Exoot: de begripsgeschiedenis van de invasie-ecologie, van Linnaeus tot Darwin

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— ENGLISH SUMMARY —

ALIEN - A CONCEPTUAL HISTORY OF INVASION ECOLOGY, FROM LINNAEUS TO DARWIN

This is not a dissertation about the history of alien plant species, but about the history of our understanding of them. This topic has been taken up before. Matthew Chew, in his dissertation entitled *Ending with Elton: Preludes to Invasion Biology* (2006), convincingly shows that the conceptual history of invasion ecology stretches much further back than Charles Elton's *The Ecology of Invasions by Animals and Plants* (1958), often regarded as the field's founding text. However, Chew overlooks the decisive role of Linnaeus in shaping early thinking about plant nativity and human agency in dispersal. This is where my dissertation diverges and takes a different path. Chronologically, I place the beginnings of the European conceptual history of invasion ecology in the work of Carolus Linnaeus. This eighteenth-century Swedish naturalist was the first to engage thoroughly with the distinction between native and alien. Methodologically, too, I take a different approach. I argue that our understanding of alien plants was shaped not merely by a quantitative increase in alien species, but by qualitative conceptual shifts. This perspective offers new answers to questions such as: When did a distinction between alien and native arise? How did naturalists first come to recognize human agency in plant dispersal? And when do they begin to notice alien species escaping and establishing themselves in the wild?

The awareness of alien plants is intricately linked to the rise of phytogeography, the study of plant distributions. Linnaeus played a pivotal role in its early development. He spoke of botanical topography and was the first to engage thoroughly with the European tradition of floras. His own cataloguing of the flora of Sweden set the gold standard for floras, providing a methodological framework that would influence generations to come. Through careful study of plant distributions, exotic influences became apparent to Linnaeus and his "apostles." Recognizing these influences required a sensitivity to the distinctions between the familiar and the strange, the native and the alien. Yet, this sensitivity was not the only prerequisite. The central claim of this dissertation is that our understanding of alien plants is inextricably tied to three earlier semantic shifts. Each shift illuminates a different

aspect of the alien, revealing it in turn as a *colonist*, as an *invasive*, and as a *weed*.

The conceptual history of invasion ecology begins with a shift in the meaning of the word *colonist*. This shift can be traced back to the work of Carolus Linnaeus and his student Jon Flygare, who in 1768 published the dissertation *De coloniis plantarum*. It represents the earliest systematic attempt to document the arrival and establishment of alien plants in Sweden and Europe. Strikingly, they employ the term "colonist" to describe these botanical newcomers. Applying such a term to plants was far from trivial: it marked a crucial conceptual shift, reflecting an early attempt to understand the presence of recent arrivals within the native flora. For Linnaeus, the term "colonist" was not limited to plants introduced through human action. Humans were only one among several dispersal agents, alongside wind, water, and animals, but an important one. For the first time, Linnaeus identified the various ways in which people, by accident or by design, contributed to the introduction of alien plant species.

How does the arrival and establishment of colonists fit within Linnaeus' broader conception of plant distribution? At first glance, *De coloniis plantarum* appears anomalous, seemingly at odds with prevailing interpretations of his phytogeographical and ecological ideas. On the one hand, Linnaeus is portrayed as adhering to a static view of nature, convinced of the fixity of species and of place. On the other hand, he is also presented as embracing a dynamic view, in which species were mutable and capable of moving and acclimatizing to new regions. Both interpretations, however, oversimplify Linnaeus' position. A close reading of texts such as *Critica botanica* (1737) and *Stationes plantarum* (1754) reveals a more nuanced conception of place, simultaneously static and dynamic.

Linnaeus achieved this duality by distinguishing three interrelated aspects of "birthplace" (*locus natalis*), namely "soil/substrate" (*solum*), "frequency/prevalence" (*frequentia*), and "region" (*regio*). Of these, only "soil," later reinforced by the synonym "station" (*statio*), formed the necessary link between plant and place. Region and frequency, however, were in flux. As Augustin Pyramus de Candolle later noted, Linnaeus differentiated between *habitation* and *station*. *Habitation* referred to the specific geographical region where a plant is native, whereas *station* denoted the type of place, or "special nature of the locality," in which it grows – what we today would, somewhat confusingly, call its habitat.

The white waterlily (*Nympha alba* L.) illustrates this distinction. Its habitat is freshwater lakes and rivers, yet it does not occur in every lake or river under similar environmental conditions. Its native range is limited to Western Europe, Asia, and Northern Africa. In Linnaeus' view, however, this could change if the species migrated to similar stations in different regions. In this way, he could argue that plant distribution exhibited a kind of dynamic stability: the topography of plants was continuously changing, yet the fixity to a soil or station meant that plants could only colonize places suited for their flourishing.

Within Linnaeus' broader natural-theological framework of species distribution, set out in *De telluris habitabilis incremento* (1744), every plant turns out to be a colonist. All species, he claimed, originated in the Garden of Eden before dispersing across the expanding habitable landmass. He envisioned this garden as a mountainous island near the equator. In a prismatic sense, this island encompassed the variety of soils and climates found across the globe in one place. It is difficult for us today to recapture the conviction that nature discloses harmony, order, and a designing hand. Linnaeus' attempt to harmonize scripture with natural science was neither insincere nor forced. He was convinced that the two were complementary sources of truth. His natural theology even encouraged him to pursue several promising lines of research, namely on the fecundity, dispersal, and succession of plants, which would later exert a profound influence on Charles Darwin.

When discussing plant colonization, Linnaeus employed a rich vocabulary. He contrasted the term *indigena* ("indigenous," "native") with three others: *advena* ("newcomer," "refugee"), *peregrinus* ("foreigner"), and *alienigena* ("foreign"). The category *advena* was reserved for plants unintentionally transported to new regions, whereas *peregrinus* served more broadly as the counterpart of *indigena*. For Linnaeus, however, there was no strict demarcation between *indigena* and *peregrinus*; like humans, plant species can change their "civil status." The rights of "full citizenship" were granted only to colonists that had become widespread. This vocabulary played a significant role in the formalization of the scientific language of phytogeography and, later, invasion ecology.

Linnaeus described alien plants using vivid metaphors drawn from medicine, household management, military, and political imagery. Colonists could "infest" farmers' fields, yet beyond the anthropogenic realm these same colonists were no nuisance and, if fruitful, could even secure a permanent place in the "household of nature." He also imagined colonists as "foreign legionnaires" reinforcing the ranks of "Europe's veteran army of plants"; while the most fortunate, thoroughly established colonists acquire "civil rights." Two of these metaphors also became the subject of formal publications, namely *Oeconomia naturae* (1749) and *Politia naturae* (1760). In both works, nature was conceived as a state of dynamic stability, where opposing and cooperative forces are perpetually in balance. To Linnaeus, it would have been inconceivable that any place in this household, any rank in this army, or any office in this state would vanish from the face of the earth.

Linnaeus' metaphors continue to resonate today. The household metaphor, for instance, persists in the Dutch dualism between *inheems* ("indigenous") and the out-of-place *uitheems* ("alien," or "non-indigenous"), with *heem* etymologically related to "home." Like Linnaeus, invasion ecology still uses political language, employing terms such as "naturalise" and "naturalization." Plants outside of their natural ranges or often described as "adventive" plants, or even "refugees" or "migrants". The military metaphor plays an even more prevalent role, with inva-

sive species depicted as "enemies," "intruders," or one of the "horsemen of the biodiversity apocalypse." Finally, contagion metaphors, such as "pest," "infestation," "plague," and "epidemic," are frequently employed to frame the spread of alien plants.

The second semantic shift in the early conceptualization of alien plants marks a turning point in the evaluation of newcomers. Linnaeus spoke in predominantly positive terms about successful plant colonists, with one notable exception. In farmers' fields there was the potential threat of infestation through the import of seeds. Here, he relied on the traditional definition of weeds as plants out of place and as a general nuisance to humans. In the mid-nineteenth century, however, a new class of weeds emerged. Its rise became evident in a historical episode that briefly held the European continent in its grip: the rapid spread of Canadian pondweed (*Elodea canadensis* Mich.) from Great Britain to the rest of Western Europe. A discovery first regarded as benign suddenly took on an acute seriousness once the plant's exotic origin was recognized. This newly discovered native species was quickly recast as a troublesome foreign weed, but of an unusual sort. Weeds had until then been limited to human spaces: fields, gardens, parks, and roadsides. Like all weeds, Canadian pondweed was treated as a plant out of place and a nuisance to humans. However, what makes this case truly remarkable is that it was deemed out of place in nature itself. As if nature had its own category of weeds, taking up space, choking rivers, displacing natives, and disrupting wild habitats. What set this case further apart was its societal impact. For the first time, an alien plant became a matter of public concern, drawing coverage in newspapers and popular science articles, and even prompting government action. With the success of Canadian pondweed, the association between alienness and weediness was firmly established, laying the groundwork for later anxieties about invasive alien plant species.

The swift conquest of Canadian pondweed marked Europe's first encounter with a foreign plant plague. This outbreak unfolded against the backdrop of the supplanting of plant topography by plant geography, a shift pioneered in the early nineteenth century by Alexander von Humboldt. In the decades before the arrival of pondweed, plant geographers like John Henslow and Hewett Cottrel Watson had begun to scrutinize plant nativity, particularly in cases where human agency was suspected. Unlike the later alarm over Canadian pondweed, no negativity was voiced, nor was any moral judgement passed on these foreign influences.

An important difference between Linnaeus' plant topography and the emerging field of plant geography lay in the classification of colonists. The latter began to make a sharp distinction between natural and human-mediated dispersal, a distinction deemed crucial for uncovering the laws governing the distribution of plant species in time and space. While Linnaeus interpreted this distribution within the narrow confines of the Biblical timescale, plant geography expanded the temporal horizon by embracing the concept of deep geological time. These eons, unimagin-

ably long by human standards, revealed a dynamic distribution of flora and fauna, if one that still exhibited order. Alfred Russel Wallace highlighted an important link between the geographical and geological distribution of species. Based on biogeographical and fossil evidence, he proposed the following law: "[E]very species has come into existence coincident both in space and time with a pre-existing closely allied species." With a notable exception, of course, in cases of colonization, where plants suddenly appeared far from their nearest relatives.

Identifying plants introduced by humans was no easy task, especially when they hitched a ride unnoticed. Reliable plant geography observations were still a relatively new development. Earlier records, such as those in herbals, offered a hotchpotch of credulous and questionable accounts. Often, only piecemeal information existed to support claims of human-mediated migration, especially the plants that quickly "naturalized" by becoming well-established in the wild. Where Linnaeus could speak with some certainty about a species' foreign origin, plant geographers faced uncertainty and had to speak in terms of differing degrees of probability. The "civil status" of plants came under closer scrutiny and was subject to further taxonomic splitting, which gave rise to a new terminology to classify species based on their origins. Most importantly, human-assisted migration was regarded as a disruptive force. It obscured efforts to reconstruct plant distributions and complicated the attempts to derive 'laws' from nature.

The third and final aspect of alien plants discussed in this dissertation is their invasiveness. This aspect first appears in the travel writings of Charles Darwin, whose voyage on the *Beagle* marks a turning point in the conceptual history of invasion ecology. While travelling through the Paraguayan and Argentinian Pampas, he observed the rapid spread of a Mediterranean cardoon (*Cynara cardunculus* L.). Darwin´s journal marks the first recorded use of the word "invasive," capturing the impact of cardoon on the native flora and showing how their proliferation came at the expense of indigenous species. He also noticed that these invasions did not occur in isolation. The spread of the cardoon was further facilitated by other anthropogenic introductions, such as cattle and sheep.

On subsequent stops along his journey, Darwin documented further examples of the far-reaching effect of European colonists on indigenous flora and fauna. To make sense of these observations, he drew on Charles Lyell's *Principles of Geology* (1832), which emphasized the continual geological reshaping of regions through erosion, volcanic activity, and other processes. This perspective allowed Darwin to see landscapes and species distributions as dynamic rather than fixed, marked by migration, colonization, replacement, and extinction. He would later supply the mechanism of natural selection by which species could adapt to different climates and soils, and fit new places.

After his voyage, Darwin kept a keen interest in invasive plant species. Like Linnaeus, he began compiling a "table of colonists" to study the influence of European

flora on North America and vice versa. Correspondence with Asa Gray revealed the remarkable spread of European plants in the Americas. This Midas' touch contrasted with the limited spread of American species in Europe, with Canadian pondweed or horseweed (*Erigeron canadensis* L.) as notable exceptions. Crucially, Darwin did not view invasives as anomalies. Rather, he saw them as windows into a far older history of plant invasions, independent of human influence. However, this analogy built on the hypothesis that plants could disperse over long distances without the aid of human maritime activity.

To investigate the problem of plant dispersal, Darwin conducted a wide range of experiments on long-distance migration of seeds to explain how plants reached far-flung regions. At the time, there was no scientific consensus on the range of plant dispersal, and empirical evidence was scarce. Darwin's mentor, John Henslow, believed there were unsurpassable natural limits to migration. Joseph Dalton Hooker held a similar view. And Louis Agassiz went further still, arguing for a static view of plant distribution in which species were fixed to their places. Darwin challenged these assumptions, demonstrating that long-distance dispersal was possible and by no means merely a human phenomenon. Furthermore, invasive alien species gave insight into the effects of these migrations and Darwin displayed scientific curiosity for the spread and establishment of Canadian pondweed and other invasive flora.

Invasive alien species play an understudied yet meaningful role in *On the Origin of Species* (1859). Their long-distance dispersal, rapid reproduction, and unchecked spread exemplify several of Darwin's core themes. Understanding these invasions was important proof of the power of geometric increase, as laid bare by Thomas Malthus. They also offered insight into the struggle for existence and the principle of divergence. Where Darwin initially conceived of place as a discrete unit for which different species struggled, he came to see that places, like species, were not immutable. The physical diversification of the earth's surface, together with the growing complexity of relations among organisms, meant that new places could continually originate as old ones disappeared.

On a metaphorical level, both Lyell and Darwin reinterpreted Linnaeus' imagery, emphasizing the disruption and disorder of the household, army, and state of nature. Species had to struggle to maintain their place, rank, or office. Yet Lyell still envisioned a dynamic balance or harmony within the natural order. In *On the Origin of Species* Darwin revealed a harsher vision of the "economy of nature," where species were locked in a continuous struggle to hold their place. The military image of *invasive* alien species, among others, offered insight into an ever-changing household or state of nature. Their prosperity proved that places, roles, and relations in nature's household were never fixed. Just as species could go extinct, so too could they be ousted from places by new occupants. Newcomers were no longer reinforcements to an existing plant army, but invasive hordes, expanding at the expense of indigenous inhabitants. This revealed an essential vulnerability that

extends to humanity itself: all places, even our own, are contingent, unstable, and open to replacement.

In Darwin's writings, the three aspects of alien plants converge. In his observations and notes, he employs all three terms: colonist, weed, and invasive. Yet his reflections on these newcomers remain normatively ambiguous. Upon returning from his *Beagle* voyage, he wrote: "Where the European has trod, death seems to pursue the aboriginal." Yet his sustained interest extended far beyond this grim assessment. In a descriptive sense, these aliens revealed something fundamental about the plant kingdom and life itself. Invasive, colonizing, and weedy tendencies dwell in every plant. Each plant descends from a line of successive and successful colonization events. Somewhere in evolutionary history, each has had its day in the sun, has taken root on distant shores, and conquered new territory. In Darwin's metaphorical household or state of nature, no plant is permanently bound to a single place. Every plant, however anchored in place it may appear, carries a measure of placelessness in its fibers.