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BIODIVERSITY RESEARCH

The first steps towards unifying concepts in invasion ecology were made one hundred years ago: revisiting the work of the Swiss botanist Albert Thellung

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ABSTRACT

Aim Biological invasions are a major threat to biodiversity, and *The ecology of invasions by animals and plants* by Charles Elton (1958) is often recognized as the starting point for modern invasion research. Yet there were predecessors in invasion research whose contribution to the development of ideas and concepts in this field is often underestimated. To contribute to a balanced perception of pioneers in invasion research, we retrace the work of the Swiss botanist Albert Thellung (1881–1928) whose main work, *La flore adventice de Montpellier*, appeared 100 years ago, in 1912, and illustrate how his ideas contributed to the current state of the art in the fields of invasion science and biogeography.

Location None.

Methods We discuss conceptual approaches in the invasion-related work by Albert Thellung.

Results Thellung's early work covered topics that are still central to widely used invasion frameworks. He promoted concepts to classify alien species (degree of naturalization, introduction pathways and time period of introduction) and adopted these systematically at a regional scale in his alien flora of Montpellier, comprising 800 non-native species. He introduced an exact population-based definition of naturalization, with links to environmental barriers, and elaborated the first assessment of pathway efficiency by relating introduction modes to naturalization. With conceptual papers and a first review of human-mediated plant introductions, Thellung stimulated further research on plant invasions as well as modern terminological frameworks for alien plants.

Main conclusions Albert Thellung was an outstanding member of the group of pre-Eltonian invasion scientists. He opened up focussed research in the field of alien plants in Europe, and his theoretical approaches were a powerful step towards unifying concepts in invasion ecology.

Keywords

Biological invasions, conceptual frameworks, exotic floras, introduction pathways, invasion ecology, naturalization, wool aliens.

INTRODUCTION

The English ecologist Charles Elton was the first who clearly recognized the global dimension of impacts associated with the introduction and spread of alien organisms. His book *The ecology of invasions by animals and plants* (Elton, 1958) is generally renowned as the starting point for the focussed scientific attention on biological invasions (Richardson & Pyšek, 2007, 2008; Richardson, 2011). Today, biological invasions are broadly perceived as a major driver of change in biotic patterns and one of the most important causes of biodiversity loss world-wide (Millennium Ecosystem Assessment,

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2005; Pyšek & Richardson, 2010). As Richardson & Pyšek (2007) state, Elton's book has been, and still is, extensively used as a source of ideas and stimulus for fundamental concepts in invasion ecology. The authors thus conclude that Charles Elton 'was a visionary scientist who fostered considerable cross-disciplinary synergy', a view 'shared by most prominent researchers in the field' (Richardson & Pyšek, 2007, 2008, p. 163).

Given that Charles Elton is the father of modern invasion ecology, there were indeed several generations of grandfathers and great-grandfathers who paved the way to systematic research in invasion topics (see Trepl, 1990; Chew, 2011 for reviews). The phenomenon of introduced species has been addressed since the 16th and 17th centuries, and in the late 19th and early 20th centuries, it was mentioned in the writings of prominent scientists, including Charles Lyell (1767–1849), Alexander von Humboldt (1769–1859), Joakim Frederik Schouw (1789–1859), Alphonse de Candolle (1806–1893), Charles Darwin (1809–1882) and Joseph Hooker (1817–1911; see Trepl, 1990; Chew, 2011; Richardson & Pyšek, 2008). Moreover, in different European regions, several systematic studies emerged that led not only to a wealth of inventories of non-native species (e.g., Büttner, 1883; Lehmann, 1895; Probst, 1949), but also to the earliest concepts to classify them rigorously. Most prominent among the latter are Watson's *Cybele Britannica* (Watson, 1847) and de Candolle's *Géographie botanique raisonnée* (de Candolle, 1855) and, later, the floras by Thellung (1912) and Linkola (1916, 1921). Yet often written in other languages than English and not being included in the Web of Science, these works are not easily accessible to many invasions scientists today. This clearly brings about risks of underestimating the contribution of older authors to the evolution of ideas and concepts in invasion ecology. As early as in the 1950s, the Finnish botanist Jalas (1955) indirectly pointed to the richness of existing terminological and conceptual frameworks when he complained about a terminological confusion – similarly as Blackburn *et al.* (2011) did about 50 years later when considering the current conceptual diversity in plant and animal ecology or terrestrial and marine ecology, respectively.

Here, we retrace some lines in the scientific work of the Swiss botanist Albert Thellung whose contribution to invasion science appears to be strongly underestimated. Chew (2011), in his review of predecessors of modern invasion biology, shortly refers to Thellung, but mostly with a focus on terms and without reflecting conceptual ideas behind. Thellung is not totally forgotten though, as illustrated by 97 references to his main work, *La Flore adventice de Montpellier* (Thellung, 1912), in Google Scholar. Yet the number of 3930 references to Elton's *The ecology of invasions by animals and plants* in the same database is higher by a factor of about 40 (access to Google Scholar on 24 July 2012). One-third of these citations have appeared since 2008, that is, the year in which the 50th anniversary of Elton's work was commemorated in a special issue of *Diversity and Distributions* (Richardson & Pyšek, 2008). In contrast, only 12% of total references to Thellung's *Flore adventice* are related to the same reference period. The Cited Reference Search tool in the Web of Science revealed 2616 references to Elton's book, a number that is higher by a factor of about 85, compared to only 31 references to Thellung's volume (as of 25 July 2012).

To contribute to a more balanced perception of important pioneers in invasion science, we take the 100th anniversary of the first publication of the *Flore adventice de Montpellier* in 1912 to highlight Albert Thellung's status as an outstanding member of the group of pre-Eltonian invasion scientists and illustrate how his ideas contributed to the current state of the art in the fields of not only invasion science, but also conservation biogeography in general. This is because, as we show below, Thellung's research on alien species had a strong biogeographical focus and his concepts and ideas are tractable in modern frameworks of biological invasions.

ALBERT THELLUNG: A PIONEER IN INVASION RESEARCH

Albert Thellung (Fig. 1) was born in Enge, Zürich on 12 May 1881, and passed away in the same city on 6 June 1928. Thellung started his studies of natural sciences at the Universität Zürich in 1900 and passed his final exam (with distinction) in 1904. Since October of the same year, Thellung worked, with some interruptions, as assistant lecturer (wissenschaftlicher Assistent) at the Botanical Museum of the Universität Zürich (today: Institute of Systematic Botany). He completed his doctoral thesis, a monograph on the genus

Figure 1 The Swiss botanist Albert Thellung (1881–1928), an important pioneer in invasion research (photograph from Pfeifer & Rutishauser, 2000, by courtesy of Rolf Rutishauser).

Lepidium (Thellung, 1906), in 1905, again with distinction. Thellung habilitated in 1909 and received the grade of a titular professor in 1921. Apart from a research stay of about 1 year in Montpellier, France, Thellung worked mainly in Zürich. Hans Schinz, who was the director of the Botanical Museum and in this position both a superior and friend of Thellung, published an obituary in the year of Thellung's death (Schinz, 1928) with the previously cited details on Thellung's academic career. Schinz also reported that Thellung had a weak constitution that forced him repeatedly to interrupt his work.

The scientific work of Albert Thellung includes about 240 publications, which appeared between 1902 and 1930 and which are listed in the obituary by Schinz (1928). Thellung's main contribution to invasion science was certainly the promotion of conceptual approaches to classify introduced species (Thellung, 1905, 1912, 1918/19) and efforts to apply these concepts systematically to regional alien floras (Naegeli & Thellung, 1905; Thellung, 1912).

Moreover, Thellung participated in working on the flora of Switzerland (Schinz, 1914) and on Hegi's famous *Illustrierte Flora von Mitteleuropa* (e.g., Thellung, 1913a) and published a wealth of taxonomic and floristic studies, including many papers on alien species (e.g., on the genera *Aster* and *Helianthus*; Thellung, 1913b) and contributions to the alien flora of Switzerland and other regions (e.g., Thellung, 1907). His last work on the origin of cultural species appeared 2 years after his death (Thellung & Braun-Blanquet, 1930). Although Thellung worked in Zürich and also spent some time in Montpellier, he was not associated with the Zürich-Montpellier-School as reported by Chew (2011) because this school is usually related to phytosociology, that is, the classification of plant communities, while Thellung's scientific focus was on species.

One hundred years ago, in 1912, Thellung's main work in the field of invasion science appeared, in French, comprising work that was accepted in 1909 as his habilitation thesis by the Universität Zürich: *La flore adventice de Montpellier* (Thellung, 1912; available online at http://archive.org/details/lafloreadventice00thel). For this volume, Thellung compiled an account of the alien flora of Montpellier, a city in southern France with about 80,000 inhabitants in 1911, and its wider surroundings, the Hérault department (6101 km^2). As this region had a very rich and long history of botanic records owing to the work of several well-known French botanists (e.g., Pyramide de Candolle, Cosson, Delile, Godron, Flahault), Thellung was able to retrace the arrivals of some alien plant species since the 17th century, and in particular their entry associated with the wool processing activities at Port-Juvénal, a site near Montpellier, which had been connected with the Mediterranean sea by a canal to establish wool stores. As imported wool had been stored, washed and laid out for drying here, this site functioned for a long period (1750–1880) as the main gate of entry for hundreds of non-native species introduced with wool ('wool aliens') and emerging thereafter in the surroundings. These species formed the so called *Flora Juvenalis* (Groves, 1991). Thanks to the excellence in plant recording and identification, to which Thellung himself contributed greatly, the long-term record of the *Flora Juvenalis* provides an outstanding example of the efficiency of a specific introduction pathway, and the role it can play in dramatically increasing and subsequently decreasing, once the wool production has been ceased, on the richness of a local alien flora (Groves, 1991). In 1950, only six species remained of about 500 wool adventives that had been recorded 200 years earlier (Rioux & Quézel, 1950).

What makes Thellung's *Flore adventice* a milestone in invasion ecology is its combination of systematic, in-depth floristic research at a regional scale with conceptual approaches that capture the principles of invasion processes and associated drivers long before invasion ecology emerged as a distinctive field. The underlying theoretical concepts – in liaison with the main results from the Montpellier study – had also been published separately, with slight differences (Thellung, 1905, 1918/19), including an extensive review on human-mediated plant migration (Thellung, 1915). Hence, the following points refer to several of Thellung's publications and illustrate important points which clearly stimulated the evolution of concepts in the field of invasion ecology.

Alien floras

In the second half of the 19th century, the influx of non-native plant species to Europe increased exponentially (Lambdon *et al.*, 2008) and, as a response, many botanists reported on newly arrived species, an emerging research field (so called 'adventive floristics'; Trepl, 1990). As cities function as important points of entry of non-native species, many reports on alien species had an urban context, but floristic inventories mostly focused on selected habitat types without covering the whole city area (Sukopp, 2002). Albert Thellung compiled two extensive alien floras that cover both large cities and their surroundings. The first inventory was compiled for the canton of Zürich, Switzerland, and was published as part of *Die Flora des Kantons Zürich* (Naegeli & Thellung, 1905). The second alien flora was Thellung's major work, *La flore adventice de Montpellier* (Thellung, 1912).

Unlike other authors, Thellung did not only compile selected lists of interesting, frequent or naturalized species. Instead, his *Flore adventice* represents a complete regional inventory of 800 non-native plant species, based on extensive historical and contemporary records and including also a wealth of recent and extinct casual species that encompassed in total 87% of the flora. Moreover, Thellung (1912) adopted a comprehensive terminological framework to classify all non-native plant species in the *Flore adventice*.

Terminological framework

Thellung promoted very successfully a concept to classify non-native species according to three main criteria, which are still in the centre of invasion science (Blackburn *et al.*,

2011; Kühn *et al.*, 2011): (i) the stage of the invasion process, (ii) the main pathway of introduction (deliberate versus accidental) and (iii) the temporal differentiation between old and young introductions.

Many terms within this concept had been originally coined by Rikli (1903); Thellung adopted some, refined others and introduced some new terms such as 'ephemerophytes' or 'ergasiophytes' (see Table 1). Moreover, Thellung developed schemes to differentiate important introduction pathways and assigned 800 of the non-native *Flore adventice* species to these, as well as to degrees of naturalization (Thellung, 1912, 1915, 1918/19; see Table 2).

Thellung's terminological approach has sometimes been criticized because of its complicated terms. All were neologisms in Greek, a language that was accessible to many scientists at his time, and some inconsistencies remained within the terminological framework (Scheuermann, 1948; Trepl, 1990). Thellung himself changed the definition of some terms within the suite of his conceptual papers, and other authors did the same or developed their own schemes based on the Thellung's one (e.g., Holub & Jirásek, 1967; Schroeder, 1969). Still, Thellung's merit is that his terminological framework – and mainly the concept behind – depicted important directions of research on non-native plant species and stimulated many other European scientists (Trepl, 1990) as well as modern terminological frameworks on alien plants (Richardson *et al.*, 2000; Pyšek *et al.*, 2004).

Invasion processes

Many approaches have been developed thus far to define invasion processes as a series of stages a species must pass through following its introduction to a new range (Williamson & Brown, 1986; Williamson & Fitter, 1996; Richardson *et al.*, 2000; Inderjit *et al.*, 2005; Blackburn *et al.*, 2011). These approaches vary strongly in terminology and focus, with two main directions as depicted by Blackburn *et al.* (2011): concepts that define invasion processes as a sequence (i) of environmental barriers a species has to get over (e.g., Richardson *et al.*, 2000) or (ii) of stages of population establishment a species may undergo in the new range (e.g., Williamson & Fitter, 1996). Blackburn *et al.* (2011) recently illustrated a way to combine both approaches into a unifying concept that can be broadly adopted across subdisciplines in invasion science.

Albert Thellung was, to our knowledge, the first who not only developed a comprehensive framework on invasion stages (Thellung, 1905, 1912, 1915, 1918), expanding on previous work (see Table 1), but also adopted this concept at a regional scale to complete floristic inventories (Naegeli & Thellung, 1905; Thellung, 1912). Interestingly, Thellung did not use the term 'invasion' although by then, this term had been already introduced by Goeze (1882, pp. 106ff., 'Pflanzeninvasion', 'Invasion') and Lehmann (1895). The work of at least the latter author was likely accessible to Thellung as he cited another of Lehmann's papers (Thellung, 1912; p. 487). Instead of invasion stages, Thellung referred to different degrees of naturalization (see Table 1) and generally spoke of human-mediated plant migration ('Pflanzenwanderungen unter dem Einfluss des Menschen'; Thellung, 1915).

Concepts to differentiate invasion processes as a suite of naturalization stages indeed took root in the 19th century, as botanists such as Watson (1847) or de Candolle (1855) early on assigned introduced species to different naturalization stages. Thellung's naturalization concept and related terms (Thellung, 1915, 1918/19) differ in one important point from those of earlier authors (Table 1): its general applicability to all alien species, independent of their mode of introduction or habitat types considered. Previous concepts were ambiguous because they excluded important groups of alien species or combined information on naturalization with other issues. De Candolle (1855), for example, did not consider the naturalization of weeds of fields and gardens, and Rikli (1903) applied his naturalization approach only to accidentally introduced species, hence excluding the important group of deliberate introductions; Watson (1847, 1870) merged naturalization stages with assessments of the certainty about the non-native status. De Candolle (1855) criticized the latter as lacking clear differentiation between alien and native species.

Thellung's naturalization concept thus evolved on conceptually prepared grounds but yielded important progress in general applicability. Consequently, Scheuermann (1948) stated that – although scientists had addressed invasion topics for about 100 years – Thellung's concept was very important as the first comprehensive and convincing approach to classify non-native plant species. In current approaches, the naturalization stage is still highlighted as a key phase in the invasion process (Richardson & Pyšek, 2012).

Definition of naturalization

Thellung (1915, p. 55, 1918/19, p. 41) provided the following definition of the naturalization of species that are established either in man-made or in natural habitats (translation by IK): '*A plant species which had been introduced deliberately or accidentally by humans ... is naturalised when it is capable, with all characteristics of a native species, of* [1] *reproducing extensively without direct human interference by naturals means, i.e. by seeds, tubers, bulbs, sprouts ... depending on the species' characteristics,* [2] *colonising more or less regularly adequate sites and* [3] *surviving also some unfavourable climatic periods.*'

Thellung's definition specifies a similar definition by de Candolle (1855, p. 608) and expands a related one by Watson (1870, p. 60). It combines two approaches that are also constitutive of the unifying concept of Blackburn *et al.* (2011): first, a population-orientated approach leading to a differentiation of established and casual species; second, an environment-related approach referring to barriers that may prevent species' establishment, that is, the barriers of transport, survival, reproduction and environment (suitable habitats, climatic conditions) as defined by Blackburn *et al.* (2011).

Table 1 Invasion-related key terms used by Albert Thellung and their correspondence to terms used by other authors.

Current terms	Thellung (1905ff.)	Rikli (1903)	Watson (1847ff.)	de Candolle (1855)
Alien, exotic, introduced, non-indigenous, non-native species; neobiota	Anthropochoren (Rikli, 1903; emend. Thellung, 1905; p. 232): umbrella term for accidentally or deliberately introduced non-native species	Anthropochoren (Rikli, 1903): combined group of non-natives and of those natives that colonize man-made habitats, that is, followers of man	Introduced species (Watson 1847, p. 65)	
Cultivated species	Ergasiophyten (Thellung, 1905; p. 233): non-native species that are cultivated and maintained at agricultural sites and in gardens; related terms are Ergasiolipophyten (Thellung, 1905; p. 233): cultural relicts in the wild (formerly planted); Ergasiophygophyten (Rikli, 1903): escapees from cultivation			Combination of natives and non-natives in two groups: espèces cultivées (de Candolle, 1855, p. 642), including cultivated species (espèces cultivées volontairement) and agricultural weeds (espèces cultivées involontairement); espèces spontanées (de Candolle, 1855, p. 643): species occurring spontaneously outside of gardens and fields
Naturalization stages: Casuals	Ephemerophyten (Thellung, 1905; p. 234): non-native species without permanent populations	Ephemeren (Rikli, 1903): same as Thellung's Ephemerophyten, but restricted to accidentally introduced species	Casuals (Watson, 1870): not established non-native species Alien (Watson, 1847; p. 63): 'now more or less established'; presumed or certainly introduced	Adventives (de Candolle, 1855, p. 643): introduced, but poorly established outside of gardens and fields
Established, naturalized species	Epökophyten (Thellung, 1905; emend. Thellung, 1918/19): non-native species, established on man-made sites, but depending on further human agency; a subgroup are Archaeophyten (Rikli, 1903; emend. Thellung, 1918/19) as established weeds of arable land and gardens, introduced in prehistoric times	Colonophyten (Rikli, 1903): same as Thellung's Epökophyten, but restricted to accidentally introduced species Archaeophyten (Rikli, 1903): same as Thellung's Archaeophyten, but without considering the degree of naturalization	Colonist (Watson, 1847; p. 63): weeds of cultivated land or about houses, mostly at man-made sites; natives are not explicitly excluded from this group	Naturalisées (de Candolle, 1855, p. 643): established outside of gardens and fields, with two subgroups formed according to the certainty of having been introduced (probablement/peut-être d'origine étrangère)
	Neophyten (Rikli, 1903; emend. Thellung, 1915; p. 53): non-native species, established on natural sites among native vegetation, independently of further human agency	Neophyten (Rikli, 1903): same as Thellung's Neophyten, but restricted to accidentally introduced species	Denizen (Watson, 1847, p. 63): established without the aid of man; likely having been introduced Naturalized species (Watson 1859, p. 66f.): Species established among native vegetation without aid of man, including species from man-made sites	

Table 1. Continued

Current terms	Thellung (1905ff.)	Rikli (1903)	Watson (1847ff.)	de Candolle (1855)
Main characteristics of the approach	Clear focus on non-native species; general definition of three naturalization stages	Assignment of thee naturalization degrees only to accidentally introduced species	Five naturalization stages merged with assessments of certainty about non-native status; possible overlaps with native species	Two naturalization stages assigned to non-native species outside of gardens and fields

Table 2 Assessment of pathway efficiency by relating pathways of introduction to naturalization success (i.e., differentiation between casual and naturalized species) in the Flore adventice de Montpellier (adopted from Thellung, 1912).

		Casual species No.		Naturalized species No.	
Pathway of introduction	Total species No.	No.	%	No.	%
Total species	800	693	86.6	107	13.4
Deliberate introductions	148	87	58.8	61	41.2
Accidental introductions with	621	575	92.6	46	7.4
Wool	526	507	96.4	19	3.6
Seed and feed grains	40	31	77.5	9	22.5
Grain crops	18	18	100.0	0	0
Ballast materials	19	10	52.6	9	47.4
Transportation vehicles	18	9	50.0	9	50.0
Resulting from hybridisation	31	31	100.0	0	0

Naturalization stages

Thellung's naturalization concept is basically population-oriented as it serves to ascribe non-native species to one of a sequence of naturalization stages that reflect the capacity of a species to propagate in the new range and, eventually, to establish self-replacing populations (Table 1). This concept of naturalization stages generally matches current approaches to discern invasion stages by differing between (i) introduced, but not propagating, species (ii), propagating, but not established, species and finally (iii) established species. Moreover and different from current concepts, Thellung discerned two categories of established species. These reflect the capacity of a species to establish self-replacing populations either due to further human interference or independently of the latter. This idea resulted in a differentiation of 'Epökophyten' (epecophytes) from 'Neophyten' (neophytes; Table 1), with the latter passing to the final stage in Thellung's only implicit model of an invasion process: species able to establish permanent populations even under natural conditions without being further dependent of human activities.

This stage thus describes a new quality within the course of an invasion process and goes far beyond the question of 'only' establishing permanent populations under unspecified environmental conditions as other approaches do. In recent (European) invasion terminology, these species are called agriophytes (Kamyshev, 1959; Schroeder, 1969), while the term neophyte is now used to specify the introduction time, that is, to differentiate archaeophytes as older (pre-1492) from neophytes as younger (post-1492) introductions (Kreh, 1957; Schroeder, 1969). A modern analogy of Thellung's approach is reflected in the scheme of Richardson *et al.* (2000) where two invasion stages are implicated, depending on whether the species overcome barriers imposed by vegetation in human-made or natural habitats.

By considering the dependence of naturalization on human interference, Thellung merged an approach of natural sciences, that is, assessing population establishment, with a cultural perspective, because he also considered the (eventually missing) functioning of human agency as a driver of population establishment when assigning species to naturalization stages. Thellung's concept and his main idea of discerning aliens established under human-shaped or natural conditions have been rather influential in central Europe (e.g., Holub & Jirásek, 1967; Schroeder, 1969; Lohmeyer & Sukopp, 1992; see Trepl, 1990) but not beyond. The conceptual merging of biological and cultural perspectives has been criticized (Trepl, 1990). Yet one may also argue that it is exactly the interface between nature and culture that reflects a main paradigm of invasion science, because non-native species are defined as those expanding their natural range by human interference. There is some logic, although, in defining the last stage of an invasion process with reference to the emancipation from the functioning of just that force, the human agency that initially induced the invasion process – an idea that might be considered when further elaborating on unifying concepts in invasion science as proposed by Blackburn *et al.* (2011).

Introduction pathways and their efficiency

Identifying introduction pathways and assessing their efficiency is still a major challenge in invasion research (Carlton

& Ruiz, 2005; Kowarik & von der Lippe, 2007; Hulme *et al.*, 2008). Thellung's review from 1915 on human-mediated plant introductions is likely the first in this field. In this paper, Thellung reported the state of the art on introduction pathways, human-mediated plant dispersal and naturalization success of introduced species – also with clear links to conservation issues. This conceptual paper was strongly backed by pathway analyses from his *Flore adventice*. As a novel approach, Thellung (1912) assessed pathway efficiency by combining two approaches (Table 2). First, he assigned the components of a large regional species pool to a main group of introduction pathway, that is, deliberate versus accidental. Interestingly, Thellung also realized that hybridisation among introduced or between native and introduced species may lead to a new category of non-native species, 31 of which he listed in his flora (Table 2). Moreover, he specified several modes of accidental introduction pathways such as the influx of non-natives with wool, seed and feed grains, grain crops, ballast materials or transportation vehicles. Second, Thellung assessed the vector efficiency also in terms of naturalization by relating species' modes of introduction to their degree of naturalization (established or casual).

This approach led to the first analysis of pathway efficiency at a regional scale and illustrates that accidental introductions can dominate a non-native species pool but are clearly less important among the naturalized species than are deliberately introduced species. For example, only < 4% of the wool aliens, which clearly dominated the group of accidentally introduced species, became naturalized. In contrast, a much higher share of the deliberately introduced species (41%) went through this invasion stage (Table 2). It took about one hundred years to submit such inter-relationships between introduction pathway and invasion success to rigorous statistical testing (Pyšek *et al.*, 2011).

Temporal dimension of plant invasions

Thellung (1918/19) was aware of the existence of a subset of alien species, mostly weeds of agricultural land, gardens or ruderal places, which had been introduced long ago, often in prehistoric times. The character of these species as human-mediated introductions can thus often only be recognized by indirect, for example archaeobotanical, methods. He addressed these old introductions as 'archaeophytes', a term that had been originally coined by Rikli (1903) and is currently still used in Europe to disentangle 'old' (pre-1492) from 'new' (post-1492) plant introductions. Yet Thellung (1918/19) was inconsistent in this point as he applied the temporal classification of archaeophytes only to naturalized agricultural weeds and thus excluded deliberate introductions (Table 1). Since Kreh (1957) and Schroeder (1969), the differentiation of introduction time (archaeophytes versus neophytes) is generally related to all alien species. The temporal stratification of alien species by Thellung, regardless of the above-mentioned inconsistency, has proved of high ecological relevance and has provided important insights into understanding the dynamics of invasions on an historical time-scale (e.g., Pyšek *et al.*, 2005; Jarošík *et al.*, 2011).

Context dependence of invasion success

Invasion success and impacts can clearly vary among different environmental conditions (Fischer *et al.*, 2009; Jäger *et al.*, 2009; de Moura Queirós *et al.*, 2011), and exploring this kind of context dependence is still an intriguing research topic in invasion science (Kühn *et al.*, 2011). Thellung was already fully aware that environmental conditions are major drivers of invasion success. A first example from his work relates naturalization success to accessibility to suitable habitats. Thellung (1915) explained the rather low naturalization rate of wool aliens in Montpellier (3.6%) by the lack of sites that may facilitate species' establishment in the vicinity of the wool processing plant in Port-Juvénal. As support for this hypothesis, he pointed to a much higher share of naturalized wool aliens (13%) in the rural surroundings of a wool processing plant in Bédarieux, which was also situated in the Hérauld department (Thellung, 1915, p. 66).

A second example refers to the naturalization of introduced species that had been released deliberately to the wild to 'enrich' nature. Thellung (1915, p. 39) clearly recognized the role of environmental matching between donor and recipient regions when explaining the failure of annual steppe species, which had been released at the turn of the 17th to the 18th century in montane forests in southern France, while plants stemming from riverine systems such as *Elodea canadensis* Michx., *Acorus calamus* L., *Aponogeton distachyus* L.f. or *Ludwigia grandiflora* (M. Micheli) Greuter & Burdet proved to be successfully naturalized after their release.

Invasions impacts and conservation issues

Thellung's focus was on the classification of alien plant species, taxonomically and with regard to introduction pathways and naturalization stages. He did not study impacts of introduced species but was clearly aware of their ecological relevance in relation to conservation issues. By incorporating this applied issue in his review on human-mediated plant migration (Thellung, 1915) and the later conceptual paper (Thellung, 1918/19), Thellung raised awareness of the negative impacts of plant invasions on resident vegetation. He reported, for example, that naturalized species, such as those of genera *Solidago* or *Aster*, can often significantly suppress or even replace native vegetation and become dominant at the landscape scale (Thellung, 1918/19; pp. 40f.) and referred to the dramatic effects of some European species in North America or Australia ('dangerous and devastating weeds'). He also addressed implicitly the enemy release hypothesis by stating that the success of alien species may rely on their lacking competitors or enemies in the new range (Thellung, 1915, p. 62). He was also conscious of the fact that island floras are particularly threatened by introduced species.

CONCLUSIONS

Albert Thellung was an astute observer who was well aware of the dynamic nature of plant invasions and their consequence long before the principles of the field were put on firm ground in the 1950s. Already, his contemporaries highly appreciated his scientific work (Schinz, 1928) and so did many European scientists who worked in the field of biological invasions. Scheuermann (1948), for example, started a paper on classifying alien species with an enthusiastic appraisal of Thellung by stating that this scientist 'opened up research in the field of alien plants' and that his terminological framework was the first convincing approach in classifying alien plant species. Indeed, Thellung's main approach to classifying non-native species according to their degree of naturalization, the main pathway of introduction and the time period of introduction, clearly expanded the work of previous authors and was trend-setting, at least in Europe, even though the followers later often used other terms than Thellung himself (Holub & Jirásek, 1967; Schroeder, 1969; Trepl, 1990). It was thus the concept behind the terms and its application in classifying regional alien floras that stimulated many other scientists and directed further research in plant invasions. As a consequence, important parts of modern classification schemes about non-native species appear to have evolved, or to have been elaborated independently, on Thellungian grounds. He was also ahead of the times when assessing the efficiency of introduction vectors by relating them to species' naturalization success. The *Flore adventice de Montpellier,* published 100 years ago, is thus a milestone in invasion research. Thellung's concept to discern naturalization stages only implicitly referred to an invasion model. Yet this approach – population-based, with clear links to environmental barriers a species has to negotiate – can be seen as a first step to unifying concepts in invasion ecology. Albert Thellung is worthy to be rewarded as an important pioneer of modern invasion research.

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