Evo–Devo–Eco and Ecological Stem Species: Potential Repair Systems in the Planetary Biosphere Crisis

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Contents

Abstract We draw on well-established domains of the biology of evolution (EVO), development (DEVO), and ecology (ECO), particularly of plants, to develop the new concept of "stem species" based on "EVO–DEVO–ECO." In EVO the evolutionary

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theory of punctuated equilibrium of NILES ELDREDGE and STEPHEN JAY GOULD is thought provoking. These authors make use of spandrels, exaptations, and functional shifts to explain interruptions of stasis by punctuated speciation. In DEVO it is epigenetics where environment-induced chromatin methylations constitute heritable memories of experienced stress. In addition, spandrels, exaptations, and functional shifts shape the phenotypes emerging from reading the genome information. By feedback of development through the evolutionary selection of phenotypes, EVO–DEVO is more than the evolution of development. In ECO the thoughts dwell on the ecological impacts on development of phenotypes as well as the environmental pressure causing selection in evolution. EVO, DEVO, and ECO are nodes of a network with strong interactions between them. The "stem species" idea is issued by comparison with stem cells. In analogy to stem cells in organisms, "stem species" in ecosystems have multipotency and they fulfill repair functions in deteriorating and destroyed habitats. "Stem species" differ from invaders, nurse species, and pioneer species. This is exemplified. "Stem species" may strengthen optimism regarding self-repair and sustainability of the biosphere on Earth in a current time of extraordinarily irritating global changes.

1 Introduction

In the "Origin of Species" CHARLES DARWIN (1809–1882) above all developed the theory of EVOLUTION: EVO. He was much interested in DEVELOPMENT and growth on which many of his arguments were much founded (Friedman and Diggle 2011). He called DEVELOPMENT and embryology the most important aspects of natural history: DEVO. He did not outspokenly deal with ECOLOGY. ERNST HAECKEL (1834–1919) coined the term "ECOLOGY" in 1866, i.e., 7 years after the first publication of the "Origin" by DARWIN in 1859. However, the selective pressure of environmental conditions on organisms in evolution is an eminently ecological theme. This is the driving force of evolution considered in the "Origin": ECO. EVO–DEVO is well established in a large body of more recent literature. It is "the evolution of development" (Gould 2002). This can be extended as there is also feedback from development to evolution. Another extension is to take it a step further and add ECO arriving at an EVO–DEVO–ECO-concept (see Müller 2007; Gilbert and Epel 2009; Lüttge 2010a). An exegesis of the "Origin" could already bear out the entire EVO–DEVO–ECO-concept.

Ecology may lead us on to consider relations between environment and evolution on more global scales including the current planetary crisis. There have always been large ecological crises of global dimensions with waves of massive extinctions of species. We know of five large waves of massive species extinction during the last 450 million years occurring at intervals of 45–140 million years (100 million years on average), i.e.,

- 444 million years ago at the change from the Ordovician to the Silurian
- 364 million years ago at the change from the Devonian to the Carbonic
- 251 million years ago at the change from the Permian to the Triassic, when 90–95% of all existing species where extinct including the well-known trilobites
- 206 million years ago at the change from the Triassic to the Jurassic, when extinction was associated with the appearance of the dinosaurs
- 65 million years ago at the change from the Cretaceous to the Tertiary when 75% of all existing species were extinct and with them the ammonites and also the dinosaurs, which led to the tremendous proliferation of the mammals on Earth

(see Matyssek and Lüttge 2012).

All these waves of extinctions were due to environmental changes without any influence of man who did not exist at those times. We might call them natural environmental changes, but this would get us involved in the argument if we must not consider man as part of nature (Lovelock 1979, 2009; Wobus et al. 2010). Currently man is so severely affecting the planetary environment by output with overexploitation of natural resources and by input with pollution that we presently live in a sixth and evidently this time manmade planetary crisis.

The waves of extinctions were always followed or accompanied by innovations. New forms of life emerged with the expression of new traits making organisms fit for the changed environment. For examples of this feedback of ECO on EVO see Matyssek and Lüttge (2012).

Returning our view to DEVO we note that at the organismic level differentiation and development originates from omnipotent stem cells. If there are defects, omnipotent or pluripotent stem cells may also build up repair systems. This means that there is some potential of self-organization and self-sustainment in organisms, where stem cells are key elements in control and regulation. In this essay we ask the question whether there are mechanisms in habitats, ecosystems, or biomes up to the entire planet, which are similar with the only difference being scalar levels.

In 1979 Lovelock has conceived the entire biosphere of the planet including man as a supra-organism, which he named Gaia after the ancient Greek goddess of the Earth. He took Gaia as a self-organizing, self-sustaining entity stabilizing life. Indeed, notwithstanding large amplitudes of perturbations and the extinction waves and although survival of particular forms of life as such were never assured, life itself experienced sustainment throughout geological times. In another book 30 years later he proves much less optimistic (Lovelock 2009; Matyssek and Lüttge 2012; Lüttge 2012). In the current planetary environmental crisis, repair systems are needed for which particularly equipped species will be required. At the higher scalar levels of habitats and ecosystems such species should function in analogy to stem cells at the lower scalar level of organisms, so that we may call them “stem species” (Scarano and Garbin 2012).

We may reflect if the mammals following the dinosaurs after their extinction in the fifth of the waves named above as evolutionary innovations can be considered to have been such “stem species.” However, after inspecting some basic properties of stem cells, we will rather explore the possible properties and nature of “stem species” in actual extant ecosystems. Action of “stem species” as part of natural repair systems strengthens the ECO-part of the EVO–DEVO–ECO-concept.

2 EVO–DEVO–ECO

2.1 Evolution

2.1.1 Gradualism and Punctualism of Evolution

In evolution the selection leads to fixation and establishment of genotypes. In contrast to a provocative view (Dawkins 1976) selection never works on individual genes (Gould 2002, and Sect. 2.2). CHARLES DARWIN considered selection to act on individual organisms while STEPHEN JAY GOULD (1941–2002) argued that selection is also acting on species (Gould 2002). Both may occur. The selection of stem cells and their functions in development and in organismic repair systems might have been shaped by a DARWINian mechanism of selection at the level of individual organisms. Stem species as elements of repair systems of ecosystems more likely are subject to GOULDian selection at the species level. Some exegesis of Gould (2002) and the distinction of DARWINian gradualism and ELDREGEian/GOULDian punctualism of evolution are very useful for developing ideas how "stem species" may function. Comparisons highlighted in Table 1 demonstrate the essence of differentiation between gradualism and punctualism. The key difference is that according to DARWIN new species evolve gradually, whereas ELDREDGE and GOULD propose a "punctuated equilibrium" where species remain stable for long periods of stasis in geological time ("equilibrium") and speciation is rather rapid interrupting or punctuating the equilibrium. In principle it appears that both concepts are not mutually exclusive and both might operate in different cases. However, punctuated equilibrium allows us to deduce some key elements of the "stem species" hypothesis we aim to develop in this essay.

2.1.2 Spandrels or Exaptive Surprise by Nonawaited "Stem Species?"

Spandrels and exaptation are in the core of the mechanism of punctuated equilibrium. Spandrels especially in ecclesiastical architecture are the very poetic and esthetic structural metaphor used by GOULD for explaining exaptation. There are functional elements in architecture, e.g., in a two-dimensional view arches in a linear row or in a three-dimensional view hemispherical domes mounted on a set of four rounded arches meeting at right angles to form a square as in GOULD's favorite example of the dome of the Cathedral of San Marco in Venice. These elements serve a distinct architectural and static purpose. However, unavoidably the two-dimensional arches leave triangular spaces between them, and similarly in the three dimensions curved triangular pendentives form as a structurally necessary side consequence under the arches supporting the dome. These spaces or spandrels arise as geometric byproducts completely nonadaptive to the actual function. However, such forms not explicitly chosen to serve a purpose may unexpectedly turn out essential for marvelous use, i.e., in the case of the architectural spandrels for the most artistic ornamentation by mosaics or frescos.

Table 1 Comparison of gradualism and punctualism of evolution

DARWIN: gradualism	ELDREDGE and GOULD: punctualism
New species evolve gradually without periods of stasis	New species evolve rapidly and are then subject to long periods of stasis
Within the lineages of organisms fossils should display many forms of transitions	Fossils should display few forms of transitions and the maintenance of given forms over long periods of time
New species originate from transformation of the whole parent population lineage	New species have their origin in the splitting of lineages
The parent population is completely integrated in the new species	A small sub-population is the origin of the new species
The entire geographic range of the species is included in speciation (sympatric speciation)	The sub-population giving rise to the new species is located in an isolated part at the periphery of the geographic range of the species (allopatric speciation)

Spandrels of architecture are equivalent to the exaptations of organisms. Like spandrels exaptations are not forms explicitly selected for adaptation and for serving a special purpose or function under the conditions of here and now. They are rather "structures co-opted for utility from different sources of origin .... and not directly built as adaptations for their current function" (Gould 2002, p. 43). In other words, the nonadaptive property of exaptations allows a later or future cooption for utility, i.e., later becoming the prerequisite for success.

With respect to the underlying mechanism of punctuated equilibrium of evolution, we consider accumulation of neutral mutations or spandrels. They are neither of disadvantage or lethal, and thus eliminated by selection of the individuals carrying them, nor useful at the here and now, and thus positively selected as adaptations. Such neutral mutations accumulate and become useful when the equilibrium is punctuated by speciation *sensu* GOULD. These mutants may constitute an "exaptive pool" of traits which prove useful in changed or new environments. In addition there is the option of "functional shift" where traits adaptive to certain conditions can be found exaptive for different functions under different conditions.

With this brief exegesis of some aspects of the voluminous and great pace-making book of STEPHEN JAY GOULD (Gould 2002), we realize that "stem species" are an outcome of EVO–DEVO–ECO. GOULD guides us when we attempt to underline the important features of "stem species". They must have exaptive pools and they must have capacities of functional shift. Unlike adaptation which responds to given conditions, exaptation provides flexibility for future changes or with the precision given by GOULD: adaptation has function, whereas exaptation has effect (Gould 2002, p. 1233). This is exactly what we expect from "stem species": they must have effect.

2.2 *Development*

CHARLES DARWIN proposed that transformation of organisms over time in addition to natural selection is due to modification of development (Friedman and Diggle 2011).

ERNST HAECKEL first linked phylogeny and ontogeny by what he called the "biogenetic law" saying "ontogeny recapitulates phylogeny". We now have different and molecularly founded reasons to argue that evolution and development are intimately correlated and to advocate an EVO–DEVO–concept. Selection does not act on genes or genomes but on individual organisms or phenotypes. These originate in development from expression of the genetic information. This makes it immediately evident how EVO and DEVO are interwoven (Müller 2007; Gilbert and Epel 2009).

That selection does not act on genes is shown by the observation that several genes often interact to determine a specific given trait. This phenomenon is called epistasis. The organism expressing this trait is then subject to selection. Such epistasis rules out that selection is acting on the single individual genes involved. Development is based on the regulation of the expression of genes. One has used the metaphor that a genome is like a musical instrument such as a grand piano, dead and meaningless unless a musician plays it. A genome per se and in itself cannot be the incarnation. This is readily seen when we compare genome sizes of organisms with vastly different degrees of complexity. For example, the number of genes in:

- man 25,000; about 300 genes different from the chimpanzee (1.3%);
- a little nematode (*Caenorhabditis elegans*) and the fruit fly (*Drosophila melanogaster*) 15–20,000;
- the weed *Arabidopsis thaliana* 27,000.

It cannot be a small number of genes that make up for the differences of complexity between these organisms. Regarding the comparison between humans and chimpanzees, different in about 300 genes, this was already realized quite a while ago by King and Wilson (1975) "... that the genetic distance between humans and the chimpanzee is probably too small to account for their substantial organismal differences .... that evolutionary changes in anatomy and life are more often based on changes in the mechanisms controlling the expression of genes than on sequence changes ....".

This is currently developed in the vividly emerging field of epigenetics. The basic idea of epigenesis as a principle producing the gestalt of organisms dates back to JOHANN FRIEDRICH BLUMENBACH (1752–1840, see Gierer 1998) and then was picked up with giving it more precision by CONRAD HAL WADDINGTON (1905–1975). Molecular epigenetics is a system of reading the genetic information of DNA. The molecular mechanism of epigenetic regulation is based on the structure and conformation properties of chromatin modulated by acetylation and methylation, respectively, of DNA and nucleosomal histones. Only in the state of acetylation, DNA is accessible for regulator molecules of gene activation or deactivation due to the larger size of the acetyl group as compared to the smaller methyl group. In the state of methylation the genetic information of DNA is silenced. A functional analysis and a high-resolution genome-wide characterization of DNA methylation of *Arabidopsis thaliana* underlines the overarching role gene methylation must exert in the control of biological functions of genes (Zhang et al. 2006). An example showing how this can affect gestalt is given by the ubiquitous ruderal plant *Linaria vulgaris*. This species is normally characterized by bilateral symmetry of its yellow flowers.

There is also a rare form with radial symmetry of the flowers. CHARLES LINNÉ took it for a different genus which he named *Peloria*. We now know that both have identical DNA. The only difference is methylation of the promoter DNA of a single gene (*cycloidea, Lcyc*) in *Peloria* (Cubas et al. 1999; Paulsen 2007; Daxinger and Whitelaw 2010).

Epigenetic variations may be directed by the environment (Jablonka and Lamb 1989). There is increasing evidence that chromatin methylation patterns are strongly modified by environmental stress (Bond and Finnegan 2007; Chinnusamy and Zhu 2009; Adams 2010; Daxinger and Whitelaw 2010; Verhoeven et al. 2010), such as salt stress, nutrient stress, e.g., nitrogen deficiency (Kou et al. 2011), and chemical induction of anti-herbivore and anti-pathogen defenses (Verhoeven et al. 2010).

Epigenetic mechanisms are involved in memory functions of plants. Memory processes in the control of plant growth and morphogenesis (Thellier 2012; Thellier et al. 2012) and also in priming of defense reactions by previous attack (Bruce 2010; Heil 2010; van Hulten et al. 2010) comprise a form of habituation where after exposure to a first stimulus, subsequent responses to a second stimulus of the same type are modified. Most importantly there is a second form of memory which allows storage of information and recall of that information and is therefore termed STO/RCL. Storage of information can occur for various kinds of stress, such as manipulation of plants, drought, wind, cold shock, and even low-intense electromagnetic radiation. At the molecular level proteins are involved in the STO/RCL functions. Possibly small RNAs are participating in the signaling cascades because, as we shall see in a moment, epigenetic modifications where small RNAs are involved (Chinnusamy and Zhu 2009), could well be the major mechanism of STO/RCL. Stress memory appears to be epigenetic (Chinnusami and Zhu 2009; Verhoeven et al. 2010). This requires that stress-induced methylation patterns are not reset to the basal level when the stress is relieved and that therefore methylation is kept as the stress memory (Chinnusamy and Zhu 2009). The physiological experiments show that storage of information is robust, and it can be recalled after many days and weeks (Thellier 2012; Thellier et al. 2012). Studies of epigenetics demonstrate that information of stress received by plants can even be transferred to subsequent generations. Stress-induced methylation changes that are not reset can be transmitted through the germ line and are mostly heritable. They can be transferred through several generations (Jablonka and Lamb 1989; Bird 2002; Molinier et al. 2006; Bond and Finnegan 2007; Saze 2008; Verhoeven et al. 2010).

The inheritance of epigenetically established traits has evolutionary implications. One example, which we have already seen above, is that of the morphologically so different phenotypes of *Linaria vulgaris* and *Peloria*. Phenotypes resulting from heritable epigenetic variation will be subject to evolutionary selection (Verhoeven et al. 2010). Inherited epigenetic variations can also contribute to occupation of different niches with reproductive isolation between populations, and thus become drivers of speciation (Jablonka and Lamb 1989; Verhoeven et al. 2010). As we have seen above and as Richards (2006) focuses it, phenotypic variation as raw material on the playground of evolutionary selection is based on the two components of genetic and environmental variation. Inherited epigenetic variation modulated by environmental inputs blurs the line between EVO and ECO. Moreover, epigenetic modifications constitute a strong link between EVO and ECO (Richards 2006).

2.3 Ecology

2.3.1 The Step from EVO–DEVO to EVO–DEVO–ECO

Why is it so important to add ECO to EVO–DEVO? The term "ecology" was coined by ERNST HAECKEL in 1866 only after CHARLES DARWIN published the "Origin of Species". DARWIN does not talk about ecology although with our current understanding natural selection is eminently ecological, because the selective pressure driving evolution is exerted by cues of the environment. While evolution selects genotypes (Sect. 2.1: EVO) and selection acts on the phenotypes generated from the information of genotypes in development (Sect. 2.2: DEVO), ecology gives a frame for the responses of phenotypes to the conditions of the environment. We may distinguish two types of evolutionists (1) those who are not ecologically biased and (2) the evolutionary ecologists who have strong ecological interests. The former will consider selection of genotypes and evolution independent of the dynamics of environmental conditions. They do not need ecology for building evolutionary or phylogenetic trees from the genomics of molecular genotype comparisons (Sect. 2.3.2). The latter will strongly envisage the dynamics of environmental cues in niches, habitats, and ecosystems as the ecological frame within which evolution becomes manifest. They support adding ECO to the overall concept (Sect. 2.3.3). The distinction between the two may be gradual though.

2.3.2 Selection and Evolution Under "Constant Conditions"

The intriguing question is if selection and evolution can occur without any environmental and ecological dynamics, i.e., under constant conditions. There is now much evidence coming from both in-silico studies with digital organisms and experiments with actual living microorganisms that this is so, evolution does occur without environmental changes (Schuster 2011).

Digital organisms are computer programs that self-replicate and mutate randomly. The mutations then compete and are selected during the process. This then drives their increased fitness and hence evolution (Lenski et al. 1999, 2003). Such history of digital organisms also involves evolution of complex features by mutational modification of existing structures and functions (Lenski et al. 2003). The digital organisms share the properties of self-replication, mutation, competition, and evolution under given and constant conditions with real living microorganisms.

Given their short generation times mostly readily cultivable microorganisms, such as viruses, bacteria, and yeasts, are ideal models for following actual evolution of living organisms experimentally in real time (Elena and Lenski 2003). They can be observed under constant conditions for hundreds, thousands, and even tens of thousands of generations. Mutations that turn out to be better suited for fitness in an unchanged given environment are positively selected and outcompete less fit mutations. Progressive genetic adaptation based on mutations can continue indefinitely in constant environments. Factors determining this, and thus, driving evolution may be glucose limitation, temperature, fungicides, and the like (Elena and Lenski 2003). Mutants more fit for dealing with this win the race of evolution.

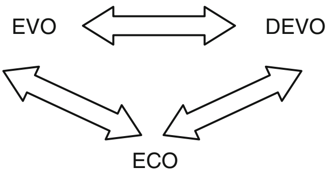
However, we must note two essential points here: The process involves (1) environmental factors albeit constant and (2) competition. Both are eminently ecological categories. Competition is dynamic, and therefore it is not even a "constant" condition. Hence while evolution definitely is possible under a stable and constant pressure of environmental factors, it cannot be said to be independent on ecological dynamics. Where competition is involved there are no constant conditions.

2.3.3 Responses of Phenotypes to Dynamic Networks of Environmental Factors

As we have seen in the previous section, we cannot dismiss ecology as part of EVO–DEVO even if we realize selection and evolution under a constant continuous rule of environmental cues. The essential role of ecology becomes still more evident, of course, when we consider the influence of dynamic changes of environmental conditions, which is the much more normal situation in nature as compared to experiments with microbial cultures.

Selection is on organisms. Irrespective of whether the selective pressure is on individuals (DARWIN) or species (GOULD) (see Sect. 2.1), it is always on the expressed phenotypes. When expression of the genotype information under certain environmental conditions generates a certain phenotype, the individuals carrying this phenotype will have to cope with the conditions given. However, under the environmental input which they receive the phenotypes can exert feedback on the genotype. If there is sufficient plasticity, ontogenetic development can set in, where expression is changed and modification of the phenotype is reached (Lüttge 2005). An example is given by C_3-photosythesis/crassulacean acid metabolism (CAM) intermediate plants, such as *Mesembryanthemum crystallinum*, species of *Clusia,* and several others (Lüttge 2005). Under nonstressful conditions these species perform C_3-photosynthesis. CAM is an ecophysiological biochemical adaptation to stressful conditions mainly affecting water relations under the effect of often network-like interacting environmental factors, such as limited water supply itself, irradiance, temperature, and salinity (Lüttge 2004). Under environmental changes individual plants of these species can switch between the physiological phenotypes (= physiotypes) of C_3 and CAM, respectively. In *M. crystallinum* the switch between C_3-photosynthesis and CAM is accompanied by stress-induced specific cytosine methylation of satellite DNA and therefore most likely under epigenetic control (Dyachenko et al. 2006; Chinnusamy and Zhu 2009).

Looking at these environmental influences, it becomes quite evident that ecology comes into the play of feedback and feedforward interactions between EVO and DEVO to constitute the network of



Epigenetics is a matter of development where stem cells have central functions. We shall consider their basic properties next to lay the ground for our thesis that at the higher scalar level of habitats and ecosystems in analogy, we can consider "stem species" as fundamental elements of hierarchical organizational systems.

3 Stem Cells in Development

As a basis for our aim to introduce a "stem species" concept in this essay, we must undertake here a very brief excursion to the stem cells in mammals and in plants. Some basic definitions and features of stem cells need to be looked at for comparison with what we may call "stem species" at a higher scalar level above organisms. May we use stem cells only as a metaphoric analogy of "stem species" or may we even speak of homologies?

3.1 Mammalian Stem Cells

The term and concept of stem cells comes from animal embryology and development, predominantly from mammals including humans. It plays an increasing role in medicine for therapies and for regenerative medicine.

A lexical definition is:

> Stem cells are biological cells found in all multicellular organisms, that can divide through mitosis and differentiate into diverse specialized cell types and can self renew to produce more stem cells. (Wikipedia 2011)

We might expand that a bit (Alberts et al. 2004). Stem cells are nondifferentiated cells that can divide continuously and indefinitely having an unlimited developmental potential. The daughter cells can either remain nondifferentiated or differentiate to specific kinds of cells. With respect to their occurrence within the organisms, we may distinguish the following types:

- embryonic stem cells,
- adult stem cells
    - somatic stem cells derived from an organ of the organism,
    - germ line stem cells.

Essentially stem cells are self-renewable and have different degrees of potency. The latter criterion allows distinguishing different classes:

- Totipotency or omnipotency: Such stem cells can construct a complete viable organism. Strictly totipotent are only the fertilized egg, i.e., the zygote, and its immediate descendent cells originating from division of the zygote.
- Pluripotency: Such stem cells can differentiate into nearly all cell types of an organism.
- Multipotency: Such stem cells can differentiate into a number of cell types belonging to a closely related family of cells.
- Oligopotency: Such stem cells can differentiate only into a small number of cell types.
- Unipotency: Such cells are still stem cells as they have the property of self-renewal, but they can generate only one single type of cells.

The different degrees of potency allow stem cells to exert various repair functions. Mammal stem cells have mobility. They can replace and renew differentiated cells that have been damaged and died in various organs. Stem cell engineering now aims at using these properties for developing new therapies in regenerative medicine. These particular properties of stem cells issued the idea to search for species as analogies with similar functional properties at the ecological level and to call them “stem species”.

3.2 Plant Stem Cells

All plant tissues develop from meristems. Primary meristems are the apical meristems of shoots and roots. They originate directly from cells of the embryos, i.e., they are “primary embryonic meristems”. Meristems generate different organs in roots and shoots, therefore in the center of plant meristems there must be and there are in fact stem cells (Weigel and Jürgens 2002). In the shoot leaves, flowers and branches are generated. This can go on almost forever as life of some plants may be very long. For example, *Pinus longaeva* (D.K. Bailey) in northwestern America may get as old as 5,000 years or more. The oldest currently living tree is 4,700 years old and in 1964 a 4,950-year-old tree was felled. The stem cells which are generating leaves, flowers, and branches are immortal over all this time.

Thus, basically mammalian and plant stem cells are similar. There are some conspicuous differences though. First of all there is no critical question regarding totipotency or omnipotency of plant stem cells. By great contrast to the mammalian stem cells, totipotency is not restricted to the zygote and its immediate descendent cells. In contrast to the determinate ontogenies of most animals, there are the indeterminate growth patterns of most plants (Friedman and Diggle 2011). Whole plants can be regenerated from meristems of all kinds, from tissue slices and even from single isolated somatic cells, a process called somatic embryogenesis. Totipotency is known from a variety of experiences and observations, such as pruning, grafting, development of adventitious plants from leaf cells, e.g., in the genus *Kalanchoë*, and on tillers, etc. Another difference is that in contrast to mammalian stem cells, plant cells have no motility within the organism and its organs due to their cell walls and their position in the center of meristem tissues.

In conclusion, like mammal stem cells plant stems cells have amazing regenerative powers and repair functions (Weigel and Jürgens 2002).

4 Invaders, Nurse Species, and Pioneer Species in Ecosystems

Before we can consider "stem species" as a new category, we must be able to distinguish them from other established categories of functional classes of species, such as invaders, nurse species, and pioneer species.

4.1 Invaders

Invaders are species which newly arrive in existing ecological systems such as niches, habitats, or ecosystems. They get established in their new host systems by outcompeting resident species, and thus, disturbing and modifying the host systems. They display exaptation based on their exaptive pool of dormant traits. The classic work of Elton (1958) was a pioneer study to indicate the impact of invasive species. An invasive species is by definition exotic to the system it invades, which often generates the mistaken notion that all exotic species are invaders (D'Antonio and Meyerson 2002). Sakai et al. (2001) have demonstrated the strong correlation between certain bionomic traits and the invasive potential of species, which strengthens the predictive power of science to determine invaders and therefore to manage them. Thus, even native species can have dormant traits that manifest themselves upon disturbance. Scarano (2009) reviews the interesting case of *Andira legalis* (Vell.) Toledo, a tropical legume shrub that often displays small isolated populations in coastal habitats, which can turn highly abundant in response to fire and subsequently outcompete other species in such a way that local diversity is reduced. Invaders by specific contrast to "stem species" have no potential of repair. On the contrary they often accelerate devastation and change.

4.2 Nurse Plant Species: Facilitators

Nurse plants are species established in the space of a system due to their adaptation. They provide resources to other species (microbes, animals, plants) in facilitation or mutualism and/or by shaping niches in competition, so that the nursed species can also get established in the space of the system. There is natural facilitation by nurse species as well as anthropomorphic facilitation.

4.2.1 Natural Facilitation

The nurse-plant syndrome occurs when plant species shelter seedlings, young and/or adult individuals of other species throughout their ontogeny (Franco and Nobel 1989). Thus, nurse plants promote facilitation enhancing fitness, survival, and/or growth of associated species (Callaway et al. 2002; Bruno et al. 2003; Brooker et al. 2008). It often results in nucleation, i.e., formation of vegetation clumps or islands. Whenever nurse plant effects go beyond the scope of facilitation only and affect the physical space where other species live, and such direct effects last longer than the lifetime of the nurse plant species, they are called ecosystem engineers (Hastings et al. 2006), which is a concept we will come back to in Sect. 5.1.

The nurse plant syndrome and facilitation mechanisms are well known for arid and alpine zones, and fine examples emerge from the papers cited in the above paragraph. For the tropical environments some of our own studies have been reviewed in Dias and Scarano (2007) and Scarano (2002, 2009) and dwell on the examples of *Clusia hilariana* and bromeliads in a coastal sandy plain ecosystem in Brazil, named “restinga”. *C. hilariana* is phytosociologically dominant at the so-called *Clusia* scrub, which is the predominant physiognomy in the restingas at the northern coast of the State of Rio de Janeiro (Pimentel et al. 2007). It consists of vegetation islands of various sizes surrounded by white sand. This tree can be as tall as 8 m (Dias et al. 2006) and displays a number of peculiar features, such as (1) dioecy (Faria et al. 2006); (2) seedling occurrence predominantly inside the tanks of terrestrial bromeliads (Scarano 2002), which are nurse plants themselves; (3) CAM metabolism (Lüttge 2006); and (4) an aboveground biomass stock and understory litter comparable to the entire woody component of many neotropical savannas (Dias et al. 2006). Curiously, however, *Clusia* is a genus with many hemi-epiphytic stranglers and/or rupicolous species (Lüttge 2006) that live in the neighboring rainforest habitats. More importantly, *C. hilariana* is the most abundant woody species locally (Pimentel et al. 2007) and it has a positive effect on both understory seedling density and richness, which is partly related to the activity of seed dispersers that use male and female plants indistinctly. Furthermore, Dias et al. (2006) indicated that slow decomposition may play an important role on carbon accumulation and that *C. hilariana* despite its conservative strategy of carbon acquisition via CAM, gives a high contribution to biomass stock in this nutrient-poor coastal vegetation. Therefore, in addition to the positive role played on local biodiversity, this plant might also strongly affect ecosystem processes such as productivity and nutrient cycling that, in turn, are also likely to affect recruitment process and species composition. In Scarano (2009), we proposed that this combination of biotic effects with a long-lasting physical effect on ecosystem processes qualify this species as an ecosystem engineer (see Hastings et al. 2006). In Sect. 5.2, we will show why we now think it is better defined as a stem species.

4.2.2 Anthropomorphic Applied Facilitation

Perhaps the most well-known example of applied facilitation is agro forestry, where woody plants and herbaceous crops or pastures are subject to integrated management. For instance, it is often observed in tropical savannas that a larger diversity of herbal vegetation builds up underneath savanna trees. This is due to protection by the trees, lower water stress due to shading at high solar radiation, and nutrient supply by litter and perching birds. In the case of trees with symbiotic fixation of atmospheric nitrogen, such as species of *Acacia*, it was estimated that about 40 trees per hectare provide sufficient N-fertilization to support pasture or crops in agro-forestry (Lüttge 2008).

Another example is management of degraded pasture and range lands by afforestation where there was no forest before or reforestation restoring previous woodlands. In many geographic regions especially in the tropics and subtropics, exotic trees are much used for this purpose (Lüttge 2008; Feyera et al. 2002; Grams and Lüttge 2010, more references there), e.g., often monocultures of *Eucalyptus*. The advantages and disadvantages have been surveyed elsewhere (Lüttge 2008; Feyera et al. 2002). The disadvantages in places get dominating so that many attempts are started to restore secondary forests which come close to original native forest.

There is more experience of handling exotic trees than native ones. Thus, one uses the exotic trees as facilitators or nurse trees. With the appropriate silvicultural management under the protection of canopies of exotic forest plantations, up to 175 native woody species have been regrown (see Feyera et al. 2002; Grams and Lüttge 2010). In an Ethiopian plantation of *Eucalyptus saligna*, a native forest of *Podocarpus falcatus* is regenerated. The photosynthetic capacity of *E. saligna* and *P. falcatus* is similar, but the *Eucalyptus* is using much more water. With thorough thinning due to regular coppicing of the *Eucalyptus, P. falcatus* becomes competitive and can outcompete the *Eucalyptus* (details in Feyera et al. 2002; Lüttge et al. 2003; Fetene and Beck 2004; Grams and Lüttge 2010). *Eucalyptus* monocultures can destroy water relations of entire landscapes with adverse effects on adjacent agriculture and even the water supply of cities. In the National Park of Mount Entoto at the rim of Addis Ababa at 2,600–3,100 m a.s.l., one is running a reforestation experiment with a diversity of more than half a dozen of native tree species (*Acacia abyssinica, Hagenia abyssinica, Juniperus procera* (syn. *J. excelsa*)*, Olea europaea, Podocarpus falcatus, Prunus africanus*)(Ethiopia Heritage Trust, eht@ethionet.et).

It is clear from these examples that an exotic tree such as *Eucalyptus* can exert repair functions and serve as facilitator and nurse tree. However, these examples also clearly underline the difference to "stem species". In plantations *Eucalyptus* is not sustainable let alone self-renewable, because it exhausts resources, such as water and soil nutrients, and after a few generations cannot be supported longer. This definitely rules out that we call it a "stem species".

4.3 Pioneer Plant Species

Pioneer plants are species acquiring pure empty space as a resource in a stochastic manner (Grams and Lüttge 2010). They function as foundation species affecting the establishment of new ecosystems at different scalar levels. They can and most likely will develop to nurse species. There is, of course, a plethora of possible examples of pioneer species in the biosphere. Here we briefly touch some outstanding examples.

4.3.1 Biofilms and Soil Crusts

Microorganisms, especially bacteria can get established and start life on almost any imaginable bare surface including surfaces of buildings and other objects around human settlements. Biofilms are mucilaginous excretions of bacteria embedding their colonies as a joint medium that provides protection and enables for metabolic communication. Thus in the biofilms bacteria may act as pioneers for the establishment of other life.

Soil crusts are similar to biofilms but more complex (Belnap and Lange 2001). They are often microscopic and hence often overlooked ecosystems that pioneer on bare surfaces of the sand of dunes, in savannas and deserts and other dry sites where larger vegetation cannot get established or forms gaps. They represent layers of soil particles that adhere to each other *via* contacts with (micro-) organisms and/or their excretions. Such layers have a thickness of a few millimeters up to centimeters but can extend over quite extended surfaces. They constitute a complex community of organisms with cyanobacteria, eukaryotic algae, fungi, lichens and bryophytes, and small animals (nonvertebrates).

The act of pioneering by biofilms and soil crusts is acquisition of new empty space. This does not really imply an act of repair, and therefore, we would not call the species involved “stem species”.

4.3.2 Bare Rocks of Tropical Inselbergs

Inselbergs are large rock-outcrops especially from tropical savannas and rainforest (for reviews see Barthlott et al. 1993; Porembski and Barthlott 2000; Lüttge 2008; Porembski 2011). Their often rich and diverse flora originates from pioneer species that have arrived on the bare rock. Again this was not “repair” but acquisition of space. The bare rock is generally covered by biofilms of cyanobacteria and crusts with lichens. There are many different niches for life, including erosion-shaped pot holes and vegetation islands developed out of them. High irradiance and water only from rain with high losses by runoff are the major environmental stresses. The adaptation of desiccation tolerance is relatively frequent among the vascular plants on inselbergs (Porembski 2011).

4.3.3 Maritime Volcanic Islands

A favorite example in the ecological literature is maritime volcanic islands where life was arriving after volcanic outbreak and formation of the new islands. Plants can often travel long distances with their propagation units or diaspores. Thus such pioneer species show mobility like stem cells and of course also the "stem species" as discussed in Sect. 5. It is noteworthy that often the diaspores of some Asteraceae can cover large distances due to their pappus hairs as flight device. Adaptive radiation after separation from their populations of origin can lead to new speciation from the founder populations. Examples are the Asteraceae *Argyroxiphium sandwicense* and *Dubautia menziesii* on the islands of the Hawaii archipelago and the genus *Scalesia* on the Galápagos Islands (McMullen 1999). Of particular interest are the various cacti on the Galápagos Islands. They are all plants performing CAM as an adaptation to stress of water scarcity and high solar radiation (Lüttge 2004). Their success as pioneers on the bare black volcanic rocks was due to this adaptation, i.e., the preadaptation they brought with them. The further development in the cactus genera on the Galapágos Islands shows interesting differences. In the genus *Opuntia* due to evolution by radiative adaptation, there are now 6 species and 8 varieties together forming 14 different lineages (McMullen 1999; Lüttge 2010b). *Jasminocereus thouarsii* is the only species of its genus. It is morphologically variable and has three varieties. Here it might be that it found niches where the environmental pressure has not been tough enough to drive further speciation during the age of only four million years of the Galápagos Islands. By contrast *Brachycereus nesioticus* is growing solitarily on bare black sun exposed lava. It is also the only species of its genus. It may be so perfectly adapted to its niche on the lava that no further selection and speciation was effective (Lüttge 2010b).

There was no "repair" on these geologically recent islands but shaping newly emerging life by preadapted newcomers. Hence, once again the species named above will not be called "stem species".

5 Stem Species

5.1 The Concept

"Stem species" correspond to stem cells in at least two ways:

- "Stem species" have different degrees of ecological potency (see Sect. 3.1), up to pluripotency, due to their exaptive pools and functional-shift capacities for creating different life-forms corresponding to the different cell types at the stem cell level. "Stem species" can provide the basis for building up a complete new viable ecosystem.
- "Stem species" have repair function. They share the property of mobility with mammalian stem cells. They can substitute for previously present adapted species that may have vanished.

Thus, “stem species” are species getting deterministically established in spatio-functional systems. For their establishment they use functional shift of traits for exaptation as explained in Sect. 2.1.2. With their own establishment they establish new niches. In this way they exert powerful repair functions in devastated systems, building functions in new systems, and therefore, collectively, work out as a repair system for the biosphere as a whole. So they constitute the basis for self-organization eventually securing self-sustainability of the systems (Scarano and Garbin 2012).

The “stem species” share some properties and functions with nurse species, pioneer species as well as species that act as ecosystem engineers. As we have seen (Sect. 4.2) nurse species can have repair functions. Pioneer species do not act so much via repair functions but can establish new niches, habitats, and ecosystems in inorganic life-less space which is obviously free of any resources except the space itself (Grams and Lüttge 2010). Pioneer species are adapted to this particular space. When they get established in such space after their diaspores arrived, this is due to their adaptation or preadaptation as it were. Ecosystem engineers “modulate the availabaility of resources to other species, by causing physical state changes in biotic or abiotic materials” (Jones et al. 1997). Stem species share these properties with nurse, pioneer, and ecosystem engineers’ species. However, they go beyond that. They display ecological pluripotency. They do not depend on (pre-) adaptation but operate with exaptation.

5.2 *Examples*

The two examples we describe here originate from tropical vegetation, in Brazil (see also Scarano and Garbin 2012). The plants involved have in common several features (1) they have considerable ecological plasticity that allowed them to colonize novel habitats over varying time scales, (2) they have apparently low-habitat requirements, (3) they are facilitators, and (4) they have long-distance dispersal. They are also insufficiently known in regard to their ecology, physiology, and genetics.

5.2.1 *Clusia hilariana* in the Atlantic Forest Complex

The genus *Clusia* typically has many hemi-epiphytic stranglers and/or rupicolous species (Lüttge 2006) that live in rainforest habitats. In the case of the Brazilian Atlantic rainforest, some such species migrated to sandy plains, known as restingas, which were formed by the coast during the Quaternary (Scarano 2002, 2009). *Clusia hilariana* is one such species. However, the plasticity of the genus and of the species is such that in the restingas of northern Rio de Janeiro (SE-Brazil), this species occurs as an 8 m tall tree (Dias et al. 2006) and that through facilitation processes in the restinga it is largely responsible for diversity in land (Dias and Scarano 2007), soil (Kreuzer et al. 2007), and possibly even in adjacent water bodies (Pimentel et al. 2007). Thus, *C. hilariana* exerts many positive effects on community diversity. Moreover, it plays a marked functional role: its aboveground biomass stock and understory litter is comparable to the entire woody component of many neo-tropical savannas (Dias et al. 2006). It has enough ecological, physiological, and morphological plasticity to, in time, colonize novel habitats and subsequently facilitate the onset of a diverse community. Therefore, *C. hilariana* fits our concept of stem species.

5.2.2 Nitrogen Fixers in the Flooded Forests of the Amazon

Another conspicuous example of such regeneration power of the planet comes from the Brazilian Amazon. From 1979 to 1989 bauxite washing tailings were continuously discharged into Lake Batata (State of Pará, Central Amazon, Brazil) and the surrounding *igapó* forest (i.e., forest seasonally flooded by low-nutrient waters). When the discharge was halted, circa 30% of the lake area with its marginal *igapó* forest was buried by a 4–5 m bauxite tailings layer (Scarano et al. 1998). Frequent and prolonged exposure to full sunlight during the dry season has led to dehydration and consolidation of the bauxite tailings. The bauxite tailings substrate consists of 75% clay, 21% silt, 3% fine sand, and 1% coarse sand. It differs from nonimpacted *igapó* soil in the proportions of clay (49%), silt (37%), and fine sand (13%) (Dias et al. 2012), and therefore constitutes a new habitat. Perhaps surprisingly, many native *igapó* species began to spontaneously regenerate and grow on the top of this substrate, particularly in areas where water was more still during flooding. Vectors of seed dispersal in these forests are to a large extent water and fish (Mannheimer et al. 2003) and therefore sites with water currents and fast flow during flooding are less prone to establishment. Thus, a large-scale reforestation program was set in place to provide forest cover to this new environment (Bozelli et al. 2000). After over 20 years since the impact happened and 15 years since man-induced forestation started, it is now apparent that nitrogen fixing legumes (*Acosmium nitens* (Vogel) Yakovlev and *Dalbergia inundata* Spruce ex Benth.; Souza et al. 1994) are the most abundant species in the site, both due to spontaneous regeneration and to successful performance of planted seedlings (Scarano et al. 1998; Dias et al. 2012). Nitrogen fixation by these species in such a nutrient-poor substrate can possibly be a factor contributing to the high diversity found in this new habitat, which would also fit them in our stem species concept.

6 Conclusions

Plants we are here calling stem species are insufficiently known in regard to their ecology, physiology, and genetics. Plants known to science under all those angles are usually productive (agriculture or forestry) or model plants (e.g., *Arabidopsis thaliana*). Often rare or threatened species that are in the focus of numerous conservation biology studies are also studied in detail. Conversely we know astonishingly little about the comportment of the most common plants that are neither economically relevant nor rare. They are largely understudied, at least in the tropics. Some of the traits described above for stem species (high plasticity, long-term dispersal, low-habitat requirements) are often found in common species. Thus, we would argue that plants with high repair potential of Gaia, and thus, the stem species, are likely to be found among common plants and among plants with no known economic importance. These are plants that have not so much attracted scientific studies and we therefore know little about them. In this essay we have explicitly mentioned only two examples and the scientific search for more such stem species now is an important challenge. EVO–DEVO–ECO would provide us with the necessary clues for the search for the stem species. If indeed we can expect exaptative surprise by common species offering repair functions of ecosystems, outlook may be not totally pessimistic.

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