability or of a socioscientific nature, that can be explored with an evolutionary lens. For instance, in the field of biodiversity conservation, the poor adaptation of species to factors such as climate change and pollution drives the reduction in biodiversity through species extinction (Barnosky et al. 2011). Within human health, changes in diet, environment, and lifestyle (e.g., obesity, diabetes, and cancer) cause a mismatch between previously adaptive phenotypes that are frequent and new selective pressures with potential impacts on individuals' health. This is strongly related with the importance of understanding human intraspecific variation to better understand individual health risks and inform more personalised therapies in advanced trial stages (Jørgensen et al. 2019; Lipinski et al. 2013; Suzuki and Matsubara 2011). Evolution also allows us to better understand cancer—an evolutionary process occurring within individuals' bodies—to develop more effective treatment strategies (Carroll et al. 2014). The emergence and frequency increase of new or drug-resistant pathogens, such as infectious diseases is also an evolutionary process and has been recognised as one of the most threatening global health problems (Jørgensen et al. 2016; Murray et al. 2022; World Health Organization 2014). Several evolutionary processes also affect food security (Carroll et al. 2014). These include: *(i)* the rise in pesticide resistance that has led to a decline in agricultural production, thereby compromising global food supplies (Søgaard Jørgensen et al. 2020; Tabashnik et al. 2014), *(ii)* the use of artificial selection and genetic improvement in food production over the years and its importance in facing current challenges (Jacobsen et al. 2013); *(iii)* the importance of conserving genetic diversity and autochthonous varieties to ensure agricultural resilience and adaptation to environmental changes (Castañeda-Álvarez et al. 2016; Godfray et al. 2010).

To foster the development of evolutionary literacy that will enable students to understand social issues they may encounter as active members of society, we describe how the main principles of evolution can be connected to the causes of sustainability problems (fostering systems-thinking competency) and how they can help to think about the development of possible solutions (fostering anticipatory competency). We will follow the list of main principles and key concepts proposed by Tibell and Harms (2017), since they considered previously published lists summarizing and organizing them. In addition, given that Tibell and Harms (2017) exclusively established key concepts for evolution by natural selection (which are easily extended to artificial or sexual selection), we opted to also incorporate genetic drift as a main principle and adopted the key concepts proposed by Price et al. (2014). Genetic drift holds significant relevance not only in understanding evolutionary processes but also for tackling societal issues (Andrews et al. 2012; Price et al. 2014), but empirical data also suggests that this process is less often explored by teachers, curriculum and textbooks (see Mavrikaki et al. 2024 and Panayides et al. 2024 and references therein). Given this, it is not surprising that students encounter challenges in understanding genetic drift and harbor various misconceptions surrounding it (Andrews et al. 2012; Beggrow and Nehm 2012). While other concepts, like epigenetics, morphological and behavioral plasticity, also hold significant potential for enriching the understanding of evolution and sustainability (Ducatez et al. 2020; Tombre et al. 2019), these are not the focus of this paper. Further research is needed to explore how these additional concepts can be integrated into evolution and sustainability education.

Following Carroll et al. (2014) we divided sustainability issues into two main groups: the group of issues where evolution occurs too quickly, usually taking place in unwanted organisms that we want to control (Table 1), and the group of issues where evolution occurs too slowly compared to the pace of environmental changes, usually taking place in desirable organisms that we want to protect (Table 2). For each type of sustainability issue, we identified real examples that can be used to illustrate how the main principles are related to the origin of the problem and/or its solution. To better illustrate these relationships, Figs. 1 and 2 show a schematic representation of an example of a problem belonging to each of the two groups. In these schematic representations, the links between the origin of the problem and the main principles of evolution are detailed.

Although research has been more focused on developing and promoting evolution literacy (Kampourakis 2022), there are already several examples in the literature that have explored, from an evolutionary perspective, sustainability issues that students may encounter in real-life contexts. These can be used to promote the simultaneous development of students' evolutionary literacy and key competencies in sustainability. The recently published book by Sá-Pinto et al. (2022) provides

Table 1 Evolution's main principles associated with the origin of sustainability problems and/or the possible solution in rapid evolution issues

Main principles	Key concepts	Problems	Solutions	Examples
Rapid evolution—control of unwanted organisms				
Intraspecific variation	1-Origin of variation (genetic changes) 2-Individual (phenotypic) variation 3-Differential fitness (likelihood to survive and reproduce)	Populations with high genetic diversity are expected to harbor more individuals with adaptive variations and increased fitness that may survive and reproduce better, under a set of conditions	Variability can be reduced with management plans or manipulated to introduce mutations that make individuals less fit under specific environmental conditions	Health: · Emerging infectious diseases (Das et al. 2020) · Antimicrobial resistance (Bal and Gould 2011; Cooper and Shlaes 2011; World Health Organization 2014) · Cancer resistance to therapies (Aktipis et al. 2011; Cunningham et al. 2011; Gillies et al. 2012; Silva and Gatenby 2010) · Ectoparasites drug resistance (Mohammadi et al. 2021) · Pest control (Alphey 2014) Environment: · Herbicide-resistant weeds (Powles and Yu 2010; Vigueira et al. 2013) · Insect pests (Tabashnik et al. 2014)
Reproduction	4-Heritable traits 5-Reproduction	Populations with short generation times and/or higher reproductive rates are expected to generate diversity faster, which is inherited by its descendants	Create conditions to reduce populations' size and/or growth rates by stopping individuals' reproduction and/or causing stress to change the ideal conditions that favor individuals' reproduction and subsequent inheritance	
Selection	6-Selection pressure 7-Differential survival 8-Differential reproduction 9-Frequency change 10-Speciation	Inadvertent selection of phenotypes that are detrimental. For example, the attempt to solve the problem may become a selective pressure favoring individuals resistant to the solution, allowing them to survive and reproduce, changing the population in such a way that the solution is no longer effective	Manipulate the environmental conditions to: (a) favor the survival/reproduction of individuals with non-detrimental phenotypes; (b) disfavor the survival/reproduction of individuals with detrimental phenotypes; (c) decrease the speed at which population change happens; (d) change the direction of population change	
Genetic drift	1-Random sampling error happens every generation 2-Random sampling error tends to cause a loss of genetic variation within populations, increasing genetic differentiation among populations 3-The magnitude of genetic drift is inversely correlated with population size 4-In populations with small effective sizes, genetic drift can overwhelm the effects of natural selection, mutation, and migration	Genetic drift makes it harder to predict the composition of the population of unwanted species e.g. for the planning of biological control programmes, refuge and dosage regimes, and the development of vaccines and vaccinations plans	Factors that reduce population sizes and the number of individuals that reproduce are expected to reduce populations' genetic diversity and contribute to the fixation of (slightly) deleterious alleles that reduce the average fitness	

Table 2 Evolution's main principles associated with the origin of sustainability problems and/or the possible solution in mismatch issues

Mismatch—protect desirable organisms

Main principles	Key concepts	Problems	Solutions	Examples
Intraspecific variation	1-Origin of variation (genetic changes) 2-Individual (phenotypic) variation 3-Differential fitness (likelihood to survive and reproduce)	Populations with low genetic diversity will harbor fewer individuals with phenotypes that are fit in diverse environments and environmental changes, precluding the populations' adaptation to new conditions and increasing their extinction rate	(a) Manipulate the processes that introduce variation in the population (such as mutation, recombination, hybridization and migration) to increase it; (b) introduce individuals that are able to survive and leave offspring in the new environmental conditions, for example, by using varieties already selected under similar conditions	Health: · Chronic diseases (Brownson et al. 2006; Cordain et al. 2005; Gaziano and Pagidipati 2013; Woodcock et al. 2011) Environment: · Biodiversity loss due to (i) habitat reduction and fragmentation (Chase et al. 2020), (ii) habitat change (Newbold et al. 2015), (iii) non sustainable exploitation (Myers and Worm 2003; Ripple et al. 2016), and iv) invasive species (Bellard et al. 2016); · Threats to food security posed by environmental changes (Beddington et al. 2012)
Reproduction	4-Heritable traits 5-Reproduction	Populations with long generation times and/or lower reproduction rate are expected to generate diversity more slowly and pass it to the next generations through inheritance	Create conditions to increase populations' size and/or reduce environmental stress to favor reproduction near biotic potential	
Selection	6-Selection pressure 7-Differential survival 8-Differential reproduction 9-Frequency change 10-Speciation	Environmental changes have modified the conditions and selective pressures upon which current populations have been selected, causing an environmental mismatch. The fittest individuals are unable to ensure survival and reproduce enough to avoid species' reduction and extinction For humans, evolution under distinct selective pressures in the past caused divergence and local/cultural adaptations in some specific traits. When these selective pressures change due to migration and/or changes in the socio-economic conditions, the individuals under the new selective pressures may suffer health problems	(a) reduce environmental mismatch by approximating the environmental conditions to those under which populations have been selected, (b) favor the survival/reproduction of individuals with suitable phenotypes, (c) prevent extinction by promoting adaptation/exchange of populations For humans, health outcomes result from the complex interplay between several factors, including the individual's genetic traits and their environment/lifestyles. To reduce the mismatch changes in lifestyle and/or the use of specific therapies may be needed to ensure individual's health and well-being under the new environment	
Genetic drift	1-Random sampling error happens every generation 2-Random sampling error tends to cause a loss of genetic variation within populations, increasing genetic differentiation among populations 3-The magnitude of genetic drift is inversely correlated with population size 4-In populations with small effective sizes, genetic drift can overwhelm the effects of natural selection, mutation, and migration	Factors that reduce population sizes and the number of individuals that reproduce are expected to reduce populations' genetic diversity and contribute to the fixation of (slightly) deleterious alleles that reduce the average fitness	Reduce the factors that reduce population sizes and the number of individuals reproducing, such as habitat reduction and fragmentation, selection of few breeding individuals, etc	

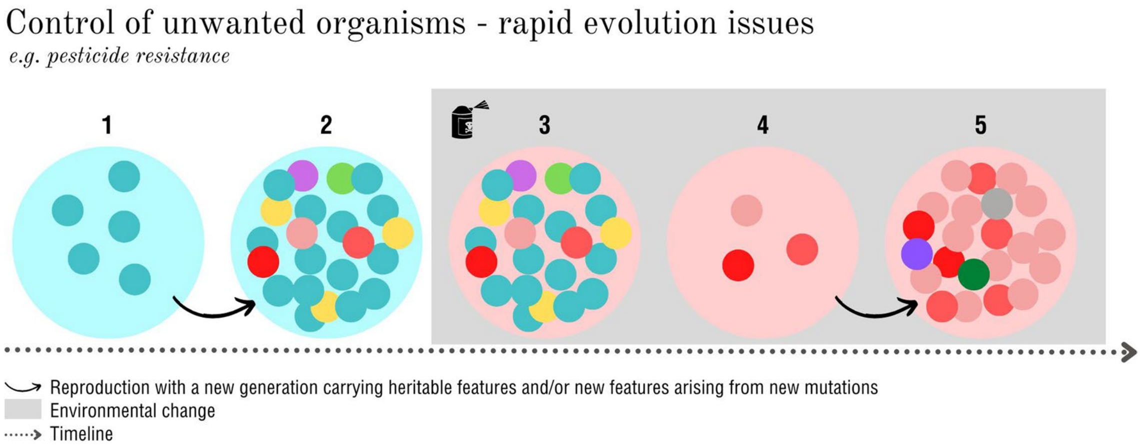

Fig. 1 Schematic representation of pesticide resistance linked with the main principles of evolution. *1*—Initial population; *2*—A population with a short generation time and/or a high reproduction rate is expected to rapidly grow through and quickly generate intraspecific variation; *3 and 4*- When the environment changes—e.g., the use of pesticides to control unwanted organisms—there is a mismatch between the organism's features and the environment, and many individuals will die. But among the high intraspecific variation of the previous population, some individuals have features that enable them to survive and reproduce more than others, passing these features to their offspring more frequently (selection); *5*—This leads to a frequency change (evolution), with the characteristics that allow their carriers to survive and reproduce more becoming more frequent over generations (selection) and reducing the effect of the solution employed to control the pest species. Some offspring will carry new mutations and may be different, increasing intraspecific variation again. This process is a good example of a downplayed problem archetype (for more information, see Moallemi et al. 2022)

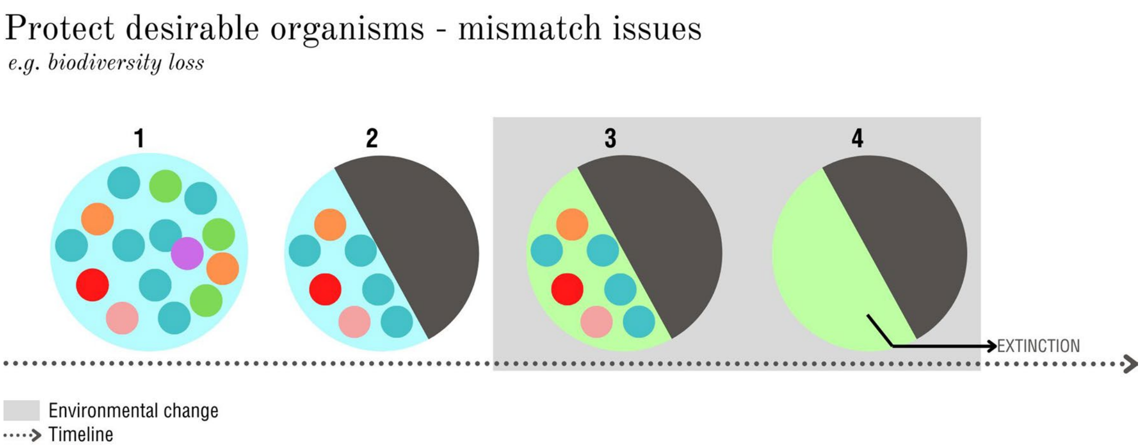

Fig. 2 Schematic representation of biodiversity loss linked with the main principles of evolution. *1*—Initial population harbors intraspecific variation; *2*—The population size was reduced—e.g., due to habitat loss—and genetic drift resulted in random changes in the frequency of traits, and in a reduction of intraspecific variation; *3*—When the environment changes, there is a mismatch between the organism's features and the environment, and many individuals will die. Low intraspecific variation decreases the probability that at least some individuals are able to survive in the new environment; *4*—A population with a long generation time and/or low reproduction rate is expected to generate intraspecific variation more slowly compared to the speed of changes in the environment. Given the low intraspecific variation, there are no individuals with characteristics that allow them to survive in the new environment, causing species extinction

several examples of these. It offers proposals related to the impact of solar radiation on our health (Ponce et al. 2022; Siani and Yarden 2022), the management of common pool resources (Hanisch et al. 2022), the decline of pollinators (Lewis et al. 2022), and genetic engineering (Schrijver et al. 2022). Additionally, there are also examples of proposals related to the conservation of biodiversity (Campos and Sá-Pinto 2013), fisheries sustainability (Pires et al. 2016), influenza virus (Nogueira and Ponce 2021), coronaviruses (Duarte et al. 2021; Institute of Science and Technology Austria 2022), and the importance of intraspecific biodiversity in food species (Afonso et al. 2021; Pessoa et al. 2024). A recent review suggests exploring socioscientific issues through evolutionary perspectives can develop key sustainability competencies but has limitations in enhancing anticipatory competency (Pessoa et al. 2022).

Teaching approaches for systems thinking and anticipatory competencies

Over the past decade, there have been several attempts to collect and analyze pedagogical approaches for developing key competencies in sustainability (Tejedor et al. 2019) and, more recently, to link these approaches to the development of specific sustainability competencies (Lozano and Barreiro-Gen 2021). In the field of education for sustainability, pedagogical approaches like eco-justice and community, project- and/or problem-based learning, community service learning, interdisciplinary team learning, mind and concept maps, jigsaw/interlinked teams, and place-based environmental education have been shown to be more effective in developing sustainability competencies than case studies, supply chain/life cycle and lectures (Lozano et al. 2019). According to the same study anticipatory competency was often developed through project/problem-based and community service learning, while systems thinking was less frequently developed. Unlike the studies in education for sustainability, in biology education, numerous studies have focused on exploring educational approaches aimed at fostering systems thinking competency in students across various fields of biology. For example, model-based instruction is one of the approaches that have been demonstrated to enhance the development of systems thinking in students, by engaging them in using, building, revising, and evaluating models (Wilson et al. 2020). Within evolution education, models have also been used to assess evolutionary knowledge and reasoning (Dauer and Long 2015; de Lima 2021).

Given the diverse pedagogical approaches employed in both education for sustainable development and evolution education and considering their potential benefits, Table 3 highlights resources that could be used to bridge these two fields. To organize and clearly present the potential of each resource's adaptation, based on the literature, we categorize them as being more suitable for the development of one particular key competency (either systems thinking competency or anticipatory competency). However, we acknowledge that some of these resources, if adapted, can be used to develop more than one competency, while others may benefit if supplemented with additional resources. Additionally, an activity proposal aimed at developing systems thinking and anticipatory competencies and evolutionary literacy, using some examples of resources presented here, can be found in Additional file 1. It should be noted that this proposal requires future implementation, testing, and evaluation to determine its effectiveness.

Systems thinking competency

To promote systems thinking competency, students should engage in tasks that allow them to: (i) recognize and understand relationships, (ii) analyze complex systems, (iii) think about how systems are embedded within different domains and different scales, and (iv) deal with uncertainty (Juuti 2021). In this paper, we do not intend to explore exhaustively the resources already identified in the literature. Instead, we will explore some illustrative examples of resources that we think could be easily adapted to evolution education:

– *Concept maps* (Brandstädter et al. 2012) are external representations of mental models composed of con-

Table 3 Examples of resources to develop systems thinking and anticipatory competencies that could promote evolution education

Resources	References	Key competency in sustainability suitable for development	
		Systems thinking competency	Anticipatory competency
Concept maps	Brandstädter et al. (2012)	✓	
Causal diagrams, causal loop diagrams, or causal maps	Cox et al. (2019), Cho and Jonassen (2012)	✓	☐
Yo-yo strategy	Knippels and Waarlo (2018)	✓	☐
Models	Wilson et al. (2020)	✓	☐
Computer simulations	Lankers et al. (2023)	✓	☐
Drawings	Julien et al. (2018)		✓
Scenarios	Julien et al. (2018)		✓
Role playing	Julien et al. (2018)		✓
Creating scenarios, visions and strategies	Withycombe (2010)	☐	✓

✓—suitable for the development of the key competency based on the literature; ☐—considered suitable for the development of the competency by the authors cepts interconnected by lines, forming a hierarchical or non-hierarchical network structure. Concept maps can be created on paper or on a computer, and the concepts may or may not be provided to students in advance. Evolution education can easily be included in this strategy by asking students to attempt to relate in their concept map the main principles, key concepts, and threshold concepts of evolution following the framework proposed by Tibell and Harms (2017), for example.

- *Causal diagrams, causal loop diagrams, or causal maps* (Cox et al. 2019; Cho and Jonassen 2012) are visual representations of cause-effect relationships within systems, using arrows to show the direction of influence. These diagrams are valuable tools for modeling complex systems, helping students grasp intricate cause-effect dynamics, such as those found in evolutionary processes. When applied to evolution education, causal diagrams effectively illustrate the multifaceted causality in evolutionary changes, enhancing students' systems thinking by encouraging exploration of multiple causal pathways (Hanisch and Eirdosh 2021). Moreover, they have been used to study evolutionary processes within social-ecological systems, offering insights into sustainability challenges in the Anthropocene (Currie et al. 2024).
- *Yo-yo strategy* (Knippels and Waarlo 2018) requires students to analyze biological phenomena by understanding the various levels of biological organization. This involves distinguishing and connecting these levels with key concepts, creating coherence horizontally (when linking with one level) and vertically (when linking with successive levels). Students should look for causal explanations by moving down and holistic explanations by moving up the levels. To develop yo-yo thinking, students should also reflect on the activities carried out and think about how and when they could apply yo-yo thinking to different biological phenomena. To adapt this strategy to include evolution education, students could explore biological phenomena at different levels of organization, ranging from molecular and genetic processes to ecosystem dynamics and evolutionary patterns over time (Tibell and Harms 2017). For example, they could examine how genetic variation within populations leads to phenotypic diversity and adaptation, and how these adaptations influence the survival and reproductive success of individuals within changing environments. Students could also investigate how evolutionary processes operate at the population, community, and ecosystem levels, shaping biodiversity, ecosystem services, and resilience to environmental disturbances. By distinguishing and connecting these levels with key evolutionary concepts, students may develop a coherent understanding of how biological systems function and evolve over time.
- *Models* (Wilson et al. 2020) are a simplified representation of a natural or social phenomenon that emphasizes specific aspects of the system (e.g., components, processes, or system function). Models are often used to represent elements of a system that are abstract, invisible, or exist on a scale that is too small or too large to be perceived, and can serve to explain and/or predict phenomena (Wilson et al. 2020). There are already some proposals based on models to foster evolution education. Namely, there are models that explore the mechanisms of evolution, such as natural selection (Grilliot and Harden 2014; Núñez et al. 2022; Peel et al. 2019; Pires et al. 2016), genetic drift (Campos and Sá-Pinto 2013), and sexual selection (Sá-Pinto et al. 2023). Nevertheless, there is room for improvement in these educational proposals to ensure they align with the recommendations of the evidence-based teaching guide 'Modelling in the Classroom', which provides instructors with a toolkit for incorporating models and modeling into their classrooms (Wilson et al. 2020).
- *Computer simulations* (Lankers et al. 2023) represent a specific category of models that provide access to complex systems by making the structure and dynamics observable. System simulations are often used to enhance systems thinking in intervention settings and from a modeling perspective. Numerous educational simulators focusing on evolution have been developed, with research demonstrating significant learning outcomes following their use. For instance:

  - Avida-ED—a digital evolution software environment designed for teaching and learning about evolution and the nature of science (Bray Speth et al. 2009; Smith et al. 2016);
  - EvoSketch—a web-based simulation software that allows learners to explore random and probabilistic phenomena associated with the process of natural selection (Fiedler et al. 2018);
  - EVOLVE—a software simulation that enables students to learn about population genetics by manipulating selection, genetic drift, and migration (gene flow), observing the effects on a population over time (Soderberg and Price 2003);
  - SimulATe—a software that can be used to model the effects of antibiotic selective pressure (David et al. 2019).

- Sim-Evolution—a simulator designed to explore three basic principles of the theory of evolution by natural selection (trait variation within a population, heritability of trait variation, and selective survival based on heritable traits; Cardoso et al. 2020);
- EvoluZion—a computer simulator designed to perform real-time simulations of virtual organisms for teaching genetic and evolutionary concepts (Zurita 2017).
- NetLogo—a multi-agent modeling tool widely used in biology and sustainability education. It enhances understanding of system dynamics and evolutionary processes. Studies have demonstrated its effectiveness in teaching evolution as an emergent process (Wilensky and Novak 2010; Wilensky and Reisman 2006) and natural selection (Dickes and Sengupta 2013). NetLogo is also applied in sustainability science, simulating scenarios like resource management and sustainable behaviors (Hanisch et al. 2023a, 2023b; Waring et al. 2017).

Anticipatory competency

Thinking about the future is inherent when we consider sustainability. However, in an educational context, thinking about the future poses a real challenge. Although many official documents emphasize the need to reflect on the future in education, they largely focus on promoting knowledge about the past and present (Julien et al. 2018) and typically only contain implicit references, not raising any questions nor presenting clear proposals to develop anticipatory competency or to ensure real implementation (Gough 1990; Hicks and Holden 2007; Jones et al. 2012). Given this, it is essential to develop educational approaches that enable the development of this competency, and specifically, when approaching biological systems, it is crucial that this competency is informed by evolution. To promote anticipatory competency, students should engage in tasks that allow them to: (i) understand and evaluate several futures (possible, probable, and desirable, (ii) create one's own visions of the future, (iii) apply the principle of precaution, (iv) assess the consequences of actions, and (v) deal with risk and change (Juuti 2021). Although evolutionary biology has been used to make predictions in various research areas related to sustainable development (Hendry et al. 2011), to the best of the authors' knowledge, there are no studies proposing the development of anticipatory competency from an evolutionary perspective. Therefore, we will explore some illustrative examples of resources that can be adapted to evolution education:

- *Drawings* (Julien et al. 2018) used as a means for students to articulate their visions of the future within a sustainability context. For instance, students may be tasked to create two illustrations: one depicting the landscape of their aspirations or idealized future (preferred future), and another based on the insights derived from researchers and stakeholders they have been exposed to (probable future). If we add the illustration of the present to this strategy, we can easily introduce evolution by comparing the various drawings and discussing their differences. Specifically, the comparison of frequencies of individual characteristics across various drawings enables an examination of evolutionary mechanisms that result in changes in these frequencies. Moreover, the illustration based on the insights derived from researchers and stakeholders, may also reflect the probable future landscape influenced by evolutionary dynamics and environmental changes. Students could be asked to try to represent evolutionary processes such as adaptation, speciation, and natural selection, highlighting how these mechanisms influence populations and ecosystems over time. This strategy, coupled with a description of what happens between the present and the future scenarios, has already been used to evaluate students' understanding of evolutionary processes (Sá-Pinto et al. 2023, 2018).
- *Scenarios* (Julien et al. 2018) are relevant tools for exploring potential futures and promoting alternatives to the present. For example, students can be tasked with constructing a model of the landscape as it might appear in a situation of climate change. They can be prompted to prioritize proposals from the most likely to the least likely. Additionally, students can be instructed to describe/label the changes in various areas of the landscape (e.g., mountain, forest, river, pastures, and village). To introduce evolution education into this strategy, it would be necessary to ask students to consider the most and least likely scenarios, taking into account evolutionary processes. For instance, they could explore if, how and how likely species are expected to evolve in response to changing environmental conditions, such as shifts in temperature or precipitation patterns or in species/individuals present in the ecosystems. They might also justify/describe those changes based on the main principles of evolution and brainstorm solutions to shift from the most probable scenarios to more desirable scenarios using strategies informed by evolutionary principles.

- *Role playing* (Julien et al. 2018) is an interpretation of a character in a situation that allows each of the students to explore various roles, develop their personal point of view through dialogue with other protagonists, and take into account different perspectives. During a role-playing activity, students assume the roles of different stakeholders, and reflect on whether they agree or disagree with the proposal and whether they align with the arguments of the characters they represent. To promote evolutionary literacy with this strategy, students could assume roles such as environmental activists, scientists, or specifically evolutionary biologists. Students representing these roles might advocate for conservation efforts and preservation of natural habitats based on evolutionary principles and/or provide insights into the role of evolution in shaping biodiversity and ecosystem dynamics. Depending on the educational level, the potential viewpoints and arguments of these characters can be prepared in advance by the teacher or developed by the students by researching information in credible sources and/or interviewing people with these roles in real life.
- *Creating scenarios, visions and strategies* (Withycombe 2010) is done by creating four students' groups—current state, scenarios, vision, and strategies. The vision group and the scenarios group will envision desirable futures, in the form of a comprehensive vision, and possible futures, in the form of scenarios, for a city fifty years from now. The vision should be collaboratively developed by students and community members. Students and community members are tasked with envisioning the city in alignment with community values and sustainability principles. Students in the scenarios group will create possible future scenarios for the city based on its current state. The strategies group will receive the results from both groups and identify recurring points of contrast between the vision and the scenarios, which will serve as key points for intervention in the strategies they will develop. In this way, different types of future knowledge are generated by students and integrated into strategies to guide the development of a city's general plan. To adapt this strategy to include evolution education, students in the scenarios and in the strategies groups could be tasked with developing scenarios, strategies and solutions integrating evolutionary principles into planning and policy-making (as suggested in Tables 1 and 2).

Future work

This paper represents a first effort at directly aligning biological evolution education with key competencies in sustainability, recognizing the fundamental role of evolutionary literacy in addressing contemporary sustainability challenges. We provide (i) theoretical support linking evolution education with the development of systems thinking and anticipatory competency; (ii) a tool for educators to bridge evolutionary key concepts with the causes and solutions of present-day sustainability issues, fostering a deeper understanding of those; and (iii) a review of a range of teaching resources that can be utilized to promote evolutionary literacy, systems thinking and anticipatory competencies.

With this approach, we aim to inspire educators and education researchers to bridge evolution literacy with the development of key competencies in sustainability, contributing to the development of evolutionary literacy as defined by Kampourakis (2022). Research on how teachers explore, use, and adapt the framework here provided is now needed to develop a functional and effective resource to be used to support and empower educators. Another limitation of this work is that it is mostly focused on the processes of evolution, not addressing other dimensions that are important for evolution's understanding (Sá-Pinto et al. 2021a; b). However, sustainability issues such as geological resource management and conservation (such as fossils for example) require a strong understanding of dimensions of the history of life (and deep time). Finally, we should also notice that this work does not illustrate every single evolutionary concept and should be acknowledged as a contribution to bridging biological evolution education and education for sustainability. In fact, to foster evolutionary literacy, there is still progress to be made. The list of key concepts could be expanded to address higher educational levels, incorporating more complex concepts such as epigenetics, behavioral plasticity and adaptive capacity, as well as concepts identified in the literature as research gaps, including macroevolution, speciation, quantitative genetics, and population genetics (Ziadie and Andrews 2018). Additionally, cultural evolutionary concepts could also be incorporated to further enhance the development of evolutionary literacy, offering a more comprehensive understanding of how both biological and cultural evolutionary processes shape sustainability challenges (Hanisch and Eirdosh 2020, 2023). Moreover, although the different teaching approaches suggested here have been shown to be useful in promoting key competencies in sustainability, additional research is needed to understand how to best use them to simultaneously promote evolutionary literacy. Thus, as working hypotheses of this paper, several questions arise that need to be tested in future research: (1) how does understanding evolution affects the development of systems thinking competency? (2) how does understanding evolution promote the development of students' anticipatory competency? (3) how does the development of key competencies in sustainability (systems thinking and anticipatory competencies) contribute to the development of evolutionary literacy? Investigating these questions will not only help refine the approach proposed here but will also provide deeper insights into the connections between evolution education and sustainability competencies.

Furthermore, we contend that school curricula and textbooks must be modified in order to articulate evolution learning goals with sustainability issues. In fact, the reduced presence of evolution key concepts in the curricula and textbooks and the lack of articulation with main biology and sustainability topics have been suggested to contribute to the general lack of understanding and acceptance of evolution (Mavrikaki et al. 2024; Panayides et al. 2024; Pinxten et al. 2020). A recent analysis of the English, Italian, and Portuguese primary school curricula revealed significant opportunities to explore socioscientific issues concerning human health and the environment (Pessoa et al. 2024 submitted), many of which can be examined from an evolutionary perspective. Using issues related to sustainability that are already present in school curricula could facilitate a more seamless change in teaching practices. However, these changes also require thorough teacher training aimed at equipping educators to delve into socioscientific issues from an evolutionary perspective (Kampourakis 2022). Investing in teacher training is essential to address the challenges posed by educators' lack of pedagogical content knowledge and their reluctance to teach evolution, as highlighted in previous studies (Cavadas and Sá-Pinto 2021; Gresch and Martens 2019; Nehm and Kampourakis 2022; Prinou et al. 2011; Stasinakis and Athanasiou 2016; Ziadie and Andrews 2018). But as highlighted by Kampourakis (2022) research on how to empower teachers to promote sustainability education and evolutionary literacy is strongly and urgently needed. There is also a lack of appropriate tools, resources, and evaluation instruments suited to various grade levels that teachers can easily adapt and use to promote and assess students' evolutionary literacy and key competencies in sustainability. In general, research priorities should be refocused to emphasize more evolutionary literacy and less evolution literacy in conjunction with sustainability competencies. This will help recognize the connections between these domains and support a more holistic educational approach. We hope this paper marks the beginning of a journey to transform classrooms into dynamic hubs of social innovation and sustainability, where evolutionary concepts come alive and inspire real-world change.

Supplementary Information

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Additional file 1.

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Author contributions
P.P., J.B.L., A.P. and X.S.P. conceptualized and designed the work. P.P., J.d.L., P.S.J. and X.S.P. reviewed and interpreted the relationship between evolution key concepts and sustainability challenges. P.P., J.B.L., J.d.L. and X.S.P. reviewed and interpreted educational strategies and resources to promote evolutionary literacy and key competencies in sustainability. P.P., J.d.L. and X.S.P. conceptualized and designed the figures. P.P. drafted the first version of the manuscript, which all authors proposed edits to and approved in its final version.

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Data availability
No datasets were generated or analysed during the current study.

Declarations

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