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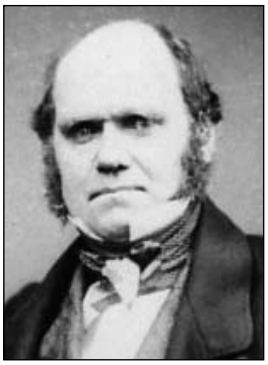

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CHARLES DARWIN AND ECOLOGICAL EXPLANATIONS OF BIOTIC INVASIONS: A HISTORICAL ANALYSIS AND MODERN CONCEPTS

Key words: Darwin, evolution, biotic invasions, invasion ecology, biogeography, flora

Abstract: The contribution of Ch. Darwin to invasion ecology is discussed. Darwin considered biotic invasions as complex but integral phenomena involving ecological, biogeographical, evolutionary, taxonomic and other aspects, such as patterns of past and present distribution, means and pathways of dispersal (and dispersal limitations), struggle for existence and natural selection, phylogenetic relationships of taxa, environmental factors, and evolutionary changes. All modern hypotheses explaining biotic invasions are evolutionary in their nature. Darwin outlined not one naturalization hypothesis but at least three invasion concepts, which may be considered as precursors of modern theories/hypotheses of biotic invasions. Thus, Darwin established foundations for all following evolutionary and ecological studies of biotic invasions, including several currently debated invasion concepts, such as Escape from Enemies, Empty Niche, Species Richness, and Disturbance hypotheses. It is demonstrated that Darwinian explanations of invasions are based on the balance between biotic/abiotic factors and ecological interactions.

Introduction

Charles Darwin is universally recognized as the author of the theory of evolution by natural selection. As Th. Dobzhansky

(1973) justly commented, «*Nothing in biology makes sense except in the light of evolution*», and because of that the Darwinian theory should be considered a cornerstone of modern evolutionary biology (Avise, 2003; Kutschera, Niklas, 2004; Lewontin, 2002; Science, Evolution..., 2008, etc.). However, the evolutionary theory was not born instantly in Darwin's mind but slowly and steadily grew from mountains of facts accumulated from many fields of knowledge in biology, geology, geography and other sciences. The synthetic scientific genius of Charles Darwin gave the unified evolutionary explanation to these facts. In his *Autobiography* (published in 1958) Darwin modestly commented on criticism against his ability to provide a great scientific synthesis: «*Some of my critics have said, «Oh, he is a good observer, but has no power of reasoning.» I do not think that this can be true, for the* Origin of Species *is one long argument from the beginning to the end, and it has convinced not a few able men. No one could have written it without having some power of reasoning. I have a fair share of invention and of common sense or judgment, such as every fairly successful lawyer or doctor must have, but not I believe, in any higher degree*.» Indeed, the Darwin's great book (Darwin, 1959) should be considered, as he expressed that, as «one long argument» in favor of evolution.

Thus, Darwin's theory was based on many foundations and, evidently, Darwin as a scientist was interested in many particular issues of biology and other sciences. He made considerable contributions to many fields of biological, geological and geographical sciences, from historical biogeography to dynamic ecology, from innovative botanical studies (movements in plants, carnivorous plants, pollination etc.) to the origin of man, from explanations of the growth of coral reefs to evolutionary paleontology, from the ecological role of earthworms to taxonomy of barnacle crustaceans (*Cirripedia*), and this amazing list of his fundamental scientific achievements can be easily continued. In addition to all that, Darwin is rightly recognized as one of scientific pioneers who first paid proper attention to the phenomenon now commonly called **«biotic invasion»**, and who in fact proposed the first evolutionary explanation (or, rather, explanations) for that phenomenon. This particular explanation is often referred to as the **Darwin's naturalization hypothesis** (Daehler, 2001; Davis, Thompson, 2000; Duncan, Williams, 2002; Hierro et al. 2005; Pyšek, Hulme, 2005; Rejmánek, 1996; Rejmánek et al., 2005; Ricciardi, Mottiar, 2006; Richardson, Pyšek, 2006), which is actively discussed until now.

Objectives and methodology

Biotic invasion are presently the focus of priority scientific research, considering the role of invasion processes in the continuing globalization of the biota, conservation issues, and human economic activities (Callaway, Maron, 2006; Davis, 2003; Elton, 1958; Goodwin et al., 1999; Global Strategy..., 2001, Mack et al., 2000; Sax et al., 2007, etc.). Explanatory hypotheses of biotic invasions, invasiveness of species, and invasibility of communities and ecosystems are especially important for our proper understanding of these complex phenomena and for developing efficient activities aimed at prevention, control, eradication, and mitigation of the environmental impact of invasive species. However, no unified invasion theory is available yet. A brief critical overview of modern

invasion hypotheses was published earlier (A. Mosyakin, 2009). All modern invasion hypotheses are evolutionary, and because of that, quite naturally, they are rooted in Darwin's ideas.

Despite active recent research in invasive ecology, no comprehensive analysis of Darwin views on invasions was available. Moreover, the so-called Darwin's naturalization hypothesis is often underestimated and oversimplified in modern publications. Now, when humankind celebrates the 200th anniversary of Charles Darwin and 150 years since the publication of the first edition of his great book, *The Origin of Species*, it would be proper to provide a historical analysis of Darwin's developing opinions on biotic invasions and his naturalization hypothesis from the viewpoint of modern theories and concepts.

In this article I consider Darwin's views on biotic invasions based on his own writings and within the historical framework. I also provide an overview of modern publications on Darwin's impact on invasive ecology. Of course, this overview cannot be considered a comprehensive treatment of the issue, but I attempted to provide here a brief historical analysis of development of Darwinian concepts on invasions based on well-known and less-known publications, and to make conclusions regarding the proper role of Darwin in laying foundation to invasion ecology.

Most citations from publications of Darwin are given following the digitized texts available on the web site *The Complete Works of Charles Darwin Online* (darwin-online.org.uk) (Darwin, 2009 onward). Citations are given *in italics*. Omitted parts of the text in citations are indicated by brackets <...>.

Discussion

Before *The Origin of Species*

The first observations on the impact of non-native plants and animals were already present in the early scientific publications by Darwin, notably in his *Narrative of the surveying voyages of His Majesty's Ships* Adventure *and* Beagle *between the years 1826 and 1836, describing their examination of the southern shores of South America, and the* Beagle's *circumnavigation of the globe* first published in 1839 (Darwin, 1839) and later published as many separate editions (e.g., Darwin, 1845). In particular, in Chapter 6 Darwin described his observation on two Eurasian plants, fennel (*Foeniculum vulgare* Mill.) and cardoon (*Cynara cardunculus* L.), completely naturalized in South America, in particular, near Buenos Aires (Argentina) and Montevideo (modern Uruguay):

«*Near the Guardia we find the southern limit of two European plants, now become excessively common. The fennel in great profusion covers the ditch banks in the neighbourhood of Buenos Ayres, Monte Video, and other towns. But the cardoon* (Cynara cardunculus) *has a far wider range: it occurs in these latitudes on both sides of the Cordillera, across the continent. I saw it in unfrequented spots in Chile, Entre Rios, and Banda Oriental. In the latter country alone, very many (probably several hundred) square miles are covered by one mass of these prickly plants, and are impenetrable by man or beast. Over the undulating plains, where these great beds occur, nothing else can live. Before their introduction, however, I apprehend the surface supported as in other parts a rank herbage. I doubt whether any case is on record, of an invasion on so grand a scale of one plant over the aborigines. As I have already said, I nowhere saw the cardoon south of the Salado; but it is probable that in proportion as that country becomes inhabited, the cardoon will extend its limits*».

As we see, Darwin noted the secondary (anthropic) geographical range of the two introduced species, indicated the invasive character of these plants and the great extent of their invasion (several hundred square miles of dense impenetrable prickly stands!), and correctly assumed that the spread of these plants was facilitated by human-caused disturbance, cattle-breeding, and colonization of the land by European settlers. Among other naturalized plants, Darwin also mentioned some escaped and naturalized fruit trees:

«*I have alluded to the invasion of the cardoon: in a like manner, the islands near the mouth of the Parana, are thickly clothed with peaches and orange-trees, springing from seeds carried there by the waters of the river*».

Some other anthropic transformations related to invasive ecology also did not escape Darwin's attention:

«*...few countries have undergone more remarkable changes, since the year 1535, when the first colonist of La Plata landed with seventy-two horses. The countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer, and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the peccari; packs of wild dogs may be heard howling on the wooded banks of the less frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills*».

Here we see the first explicit indication of the ecological impact of domesticated and feral animals upon native animal species, as well as on vegetation. Probably these observations in South America, which should be considered among the first explanatory descriptions of biotic invasions in scientific literature, initially attracted Darwin's attention to the problem of naturalized (invasive) species, to which he returned many times in his other works, especially in all subsequent editions of *The Origin of Species*. Moreover, in his *Beagle* book Darwin was probably the first who used in scientific literature the term «*invasion*» in its modern sense, as it is used in recent publications on invasive organisms.

Before the first publication of *The Origin of Species*, Darwin (1857) also discussed the issue of naturalization of plants in a little-known article *Productiveness of foreign seed* published in *Gardeners' Chronicle and Agricultural Gazette* in November 1857 as a

brief response to «*the highly remarkable article on weeds in your last Number*», in which its anonymous author expressed an opinion that «*there is too much reason to believe that foreign seed of an indigenous species is often more prolific than that grown at home*». Darwin noted that «[*T*]*he point seems to me of considerable interest in regard to the* ***great battle for life*** *which is perpetually going on all around us*». Here, as we see, the «*great battle for life*» is used, in fact, as a synonym of the well-known Darwinian term the *struggle for existence*, which was formally introduced and discussed in detail in *The Origin of Species*, especially in Chapter 3. In this article Darwin mentioned the opinion of the great American botanist Asa Gray, who believed that «*in the United States there are several plants now naturalised in abundance from imported seed <...>; and my impression is <...> that the imported stock prevails over the aboriginal*». Darwin further discussed the case of naturalization of *Sonchus* in New Zealand described by J. D. Hooker «*in his admirable Flora of New Zealand*», and naturalization of *Sinapis nigra* in Britain. It is worth mentioning that in that brief note Darwin already used the terms *invader* and *invading* in their modern meaning.

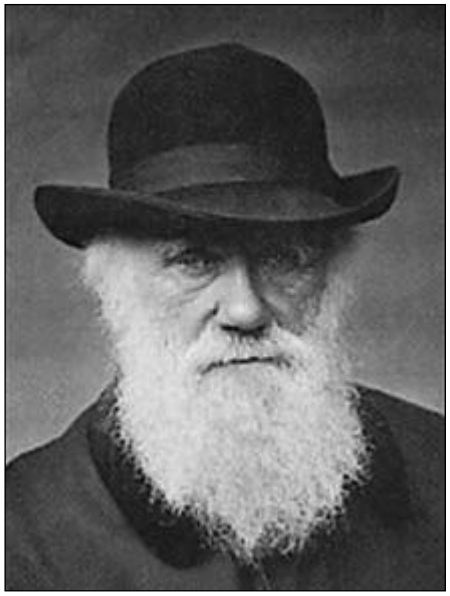
Ch. Darwin, J. D. Hooker and A. Gray on alien plants

Problems of introduced plants were also discussed in Darwin's correspondence with his eminent colleagues, especially Joseph Dalton Hooker and Asa Gray, who were leading botanists of that time in Britain and the United States of America, respectively (Darwin, 1887). Darwin's letter of 3 January 1860 to J. D. Hooker is very indicative and worth attention. He wrote this letter immediately after reading Hooker's essay *Australian Flora*, which provoked many thoughts, including ideas on plant invasions, partly mentioned and considered by Hooker in his other publications on floras of India, New Zealand, and other regions of the Globe. Of course, Darwin was very well aware of almost all botanical publications of his great friend, but especially valued the *Australian Flora*: «*To my judgment it is by far the grandest and most interesting essay, on subjects of the nature discussed, I have ever read*.»

Darwin agreed with Hooker in his opinion that the causes, means and mechanisms of introductions and invasions of plants remained unknown and unexplained, and described the situation as «*our profound ignorance of the cause of possible naturalisation or introduction*». Definitely, this recognition stimulated Darwin's thought and was partially reflected in subsequent editions of *The Origin of Species*. Admitting the excellent factual data in Hooker's publication, Darwin, however, gently criticised his lack of analysis and explanatory conclusions:

«*The list of naturalised plants is extremely interesting, but why at the end, in the name of all that is good and bad, do you not sum up and comment on your facts? <...> Should you [not] have remarked on the number of plants naturalised in Australia and the United States* **under extremely different climates**, *as showing that climate is so important, and [on] the considerable sprinkling of plants from India, North America, and South Africa, as showing that the frequent introduction of seeds is so important?*»

From that comment (as well as from other comments) it is evident that Darwin considered these examples of plant invasions integrally. He understood that for ex-



plaining the phenomena of plant invasions we should know and understand at least (1) the qualitative and quantitative patterns of past and present distribution of a species concerned, (2) means and pathways of its migrations, (3) biological and, in modern language, ecological peculiarities of the organisms considered, and (4) limitations for dispersal of organisms caused by climatic conditions and migration barriers. Darwin really had holistic and integral views on natural phenomena, which probably best explains the great success and viability of his logically flawless theory of evolution, as contrasted to pre-Darwinian evolutionary views expressed by J.-B. Lamarck, Erasmus Darwin, and many other naturalists and philosophers of the past.

Hooker correctly supposed that invasions of European and other plants in Australia were partly promoted by availability of open habitats (*unoccupied ground*), as well as certain species deficiency of the local flora. To that Darwin commented: «*With respect to «abundance of unoccupied ground in Australia,» do you believe that European plants introduced by man now grow on spots in Australia which were absolutely bare?*» From this comment it is evident that Hooker's data stimulated Darwin's considerations on invasibility of open habitats and «unsaturated» (in terms of species) communities, the invasion phenomena now mostly considered in the Empty Niche, Disturbance and Species Richness hypotheses explaining invasions (Goodwin et al., 1999; Kennedy et al., 2002; Callaway, Ridenour, 2004; Hierro et al., 2005; Rejmánek et al., 2005, Sax et al., 2007, etc.). According to the first hypothesis, species-rich, diverse and saturated climax communities are usually more resistant to invasions than species-poor and disturbed communities. In other words, biodiversity itself (especially native and rich one) is often considered as a barrier to ecological invasions (Dukes, 2002; Kennedy et al., 2002; Hierro et al., 2005; Rejmánek et al., 2005; Maron, Marler, 2007, etc.).

J.D. Hooker and Ch. Darwin were among the first scientists who recognized the threat of invasive species to native floras, thus anticipating the modern conservational concerns and recognition of alien invasive species as the second most important threat to native biodiversity. Darwin correctly commented on the novelty of Hooker's observations: «*Your remark on a mixed invading Flora keeping down or destroying an original Flora, which was richer in number of species, strikes me as* **eminently new and important**». It is also worth mentioning that some modern studies indicate that many biodiversity hotspots (including islands) are among areas most vulnerable and susceptible to alien invasions (Stolhgren et al., 2003), which to some extent contradicts the concept discussed in the previous paragraph. However, floral uniqueness and high endemism of

such biodiversity hotspots as South Africa (the Cape Province), Australia, the Hawaii, Madagascar and many other continental and insular territories is often paradoxically combined with certain species deficiency of these floras and presence of unstable and unsaturated plant communities. In that respect, in my opinion, the floristic richness should not be confused with floristic uniqueness. Moreover, this hypothesis should be considered more in ecological than floristic terms, because alien plants invade not local floras but specific plant communities.

The Origin of Species

The most detailed views on biotic invasions, naturalization and dispersal of alien species were expressed by Darwin in his famous *Origin of Species*. Here I mostly cite the first edition, and, when necessary, also the sixth edition. Darwin gave most attention to invasion and naturalization phenomena in chapters 3 (*Struggle for existence*), 4 (*Natural selection; or the survival of the fittest*), and 12—13 (*Geographical distribution*); however, other chapters also contain notes on the problem. Overcoming the geographical and ecological barriers by invasive species is also reflected in *The Origin of Species*, especially in Chapters 11—13. There Darwin clearly indicated that species usually are not optimally adapted to their environment (or, any adaptation is not absolute, but dependable on changing environmental factors), and their distribution patterns are usually limited by dispersal pathways and barriers. The much discussed issues of invasions on islands also drew attention of Darwin.

In Chapter 3 Darwin indicated that

«*As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will be more severe between species of the same genus, when they come into contact with each other, than between species of distinct genera*».

Consequently, it means that native and introduced (alien) species belonging to the same genus (congeners), or to related genera, will be competing with each other more than species belonging to distinct and phylogenetically distant genera or families. It is important to mention that already in this phrase Darwin indicated two conflicting viewpoints: (1) introduced species related to native ones are often adapted to similar conditions and have similar ecological requirements, and thus their naturalization is more likely in an area occupied by their congeners; (2) introduced species related to native ones are more likely to compete with their native congeners, just because their similar adaptations, and that may hamper the invasion success of aliens.

As we see, in just one sentence Darwin, in fact, considered the potential invasion success of alien species **as a balance between biotic and abiotic ecological interactions**. It means that so-called «*Darwin's naturalization hypothesis*» is often oversimplified in modern publications on invasion ecology. Darwin gave not just one hypothesis, but at least two alternative but complimentary explanations, one from the viewpoint of biotic competition between species, and another from the viewpoint of the *struggle for existence* against abiotic environmental factors. Thus, the invasion success of alien taxa distantly related to native taxa is possible due to little or no competition with con-

geners and because of absence of natural enemies, such as herbivores, parasites, and pathogens (biotic factors). At the same time, alien taxa related to native ones may succeed due to their preadaptation to abiotic conditions of the newly invaded area. In each case of invasion, the balance between these factors determines the fate of an invader.

Since Darwinian idea of the struggle for existence is related to Malthusian views on overpopulation and the tendency of organisms to reproduce excessively, it is no wonder that Darwin also shared, at least partly, these ideas:

«*There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair.* <...>».

He considered biotic invasions as confirmation of *«high ratios of increase»* typical for all organisms.

«*But we have better evidence on this subject than mere theoretical calculations, namely, the numerous recorded cases of the astonishingly rapid increase of various animals in a state of nature, when circumstances have been favourable to them during two or three following seasons.* <...> *So it is with plants: cases could be given of introduced plants which have become common throughout whole islands in a period of less than ten years. Several of the plants now most numerous over the wide plains of La Plata, clothing square leagues of surface almost to the exclusion of all other plants, have been introduced from Europe; and there are plants which now range in India, as I hear from Dr. Falconer, from Cape Comorin to the Himalaya, which have been imported from America since its discovery. In such cases, and endless instances could be given, no one supposes that the fertility of these animals or plants has been suddenly and temporarily increased in any sensible degree. The obvious explanation is that the conditions of life have been very favourable, and that there has consequently been less destruction of the old and young, and that nearly all the young have been enabled to breed. In such cases the geometrical ratio of increase, the result of which never fails to be surprising, simply explains the extraordinarily rapid increase and wide diffusion of naturalised productions in their new homes*».

As we see from the following quotation, Darwin considered climate and other abiotic factors even less important than the biotic factors, mainly competition with other species:

«*That climate acts in main part indirectly by favouring other species, we may clearly see in the prodigious number of plants in our gardens which can perfectly well endure our climate, but which never become naturalised, for they cannot compete with our native plants, nor resist destruction by our native animals*».

Geographical patterns of distribution and dispersal of alien species are also discussed in detail in the works by Darwin.

Darwin's naturalization hypothesis: modern opinions and tests

Leading experts in plant invasions M. Rejmánek, D.M. Richardson and P. Pyšek (Rejmánek et al., 2005) interpret Charles Darwin's naturalization hypothesis in the following way: «*it should be easier for an alien species to invade a community in which native species that are closely related to the alien species are absent than a community in*

which native species that are closely related to the alien species are present». However, they indicate that other researchers have hypothesized the reverse, and support for **both** hypotheses has been found in observational studies, with limited or missing experimental tests. Indeed, references cited in Rejmánek et al. (2005) indicate that alien taxa are more likely to invade continental areas if native members of the same genus (and/or family) are absent (Agrawal, Kotanen, 2003; Mitchell, Power, 2003), but invaders on islands seem to exhibit the opposite tendency (Duncan, Williams, 2002). The invasion of continental areas by taxa less related to native species is partly explained by the fact that many natural enemies (herbivores, parasites, pathogens) of plants usually cannot switch to phylogenetically distant taxa (though, «host jumping» or «host switching» do occur sporadically, and even leads to major evolutionary innovations). Thus, a newly introduced species initially has virtually no natural enemies in its new geographical range; this concept is within the scope of the modern Escape from Enemies (or Enemy Release) hypothesis.

In other words, Darwin's naturalization hypothesis seemingly predicts that introduced species tend not to invade areas containing closely related native species because of competition with close relatives sharing ecological preferences and natural enemies; on the other hand, introduced species may succeed in areas with native related species because alien taxa may share preadaptations to the new environment with related native taxa. A test of both hypotheses based on fish invasions showed no clear pattern supporting either viewpoint (Ricciardi, Mottiar, 2006). However, a model study of phylogenetic patterns among native and alien (including naturalized and invasive) grasses (*Poaceae*) of California, the USA, demonstrated that, at least in the case studied, exotic taxa less related to native species are usually more invasive (Strauss et al., 2006), and thus it provided additional support to the classical concept of Darwin's naturalization hypothesis. Since highly invasive grass species in California proved to be less related to native grass species than are introduced but non-invasive ones, phylogenetic relatedness of an invader can be regarded as a predictive tool for invasiveness.

However, a special study of the introduced flora of New Zealand, especially seed plant species introduced to these islands (Duncan, Williams, 2002), demonstrated that alien taxa with congeneric relatives are significantly more (not less!) likely to naturalize, perhaps because these taxa share with their native relatives some preadaptations to their new environment.

We believe that these seeming paradoxes should be analyzed from the viewpoint of mainly ecological, but not phylogenetic, aspects. As demonstrated by V.V. Zherikhin (2003), the phylocenogenesis processes are conditioned mainly by the balance of biotic *versus* abiotic interactions. Considering his concept, we can predict that invasions of alien taxa correspond to patterns of biotic *versus* abiotic competition in ecosystems. It means that communities and biomes with predominant limiting abiotic factors are more vulnerable to invasions by taxa more ecologically similar (and phylogenetically close) to the native species, while those with predominant biotic competition are more vulnerable to invasions by ecologically distinct (and phylogenetically distant) taxa. Consequently, boreal, arctic, antarctic and insular biotas are, in general, more vulner-

able to invasions by taxa preadapted to local conditions and more closely related to natives, while tropical, partly subtropical, and ecologically saturated communities are more vulnerable to invasions by ecologically distinct and phylogenetically distantly related taxa. This concept has to be analyzed and proved by special studies.

The main conclusion should be probably as follows: biotic invasions are too diverse and complicated phenomena to be explained by just one naturalization hypothesis. Some generalizations are possible, but in each case a wide range of explanations should be applied, and, *ad hoc* hypotheses will predominate in the field of invasive ecology in the nearest future, until a new ecological synthesis.

We should not consider Darwin's observations and generalizations discussed in *The Origin of Species* as the final truth, even for his times. Darwin just used the best knowledge available to provide explanations to the cases of biotic invasions known to him. Most important that he did it integrally and in a non-simplistic way, from the viewpoint of his theory of evolution. Consequently, he provided the first evolutionary and ecological explanations for biotic invasions and thus established foundations for all following evolutionary and ecological studies of that global phenomenon.

Conclusions

Darwin considered biotic invasions as complex but integral phenomena involving ecological, biogeographical, evolutionary, taxonomic and other aspects, such as patterns of past and present distribution, means and pathways of natural or human-aided dispersal (and dispersal limitations due to climate and migration barriers), struggle for existence (including competition, herbivory, predation etc.) and natural selection, phylogenetic relationships of taxa, environmental factors, and even evolutionary (microevolutionary in modern terms) changes.

All modern hypotheses explaining biotic invasions are evolutionary in their nature. Moreover, as we have seen in the discussion above, such modern concepts are rooted in ideas of Charles Darwin expressed in his publications and letters. For example, the Enemy Release hypothesis is rooted in the Darwinian concept of «struggle for existence», or biotic competition between and within species, as well as in Darwin's view on excessive rates of reproduction of organisms controlled by both biotic and abiotic factors. The first insights into the modern Empty Niche, Disturbance, and Species Richness hypotheses can be traced down to Darwin's correspondence with J.D. Hooker and A. Gray. In particular, Hooker's data on the flora of Australia stimulated Darwin's considerations on invasibility of open habitats («unoccupied ground») and «unsaturated», in terms of species, communities and whole floras. The evolving nature of naturalized plants and animals is reflected, in particular, in the Novel Weapon hypotheses, which is impossible without the evolutionary context.

Darwin outlined not one naturalization hypothesis but at least three invasion concepts, which may be considered as precursors of modern theories/hypotheses of biotic invasions. Thus, **Darwin established foundations for all following evolutionary and ecological studies of biotic invasions, including several currently debated invasion concepts**, such as Escape from Enemies, Empty Niche, Species Richness, and Distur-

bance hypotheses. We can only wonder how well he outlined in succinct phrases the main issues of the future field of invasion biology.

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1. *Agrawal A.A., Kotanen P.M.* Herbivores and the success of exotic plants: a phylogenetically controled experiment // Ecology Letters. — 2003. — **6**. — P. 712—715.
2. *Avise J.C.* The best and the worst of times for evolutionary biology // BioScience. — 2003. — **53**(3). — P. 247—255.
3. *Callaway R.M., Maron J.L.* What have exotic invasions taught us over the past twenty years? // Trends in Ecology and Evolution. — 2006. — **21**. — P. 369—374.
4. *Callaway R.M., Ridenour W.M.* Novel weapons: invasive success and the evolution of increased competitive ability // Front. Ecol. Environ. — 2004. — **2**. — P. 419—426.
5. *Daehler C.C.* Darwin's naturalization hypothesis revisited // Amer. Naturalist. — 2001. — **158**. — P. 324—330.
6. *Darwin C.R.* Narrative of the surveying voyages of His Majesty's Ships *Adventure* and *Beagle* between the years 1826 and 1836, describing their examination of the southern shores of South America, and the *Beagle's* circumnavigation of the globe. Journal and remarks. 1832—1836. — London: Henry Colburn, 1839.
7. *Darwin C.R.* Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. *Beagle* round the World, under the command of Capt. Fitz Roy, R. N. — 2nd ed. — London: John Murray, 1845.
8. *Darwin C.R.* Productiveness of foreign seed // Gardeners' Chronicle and Agricultural Gazette. — 1857 (14 November). — **46**. — P. 779.
9. *Darwin C.R.* On the origin of species by means of natural selection. — London: John Murray, 1859.
10. *Darwin C.R.* The life and letters of Charles Darwin, including an autobiographical chapter / Ed. by F. Darwin. — London: John Murray, 1887. — Vol. 2.
11. *Darwin C.* The Autobiography of Charles Darwin. 1809—1882 / Ed. with Appendix and Notes by his grand-daughter Nora Barlow. With original omissions restored. — London: Collins, 1958.
12. *Darwin C.R.* The Complete Works of Charles Darwin Online. Accessed 2009. www.darwin-online.org.uk
13. *Davis M.* Biotic Globalization: does competition from introduced species threaten biodiversity? // BioScience. — 2003. — **53**. — P. 481—489.
14. *Davis M.A., Thompson K.* Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology // Bull. Ecol. Soc. Amer. — 2000. — **81**. — P. 226—230.
15. *Dobzhansky Th.* Nothing in biology makes sense except in the light of evolution // The American Biology Teacher. — 1973. — **35**. — P. 125—129.
16. *Dukes J.S.* Species composition and diversity affect grassland susceptibility and response to invasion // Ecological Applications — 2002. — **12**. — P. 602—617.
17. *Duncan R.P., Williams P.A.* Darwin's naturalization hypothesis challenged // Nature. — 2002. — **417**. — P. 608.
18. *Elton C.S.* The ecology of invasions by animals and plants. — London: Methuen, 1958. — 181 p.

19. *Global Strategy* on Invasive Alien Species // Convention of Biological Diversity, SBSTTA Sixth Meeting. — Montreal, 2001. — ix + 52 p. [www.biodiv.org]
20. *Goodwin B.J., McAllister A.J., Fahrig L.* Predicting invasiveness of plant species based on biological information // Conservation Biology. — 1999. — **13**. — P. 422—426.
21. *Hierro J.L., Maron J.L., Callaway R.M.* A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range // Journal of Ecology. — 2005. — **93**. — P. 5—15.
22. *Kennedy T.A., Naeem S., Howe K.M., Knops J.M.H., Tilman D., Reich P.* Biodiversity as a barrier to ecological invasion // Nature. — 2002. — **417**. — P. 636—638.
23. *Kutschera U., Niklas K.J.* The modern theory of biological evolution: an expanded synthesis // Naturwissenschaften. — 2004. — **91**. — P. 255—276.
24. *Lewontin R.C.* Directions in evolutionary biology // Annu. Rev. Genet. — 2002. — **36**. — P. 1—18.
25. *Mack R.N., Simberloff D., Lonsdale W.M., Evans H., Clout M., Bazzaz F.* Biotic invasions: causes, epidemiology, global consequences and control // Issues in Ecology. — 2000. — No. 5. — P. 1—20.
26. *Maron J.L., Marler M.* Native plant diversity resists invasion at both low and high resource levels // Ecology. — 2007. — **88**. — P. 2651—2661.
27. *Mitchell C.E., Power A.G.* Release of invasive plants from fungal and viral pathogens // Nature. — 2003. — **421**. — P. 625—627.
28. *Mosyakin A.S.* (Мосякін А.С. Огляд основних гіпотез інвазійності рослин // Укр. ботан. журн. — 2009. — **66**(4). — P. 466—476.
29. *Pyšek P., Hulme P.E.* Spatio-temporal dynamics of plant invasions: Linking pattern to process // Ecoscience. — 2005. — **12**. — P. 302—315.
30. *Rejmánek M.* A theory of seed plant invasiveness: the first sketch // Biological Conservation. — 1996. — **78**. — P. 171—180.
31. *Rejmánek M., Richardson D.M., Pyšek P.* Plant invasions and invasibility of plant communities // Vegetation ecology / Ed. by E. Van der Maarel. — Oxford: Blackwell Science, 2005. — P. 332—355.
32. *Ricciardi A., Mottiar M.* Does Darwin's naturalization hypothesis explain fish invasions? // Biological Invasions. — 2006. — **8**. — P. 1403—1407.
33. *Richardson D.M., Pyšek P.* Plant invasions: Merging the concepts of species invasiveness and community invasibility // Progress in Physical Geography. — 2006. — **30**. — P. 409—431.
34. *Sax D.F., Stachowicz J.J., Brown J.H., Bruno J.F., Dawson M.N., Gaines S.D., Grosberg R.K., Hastings A., Holt R.D., Mayfield M.M., O'Connor M.I., Rice W.R.* Ecological and evolutionary insights from species invasions // Trends in Ecology and Evolution. — 2007. — **22**(9). — P. 445—471.
35. *Science*, Evolution, and Creationism / Committee on Revising Science and Creationism: A View from the National Academy of Sciences. National Academy of Sciences and Institute of Medicine of the National Academies. — Washington, DC.: The National Academies Press, 2008. — xvi + 70 pp.
36. *Stohlgren T.G., Barnett D.T., Kartesz J.T.* The rich get richer: patterns of plant invasions in the United States // Front. Ecol. Environ. — 2003. — **1**(1). — P. 11—14.
37. *Strauss S.Y., Webb C.O., Salamin N.* Exotic taxa less related to native species are more invasive // Proc. Natl. Acad. Sci. USA. — 2006. — **103**(15). — P. 5841—5845.
38. *Zherikhin V.V.* (Жерихин В.В. Избранные труды по палеоэкологии и филоценогенетике. — М.: Т-во научных изданий КМК, 2003. — vi+ 542 с.).

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ЧАРЛЬЗ ДАРВІН ТА ЕКОЛОГІЧНІ ПОЯСНЕННЯ БІОТИЧНИХ ІНВАЗІЙ: ІСТОРИЧНИЙ АНАЛІЗ ТА СУЧАСНІ КОНЦЕПЦІЇ

У статті обговорюється внесок Ч. Дарвіна до концепції екології інвазій. Учений розглядав біотичні інвазії як складний, але комплексний феномен, що охоплює екологічні, біогеографічні, еволюційні, таксономічні та інші аспекти, зокрема особливості сучасного та минулого поширення (і міграційних бар'єрів), боротьбу за існування та природний добір, філогенетичні відносини таксонів, екологічні чинники та еволюційні зміни. Всі сучасні гіпотези біотичних інвазій є, по суті, еволюційними. Дарвін окреслив не одну гіпотезу натуралізації, але принаймні три концепції інвазій, які можна трактувати як попередники сучасних теорій і гіпотез біотичних інвазій. Таким чином, Дарвін заклав підвалини всіх подальших еволюційних та екологічних досліджень біотичних інвазій, включаючи такі сучасні гіпотези інвазій, як «втеча від ворогів», «порожня ніша», «видове багатство» та «порушення». Показано, що Дарвінівські пояснення інвазій ґрунтуються на співвідношенні між біотичними й абіотичними факторами, на інших екологічних взаємодіях.

К л ю ч о в і с л о в а: Дарвін, еволюція, біотичні інвазії, екологія інвазій, біогеографія, флора

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ЧАРЛЬЗ ДАРВИН И ЭКОЛОГИЧЕСКИЕ ОБЪЯСНЕНИЯ БИОТИЧЕСКИХ ИНВАЗИЙ: ИСТОРИЧЕСКИЙ АНАЛИЗ И СОВРЕМЕННЫЕ КОНЦЕПЦИИ

В статье рассматривается вклад Ч. Дарвина в концепцію экологии инвазий. Ученый рассматривал биотические инвазии как сложный, но целостный феномен, который включает экологические, биогеографические, эволюционные, таксономические и другие аспекты, в частности, особенности современного и прошлого распространения (и миграционных барьеров), борьбу за существование и естественный отбор, филогенетические связи таксонов, экологические факторы и эволюционные изменения. Все современные гипотезы биотических инвазий в своей основе являются эволюционными. Дарвин наметил не одну гипотезу натурализации, но, по крайней мере, три концепции инвазий, которые могут рассматриваться как предтечи современных теорий и гипотез биотических инвазий. Таким образом, Дарвин заложил основы всех последующих эволюционных и экологических исследований биотических инвазий, включая такие современные гипотезы инвазий, как «бегство от врагов», «пустая ниша», «видовое богатство» и «нарушенность». Показано, что Дарвиновские пояснения инвазий основываются на соотношении биотических и абиотических факторов и экологических взаимодействиях.

К л ю ч е в ы е с л о в а: Дарвин, эволюция, биотические инвазии, экология инвазий, биогеография, флора.