

The Significance of Darwin's Origin of Species 1872 and ecology of salt-marsh plants in Northern California, USA

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ABSTRACT

In 1872, the 6th (last) edition of Charles Darwin's *Origin of Species* was published, wherein he had added a well-known section on Mivart's criticism of 1871 concerning natural selection. Here, we describe Darwin's ideas on "lower vs. higher organisms", inclusive of his hypothesis of steady "perfection" and species co-existence during the evolutionary history of life. In addition, Darwin discussed evolution with reference to ecological interactions, proposed the concept of "competitive exclusion", and, in our view, founded "evolutionary ecology". These concepts were not addressed in the first, frequently quoted text of 1859. Therefore, we present Darwin's ignored section with reference to a major recent paper on "Co-existence of plant species under harsh environmental conditions", as well as our own observations on marsh vegetation in the San Francisco Bay Estuary. We conclude that "Darwin 1872" should be recognized as the definitive version of the "Species Book", as recommended by the author himself and with reference to Letters published in the *Darwin Correspondence Project-2023*.

KEY WORDS

Darwin; Origin of Species; Species co-existence; Salt Marsh Plants; Parasitism; *Cuscuta*.

Received 13.12.2023; accepted 28.03.2024; published online 30.04.2024

INTRODUCTION

During the "Year of Darwin 2009", in most of the numerous publications dealing with the significance of the British naturalist's concepts on evolution, the authors referred to the first edition of the *Origin of Species*, published in November 1859. Unfortunately, the fact that Charles Darwin (1809–1882) (Fig. 1) considered the 6th edition, published in January 1872, as the definitive and final version of his work, was largely ignored.

However, as Figure 2 documents, Darwin only regarded the last edition as the "complete" one, and argued that earlier versions of his most important book were "outdated" when the final text was published.

This conclusion is corroborated by the *Letter*

No. 8199/ Febr. 3, 1872, from Darwin to the German biologist Anton Dohrn (1840–1909), as revealed by the *Darwin Correspondence Project* (Science News Staff, 2023). As detailed in this *Letter*, Darwin responded in the 6th edition of his "Species book" to S.G.J. Mivart's criticism concerning the alleged incompetence of natural selection to explain the incipient stages of useful structures, a topic discussed by Swain (2017) and other historians of science. However, to the best of our knowledge, other sections that Darwin had added to the final version of his "Species book" of 1872, were ignored so far.

In this contribution, we present and discuss key passages of Darwin's text of 1872 that have been overlooked so far, with reference to recent work on species co-existence, focussing on plants that live

under very harsh environmental conditions. In addition, some of our unpublished observations on salt marsh plants in the Baylands Nature Preserve of Northern California are included to illustrate Darwin's key points.

MATERIAL AND METHODS

This article consists of a theoretical and an empirical part. First, a systematic comparison of Darwin's *Origin of Species*-first vs. last edition, was carried out, and, second, salt marsh plants were studied in aquatic areas of Northern California,

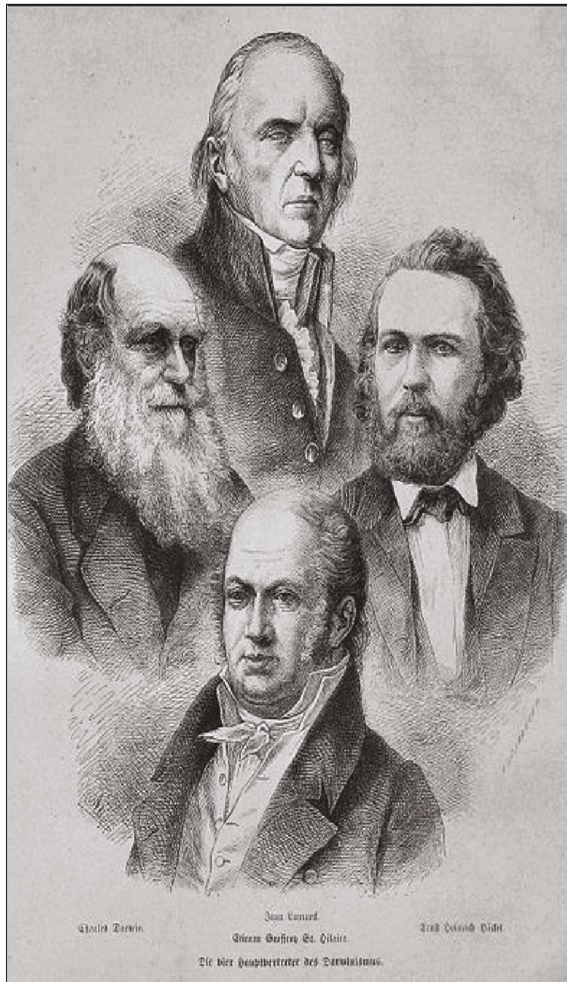


Figure 1. The four key representatives of Darwinism: Jean Lamarck (1744–1829), Charles Darwin (1809–1882), Ernst Haeckel (1834–1919), and Etienne Geoffroy St. Hilaire (1772–1844) (adapted from a drawing published in *Die Gartenlaube*, p. 711; 1873).

where recently a new leech species was identified and described in this journal (Kutschera, 2023). We used the Darwin-literature in the library of the Carnegie Institution, Dept. of Plant Biology, where many historic biology books are stored and provided for use, and noticed that the title of this major monograph had changed. The first ed. was published under the headline “*On the Origin of Species by Means of Natural Selection or, The Preservation of Favoured Races in the Struggle for Life*”, whereas the 6th ed. appeared in print under the short title: *The Origin of Species* (Darwin, 1859, 1872).

Within the context of our search for leeches and other aquatic invertebrates, we also analysed the species composition of the moist habitats of the Palo Alto Bayland Nature Preserve, Palo Alto, California 94303, USA (starting at the Visitor's Center at 2775 Embarcadero-Road) between Sept. 2009 and March 2019 (18 ca. 3 to 4 hour long excursions). The 1,940-acre Baylands Preserve is the largest tract of undisturbed marshland remaining in the San Francisco Bay Area, consisting of tidal and freshwater habitats. The Preserve is bounded by the cities Mountain View and East Palo Alto, and is characterized by a mixed plant distribution (City of Palo Alto-California-Info-Material, 2022).

RESULTS AND DISCUSSION

Darwin 1859 vs. 1872: from “the creator” to species competition

In the first section of our account, we discuss the striking differences between the 1st and final edition of Darwin's *Species Book*. As noted earlier (Kutschera 2009 a, b), the most dramatic change was, from the 2nd to the 6th edition, the addition of the phrase “by the creator” in the last sentences of the text.

However, Darwin (1872) did not explain what he meant by “the creator”; in private conversations, he revealed that, by using this phrase, he referred to “an unknown process” (Science News Staff, 2023). Nevertheless, the fundamental Christians of Darwin's time interpreted this reference to the “Creator” as indicating that the author adhered to the religious tradition of Biblical Theism. In other words, prominent creationists assumed that the

British naturalist had incorporated supernatural acts of a “spiritual being” into his interpretation of the history of life. Fortunately, this erroneous belief did dampen the “*furor theologicus*” that followed after the publication of this important book (Kutschera, 2009 a, b).

However, Darwin had added an entire new section to the 6th edition of his work that supplements the first and later versions of his masterpiece. In this new segment on the persistence of “primitive” organisms, despite the fact that natural selection should “improve” all living beings, he discussed the question as to how and why so many species, animals and plants alike, can co-exist in the same habitat. Here we present an analysis of this overlooked “Darwinian concept-1872”, with reference to recent work on species interactions and ecological relationships.

Coexistence of plant species across salt marsh waters

Four years ago, basic ideas that Darwin (1872) outlined and critically discussed in the final version of his *Origin of Species* (Fig. 2) were analysed in detail in a major paper published in the *Journal of Ecology and Environment*. Under the title “*Coexistence of plant species under harsh environmental conditions: an evaluation of niche differentiation and stochasticity along salt marsh creeks*”, Kim & Ohr (2020) provided an overview of theories that may explain species co-existence in mixed populations of plants and animals.

The following “classical” concepts are presented and discussed by the authors:

1. Co-existence maintained via niche differentiation. This idea can be summarized in the following sentence: “*Only those species differing sufficiently in resource use can co-exist, i.e., two (or more) species cannot co-inhabit the same niche*”.

2. Co-existence without niche differentiation. The concept No. 1, also described as “*competitive exclusion*”, was challenged during the 1970s, and replaced by the idea of “*retarded competitive exclusion*”.

3. Co-existence along environmental stress gradients. According to this model, very high physical stress (salt marsh, etc.) allows only extremely tolerant species to survive and maintain productive

populations; as a result, species diversity should be low, and conversely, higher under more benign environmental conditions.

In addition, many “modern” theories have been proposed to explain species co-existence. Kim and Ohr (2020) outlined and evaluated them with reference to their own observations on co-existence of plant species in salt marsh creeks in Southern Denmark. Over the past decades, we studied salt marsh plants in a prominent Estuary, the San Francisco Bay (Palo Alto Baylands). As documented in Figure 3, we observed that, in the Baylands Natural Reserve, marsh plants, such as California Cordgrass *Spartina foliosa* (Trin.), Pickleweed *Salicornia pacifica* Standl., and Pacific Coast Dodder *Cuscuta pacifica* var. *pacifica* Dodder, grow in different zones of this harsh habitat. In Darwinian-19th-century- terminology, the Pacific Coast Dodder may be labelled as a “lower”, heterotrophic-parasitic plant, whereas Cordgrass and Pickleweed can be inter-

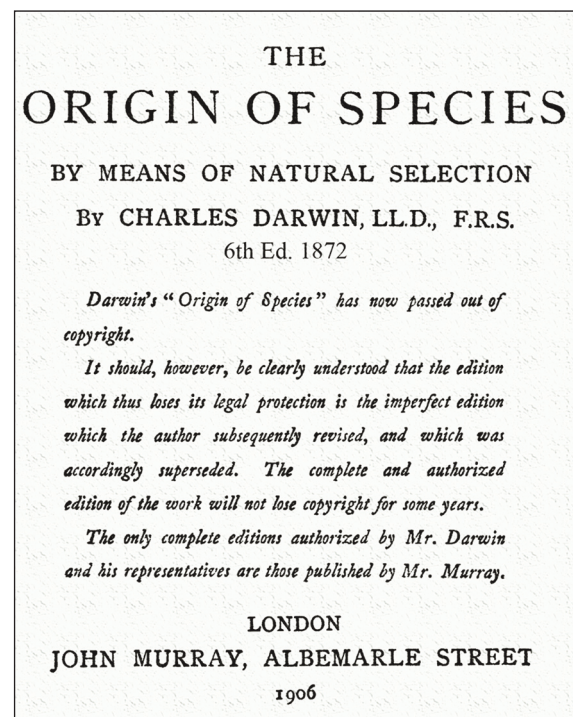


Figure 2. Note concerning the significance of the 6th and final edition of Charles Darwin's *Origin of Species*, 1872 vs. 1859, reproduced from a reprint of the last version published in 1906 (source: *Library* of the Carnegie Institution for Science, Department of Plant Biology, Stanford, California 94305, USA).

preted, with respect to their more complex morphologies, as “higher (green) plants” that are photosynthetically active “producers” of the complex biosphere (Fig. 3).

Our observations largely accord with those of Kim & Ohr (2020). These authors referred in their discussion on the co-existence-concept No. 1 to “Darwin 1859”, despite the fact that only in the final ed. of 1872, the British naturalist discussed species-coexistence from an evolutionary perspective. In the next section, we summarize and discuss Darwin’s ideas on this topic that are still relevant today.

Higher vs. lower: species-co-existence according to Darwin (1872)

In the first edition of his work, Darwin (1859) did not address the question why so-called “lower organisms” still exist today, although, according to his principle of descent with modification by means of natural selection, “higher” forms of life should steadily replace their “more primitive” ancestors.

In the 6th edition, he devoted four pages to this question (Chapter Four: “Natural Selection, or the Survival of the Fittest – On the degree to which organization tends to advance”). Here, we present key passages (see added *Headlines*) and comment on their contents, with reference to the current literature and our own observations (Fig. 3).

Specialization via natural selection. Darwin (1872) wrote that “*Natural Selection acts exclusively by the preservation and accumulation of variations, which are beneficial under the organic and inorganic conditions to which each creature is exposed at all periods of life. The ultimate result is that each creature tends to become more and more improved in relation to its conditions. This improvement inevitably leads to the gradual advancement of the organisation of the greater number of living beings throughout the world. But here we enter on a very intricate subject, for naturalists have not defined to each other’s satisfaction what is meant by an advance in organisation... If we take as the standard of high organisation the amount of differentiation and specialisation of the several organs in each being when adult ..., natural selection clearly leads towards this standard: for all physiologists admit that the specialisation of organs,*

inasmuch as in this state they perform their functions better, is an advantage to each being; and hence the accumulation of variations tending towards specialisation is within the scope of natural selection ...But it may be objected that if all organic beings thus tend to rise in the scale, how is it that throughout the world a multitude of the lowest forms still exist; and how is it that in each great class some forms are far more highly developed than others? Why have not the more highly developed forms everywhere supplanted and exterminated the lower? Lamarck [Fig. 1], who believed in an innate and inevitable tendency towards perfection in all organic beings, seems to have felt this difficulty so strongly, that he was led to suppose that new and simple forms are continually being produced by spontaneous generation. Science has not as yet proved the truth of this belief, whatever the future may reveal.

On our theory the continued existence of lowly organisms offers no difficulty; for natural selection, or the survival of the fittest, does not necessarily include progressive development – it only takes advantage of such variations as arise and are beneficial to each creature under its complex relations of life.

And it may be asked what advantage, ... would it be to an infusorian animalcule – to an intestinal worm – or even to an earthworm, to be highly organised. If it were no advantage, these forms would be left, by natural selection, unimproved or but little improved, and might remain for indefinite ages in their present lowly condition. And geology tells us that some of the lowest forms, as the infusoria and rhizopods, have remained for an enormous period in nearly their present state”.

In these sentences, Darwin (1872) used the phrase “survival of the fittest”, borrowed from Herbert Spencer (1820–1903), as a synonym for “natural selection”. Moreover, he labelled evolved organisms as “creatures”, and referred to Lamarck and his philosophical principle of the “Scala Naturae”. Darwin’s speculations as to the question of why “lower” organisms still exist today did not result in a clear conclusion.

Species co-existence and competition. In the following sentences, Darwin (1872) described the fact that different organisms can co-occur in the same habitat: “*Nearly the same remarks are applicable if we look to the different grades of organisation*



Figure 3. Salt Marsh Plants in the Palo Alto Bayland Preserve (San Francisco Bay, California, USA). Note that the yellow Pacific Coast Dodder (*Cuscuta pacifica* var. *pacifica*), see inset, grows as a parasitic epiphyte on the green, photosynthetically active organs of the underlying vegetation, such as pickleweed (*Salicornia pacifica*), and Gum plants (*Grindelia humilis*) – with yellow flowers (original photograph, March 2019).

within the same great group; for instance, in the Vertebrata, to the co-existence of mammals and fish – amongst Mammalia, to the co-existence of man and the ornithorhynchus – amongst fishes, to the co-existence of the shark and the lancelet (Amphioxus), which latter fish in the extreme simplicity of its structure approaches the invertebrate classes”.

In the next section, he explained why there is no “conflict” between “lower” and more complex forms of life on Earth: “*But mammals and fish hardly come into competition with each other; the advancement of the whole class of mammals, or of certain members in this class, to the highest grade, would not lead to their taking the place of fishes ... The three lowest orders of mammals, namely, marsupials, edentata, and rodents, co-exist in South America in the same region with numerous monkeys, and probably interfere little with each other... In some cases, as we shall hereafter see, lowly or-*

ganised forms appear to have been preserved to the present day, from inhabiting confined or peculiar stations, where they have been subjected to less severe competition, and where their scanty numbers have retarded the chance of favourable variations arising”.

Here, Darwin (1872) described the principle of “competitive exclusion” and illustrates this concept with reference to vertebrates.

Advantage vs. disservice of modifications. In the last section of this sub-chapter, Darwin (1872) explains why so many “primitive” organisms are still alive today: “*I believe that many lowly organised forms now exist throughout the world, from various causes. In some cases, variations or individual differences of a favourable nature may never have arisen for natural selection to act on and accumulate ... In some few cases there has been what we must call retrogression of organisation. But the*

main cause lies in the fact that under very simple conditions of life a high organisation would be of no service, – possibly would be of actual disservice, as being of a more delicate nature, and more liable to be put out of order and injured”.

Our comment on this key-passage is as follows. In the case of the “Pacific Coast Dodder” (Fig. 3), Darwin (1872) would have interpreted the evolutionary development of this “creature” as an example for “retrogression of organization”, an idea that was recently corroborated by analysing the genome of the parasitic plant *Cuscuta australis*, a relative of the Dodder-species that inhabits the Californian Salt Marsh investigated here (Sun et al., 2018). Darwin’s speculations as to the “disservice” of complex organization in “lower” organisms are logical, but, to the best of our knowledge, proof for this idea is lacking.

Ecological interactions. At the end of his discussion, Darwin (1872) speculated on the earliest organisms on Earth and how they may have evolved into more complex “creatures”, and concluded: “But, ... no one ought to feel surprise at much remaining as yet unexplained on the origin of species, if we make due allowance for our profound ignorance on the mutual relations of the inhabitants of the world at the present time, and still more so during past ages”.

This final remark is a clear reference to the British naturalist’s friend and colleague Ernst Haeckel (1834–1919), known in the 19th century as the “German Darwin” (Fig. 1). In 1866, Haeckel coined the word “ecology”, defined this scientific discipline as the study of interrelationships of organisms that inhabit the same area, and provided examples based on his own observations (Kutschera et al., 2019).

CONCLUSIONS: THE ORIGIN OF EVOLUTIONARY ECOLOGY

Our discussion shows that, in 1872, Darwin may have been the first to introduce the concept of “competitive exclusion” with respect to the co-existence of species. In addition, he combined evolution with ecological questions, and hence originated the research area of “evolutionary ecology”. Therefore, biologists should refer to “Darwin (1872)”,

and not to the original version of the text, published in 1859, which the author himself regarded as a superseded precursor of the final book published thirteen years later (Fig. 2).

This conclusion can be corroborated with reference to a recent example. In their major paper on the “Co-existence of plant species under harsh environmental conditions”, Kim & Ohr (2020) referred to “Darwin 1859” but, really, Darwin discussed “their topic” in the 6th, but not in the first edition of his “Species book”. In another, major article on the concept of species coexistence, published in *PNAS*, Darwin was not mentioned at all (Grainger et al., 2019). In addition, it should be noted that Eldredge (1985), who was committed to an ecological approach to organismic evolution, and Caponi (2022), in his analysis of ecological interactions from an evolutionary perspective, discussed “Darwin (1859)” – without reference to the 6th edition of this book. Probably, this neglect of the final edition of Darwin’s “species monograph”, and the corresponding focus on the 1859 version, may be due, at least in part, to the work of the German-American evolutionary biologist Ernst Mayr (1904–2005). This expert championed the view that only “Darwin 1859” expresses the views of the British scientist in “pure form”, whereas later editions blurred the original contents by added material of less significance (Mayr, 2004; Kutschera & Niklas, 2004).

We disagree with Mayr’s conclusion and, in accordance with the last will of the British naturalist (Fig. 2), recommend to study, and refer to, the “complete Darwin published in 1872”. Accordingly, we consider the edition of 1859 as a first draft-version of this great book that changed the way biologists interpret the living world – from an evolutionary (“Darwinian”) point of view (Mayr 2004, Leigh 2022).

This conclusion is corroborated by several *Letters* published recently as part of the now finished *Darwin Correspondence Project* (Science News Staff, 2023), wherein the British naturalist stressed the importance of the 6th and final edition of his monograph on the *Origin of Species* with reference to key questions in the emerging field of evolutionary biology. We think that these historical facts are important for biodiversity research, because only when species co-exist, diverse, mixed populations of “lower and higher organisms” are capable to co-occur in the same habitat (Fig. 3).

ACKNOWLEDGEMENTS

This article is dedicated to the memory of Winslow R. Briggs (1928–2019), a lab scientist and naturalist, who studied plants from a molecular and organismic perspective. The cooperation of the Authors was initiated by Alexander von Humboldt Stiftung (AvH), Bonn, Germany (AvH-fellowship 2013/14 to U.K.).

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