Tuexenia 45: 255–280. Göttingen 2025.
doi: 10.14471/2025.45.003, available online at www.tuexenia.de

Wild grapevine (*Vitis vinifera* subsp. *sylvestris*) in Germany: Is reintroduction a viable approach?

Die Wilde Weinrebe (*Vitis vinifera* subsp. *sylvestris*) in Deutschland: Ist die Wiederansiedlung ein erfolgversprechender Ansatz?

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Abstract

Vitis vinifera subsp. *sylvestris* is an endangered species in large parts of Central Europe. In the upper Rhine floodplains, Germany, less than 100 individuals have survived until the middle of the 20th century. Local reintroduction approaches began in 1967 and increased the number of individuals to 1.075 in 2018. However, the current population status and the success of these long-term reintroduction efforts are, so far, unknown, although they represent an important basis for the future conservation of *V. vinifera* subsp. *sylvestris*.

For this study, all known sites of *V. vinifera* subsp. *sylvestris.* in the upper Rhine valley were surveyed in 2017–2018. The vitality of the individuals, their growing conditions, and local threats were assessed to evaluate establishment chances, and time series of vitality data (2012, 2013, and 2018) were analyzed for reintroduction sites in Leimersheim, Lingenfeld, and Römerberg. In the most recent survey in 2018, we found 482 individuals from previous reintroduction efforts (1974 to 2016). Overall, 55% of the individuals introduced since 2012 had died. Only 16% of 456 planted individuals (for which vitality data and planting year were available) showed high vitality and reproduction potential and were therefore considered established. The remaining 84% (mostly planted in 2016) had not reached the canopy and were therefore subjected to unsuitable light conditions, with low to medium vitality. The number of adult, reproducing individuals of the total population had decreased. The risk factors that have led to the massive decline of the species are still existing in 2018. In particular, in the massively degraded Upper Rhine floodplains, the species-specific habitat requirements are largely no longer met and must be restored as part of renaturation measures to facilitate the establishment of this species. Focus should be placed on the creation of natural flooding dynamics in selected areas.

Currently, the reintroduction of *V. vinifera* subsp. *sylvestris.* is particularly difficult due to a lack of suitable habitats. Added to this are the long establishment period, the late reproductive age, dioecy, and hybridization with *Vitis* cultivars, wild *Vitis* individuals, and vine rootstocks. Due to a combination of

Manuscript received 22 August 2024, accepted 20 March 2025
Published online 10 November 2025
Co-ordinating Editor: Sabine Tischew

these factors, this species is threatened with extinction in Germany and must be protected through appropriate nature conservation and forestry strategies. The success of reintroduction efforts, the effectiveness of protective measures, and the status of the population must be monitored regularly.

Keywords: extinction, monitoring, Red List, Rhine reintroduction, *Vitis vinifera* subsp. *sylvestris*, Wild grapevine

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

According to the International Union for the Conservation of Nature (IUCN), reintroductions entail the relocation and release of organisms into regions within their former geographical range where they have become extinct or where their populations have declined to critical levels. Also known as "translocation", reintroduction is increasingly used to overcome issues associated with habitat loss, habitat fragmentation, and reproductive isolation (Quinn et al. 1994) and has become a standard technique in conservation and restoration ecology (Maunder 1992, Berger 1993). The aim of reintroduction is to establish a viable, self-sustaining population with sufficient genetic resources to adapt to environmental changes, ensuring the long-term survival of the species. Reintroduction is considered "successful" if a population grows in size and range, individuals flower and fruit, second and third generations emerge autonomously, and all features point out that survival of the population in future decades is plausible; furthermore, seeds must be released to the surrounding landscape, and satellite populations must be established (Primack & Drayton 1997). However, given the highly complex interactions among plants and other organisms, reintroductions are not a simple matter and associated with various risks, such as that rare and endangered plant species are often unable to adapt to human disturbances and environmental changes (Drayton & Primack 2012). Reintroduction thus requires careful planning, especially regarding the selection of source populations (Hufford & Mazer 2003, McKay et al. 2005) and of optimal habitats (Giorgi & Francisco 2000, Millar et al. 2007). To further guarantee the success of a reintroduction measure, good planning and careful risk assessment are pivotal (IUCN SSC 2013), along with targeted monitoring and evaluation (Sheean et al. 2012). But even then, the success rate for both plant and animal target species is often low or uncertain (Fischer & Lindenmayer 2000, Godefroid et al. 2011). Although the first reintroduction attempts can be dated back to over 100 years ago, such as the release of 15 American bison into a reserve in the US (Kleiman 1989), the associated science is still in its early stages but has received increased interest in recent years (Seddon et al. 2007, 2014, Armstrong & Seddon 2008, Sheean et al. 2012, Diekmann et al. 2015).

Wild grapevine (*Vitis vinifera* L. subsp. *sylvestris* (C.C. Gmelin) Hegi; hereafter *Vitis* * *sylvestris*) (Fig. 1) is a woody liana and the only native species of the family Vitaceae in Europe (Núñez & Walker 1989). In Germany, it generally grows in riparian forests and in floodplain areas, where this climbing plant is associated with alluvial forests and often reaches heights of over 20 m by ascending trees (Arnold et al. 1998). These habitats offer structural support and microclimatic conditions that favor its development and reproduction. In Central Europe, the species is associated with alluvial forests dominated by willows (*Salix* spp.), poplars (*Populus* spp.), *Quercus robur*, and *Ulmus laevis* (Kowarsch et al. 2019). Unlike the hermaphroditic cultivated vine (*Vitis vinifera* L. subsp. *vinifera*), *V.* * *sylvestris* is dioecious. Dispersal in the immediate vicinity rarely occurs via clonal growth (Arrigo & Arnold 2007, Biagini et al. 2016). Over long distances, the species can

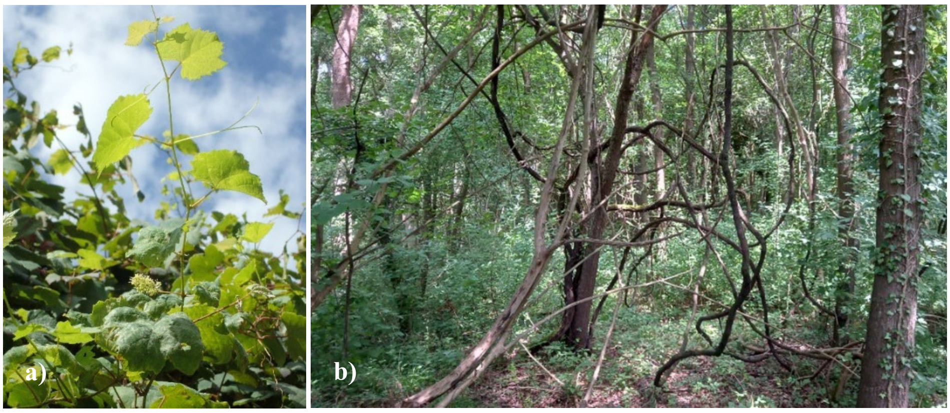

Fig. 1. *Vitis vinifera* subsp. *sylvestris* **a)** with leaves and **b)** tendrils and older individuals growing in an alluvial forest in Hördt, Rineland Palatinate, Germany (Photos: M. Niederl, June, 2019).

Abb. 1. *Vitis vinifera* subsp. *sylvestris* **a)** mit Blättern und Ranken und **b)** ältere Exemplare in einem Auwald bei Hördt, Rheinland-Pfalz, Deutschland (Fotos: M. Niederl, June, 2019).

reproduce via hydrochory; the fruits are transported (Werling et al. 2020). Its natural occurrence range is south of latitude 49° and extends into North Africa, the Caucasus, as well as western and central Asia (Arnold et al. 1998, 2005).

In Europe, the species is distributed in the Mediterranean Basin, Central France, Southwest Switzerland, the Upper Rhine Plain, and in some areas along the Danube, where it occurs in alluvial forests on moderately dry to slightly moist soils (Hegi 1995). Whilst in Central Europe, it only occurs in few locations in hardwood floodplain forests, it is still widespread in similar locations in Southeast Europe (Düll & Kutzelnigg 2005). However, since the early 20th century, it has largely been vanishing as a result of habitat destruction and overseas pathogens (Arnold et al. 1998). Based on the state of the remaining populations, *V.* * *sylvestris* is severely endangered in Europe (De Andrés et al. 2012, Ocete Rubio et al. 2012, Biagini et al. 2014, 2016) and has vanished from numerous localities in Central Europe, with massive losses in almost all countries (Arnold et al. 1998). In Switzerland (Bornand et al. 2016), Slovakia (Turis et al. 2014), and the Czech Republic (Holub & Procházka 2000), *V.* * *sylvestris* is critically endangered, whereas in Austria, it is endangered (Schratt-Ehrendorfer et al. 2022), and in Hungary, it is vulnerable (Király 2007). In France, 330 individuals were identified in 2000–2001 (Lacombe et al. 2003). In Germany, the species is considered endangered (Metzing et al. 2018), with remaining populations primarily found in the Upper Rhine region. The Rhine Island of Ketsch, for example, with approximately 90 individuals, hosts the last "large" adult population in the country (Werling et al. 2019).

The historical range of *V.* * *sylvestris* in Germany is limited to the Upper Rhine and adjacent regions near Badenweiler, Heidelberg, Büttelborn, and Bad Vilbel (Kirchheimer 1946). Historical records (Kirchheimer 1946, Issler et al. 1982, Arnold et al. 1998) describe an almost continuous occurrence of *V.* * *sylvestris* along the German and French sides of the Upper Rhine, between Basel and Mannheim. The northernmost records have been found for Bad Vilbel, 40 km northeast of Mainz. Bronner (1857) recorded thousands of *V.* * *sylvestris* specimens in the Upper Rhine floodplains in the middle of the 19th century. However, more than 150 years later, the spontaneous German *V.* * *sylvestris* population consisted of less than 100 individuals (Ledesma-Krist et al. 2013). As of 2013, the site with the largest number of spontaneous individuals was Ketsch (85). Single spontaneous specimens have survived in Hördt (2), Philippsburg (1), Otterstadt (1), and Mannheim (3) (Ledesma-Krist et al. 2013).

In Europe, numerous spontaneous forms of grapevine cultivars are naturalized. They belong to *Vitis vinifera* subsp. *vinifera*, which has been cultivated for over a thousand years, dating back to the introduction of domesticated grapevine varieties across Europe (Olmo 1995). In the last century, after the *Phylloxera* invasion, which destroyed large vineyard areas, several American and Asian *Vitis* species have been introduced as rootstock. The grafting of European varieties on these pathogen-resistant rootstocks is now standard, and numerous rootstock varieties have been developed by breeders (Arrigo & Arnold 2007).

Changes in forest management, such as clear-cutting, short rotation periods, liana control, *Phylloxera* introduction in the 19th century, and the alteration of the Upper Rhine floodplains by stream correction, drainage, the construction of barrages, and gravel mining, have led to large-scale losses of *V.* * *sylvestris* and its natural habitats (Arnold et al. 2010, Ledesma-Krist et al. 2013). Moreover, the long-term occurence of this species is threatened by small population size, genetic isolation, hybridization with cultivated vines, host tree diseases (Dutch elm disease, ash dieback), and the absence of successful sexual reproduction; although germination occurs, the seedlings generally do not survive because of the specific environmental conditions (Ledesma-Krist et al. 2013, Werling et al. 2019). In addition, cultivated vines, grapevine rootstocks, and invaders such as neophytic vines (*Parthenocissus* spp.), together with the autochthonous *Clematis vitalba*, which is highly competitive in the recent Upper Rhine floodplains, compete with *V.* * *sylvestris* for suitable sites (Arnold et al. 2010). In this context, conservation efforts are crucial to preserve these populations as they are vital reservoirs of genetic diversity and hold potential for grapevine breeding and restoration projects.

In the case of *Vitis*, the liana growth form, which differs from that of other woody plants, must be considered when determining reintroduction success. Lianas, such as *Vitis* (Mullins et al. 1992), use the stems of other woody plants to climb up to the light; they are light-demanding and reproduce once they reach the canopy (Putz 1984). *Vitis* * *sylvestris*, as a tendril climber, develops tendrils in the first year under adequate light and water conditions (pers. observation). The individual success of a liana depends on its progress in reaching a suitable host tree, or series of suitable hosts, and its ascent to the canopy (Putz 1984), where light is no longer a limiting factor. Once the liana has reached the canopy, it is generally not overgrown by canopy trees; thus, under the assumption that seedlings survive, the first ascent to the canopy is the bottleneck of individual establishment (Arnold et al. 2005, Letcher & Chazdon 2009). Transition from the seedling to the adult phase, in which sexual reproduction is possible, is completed by reaching the canopy. The occurrence of sexual reproduction, however, depends on numerous further factors such as climatic conditions, pollination distances, the presence and reaching of suitable germination niches, and herbivore pressure.

Reintroduction attempts for *V.* * *sylvestris* in Germany started in 1967, using cuttings and seeds from the Ketsch population. Subsequently, further reintroductions were realized (1974–1980, 1990–1995, 2000, 2007/2007), although the origin of the material used is largely unknown. The oldest surviving plantings date back to 1974. In 2013, Ledesma-Krist (2013) mapped and described all known sites, and the individuals were genetically tested. At that time, the entire population of spontaneous and planted individuals consisted of 375 vines. An *ex-situ* collection with approximately 80 genotype duplicates, most of them from the spontaneous population in Ketsch, was established at the Karlsruhe Institute of Technology (KIT) for research and reintroduction purposes, another one at the botanical garden in Marburg, and one at the Julius Kühn Institut, Siebeldingen (Nick 2010, 2014, Ledesma-Krist et al. 2013, Liang et al. 2019). For all subsequent plantings from 2012 onward, uniform cuttings (2 to 3 years old and treated against fungi and other vine pests during cultivation) from these *ex-situ* collections were planted between the end of October and the beginning of March (outside the growing season). A survey among different stakeholders revealed more than 1000 German *V.* * *sylvestris* individuals in 2017. *Vitis* * *sylvestris* seeds of the Upper Rhine population have a high germination capacity (Ledesma-Krist et al. 2013, Werling et al. 2019), and under suitable germination conditions, seedlings are expected in the vicinity of flowering vines (Werling et al. 2019, 2020). Given this situation, we addressed the following research questions: (1) What is the current status of the *V.* * *sylvestris* population in Germany? (2) How successful has reintroduction been so far?

To evaluate individual specimens, criteria such as living status, climbing conditions, vitality, and potential of sexual reproduction were applied. These aspects allowed us to answer questions related to survival and reintroduction.

Although currently, the European *V.* * *sylvestris* population is categorized in the IUCN Red List of Threatened Species as a "Species of Least Concern" (Kyratsis et al. 2011), we highlight the need to re-evaluate this assumption, especially for the German population. In the absence of a Germany-wide overview, we wanted to elucidate to what extent reintroduction efforts have enhanced the survival chances of *V.* * *sylvestris* in Germany and whether a downgraded threat status is justified.

2. Methods

2.1 Study area

All known occurrences of *Vitis vinifera* subsp. *sylvestris* in Germany were studied. The sites are located along the Upper Rhine, from Iffezheim to Darmstadt, in Baden-Württemberg, Rhineland-Palatinate, and Hesse. They are mostly located in protected sites, such as Natura 2000 sites, FFH (Flora-Fauna-Habitats) sites, and Special Protection Areas. Most sites are periodically flooded. The *V.* * *sylvestris* site near Stockstadt am Rhein is located in a forest area designated for the protection of natural processes. The authors are not aware of any potential management plans for these sites. Apart from the identification of the supporting tree species, no vegetation surveys were conducted in these sites.

2.2 Field survey

Overall, 15 locations were surveyed between 2017 (Ketsch) and 2018 (other sites) (Fig. 2). Each individual or each group of individuals were evaluated in July to October in both years as these months represent the flowering and fruiting seasons of *V.* * *sylvestris*. Grapevine seedlings and saplings were systematically searched within a radius of 10 m under the canopy of a female individual. Further casual findings were recorded.

2.3 Descriptors

Vine status was determined using the following definitions: 1) alive: its stem is firmly attached to the roots, it bears leaves or at least living buds; 2) presumed dead: its stem is firmly attached to the belowground roots, but there is no sprouting or the vine was not found during a recent sampling campaign but was alive when last surveyed; 3) dead: the stem is not attached to the belowground roots

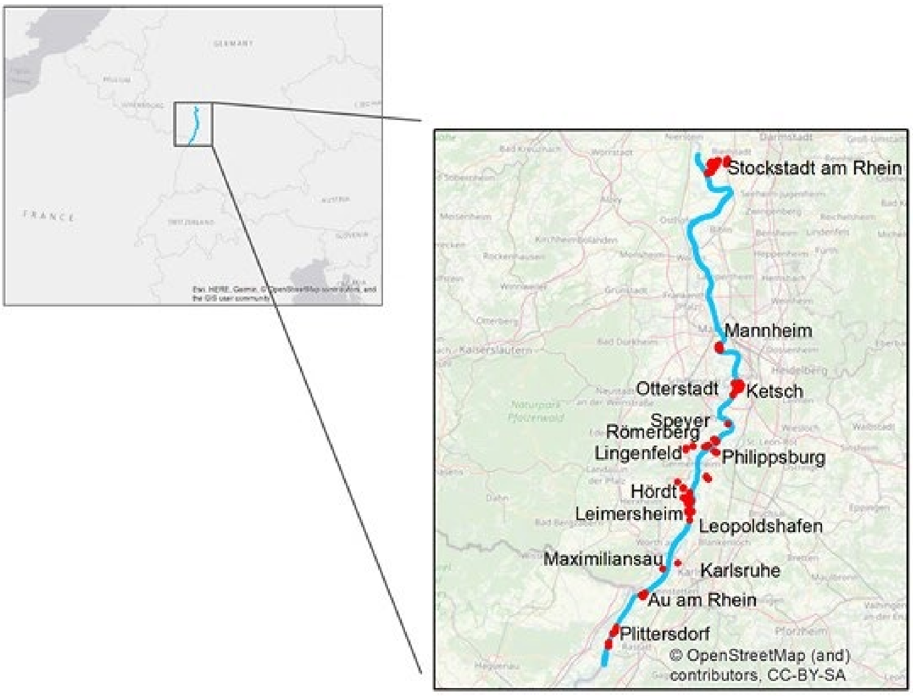

Fig. 2. Maps showing the study area and the surveyed *Vitis inifera* subsp. *sylvestris* sites along the Upper Rhine, Germany (© OpenStreetMap 2024).

Abb. 2. Karten des Untersuchungsgebiets und der *Vitis inifera* subsp. *sylvestris* Lokalitäten entlang des Oberrheins, Deutschland (© OpenStreetMap 2024).

or has died at the stem base and does not sprout or the vine was not found neither during a recent sampling campaign nor in the last survey); 4) no additional information (n. a.): the vine is alive and grows in a group, where it cannot be identified individually; alternatively, the site is inaccessible.

The light exposure level depends on the position of the liana crown in relation to the surrounding vegetation and is classified as follows: 1) high: the vine crown overgrows the host tree crown; 2) medium: the vine crown is partially exposed to direct sunlight; 3) low: low growth height and/or strong shading effect of surrounding vegetation on the vine crown.

The presence (yes) or absence (no) of fruit were recorded.

Vine vitality was assessed as follows: 1) high (h): only characteristics of high vitality are present; low (l): at least two characteristics of low vitality apply. All other combinations of characteristics result in vitality class medium (m). The three vitality classes were defined based on the characteristics given in Table 1.

The quality of the climbing conditions for at least 2–3 m high shrubs or trees (also artificial climbing aids) in the immediate vicinity was determined as follows: good (g): all relevant characteristics are met; medium (m) or low (i): one relevant characteristic applies. The characteristics are shown in Table 2.

“Other local threats” were classified as 1) none; 2) potential: weak deer browsing, presumed competition with invasive neophytes, slightly too much shade, lack of highly visible markings on host trees, or an ingrown wire basket; 3) acute: severe deer browsing, signs of high wild boar activity/wallows, presence of diseased and dying trees in close vicinity, too much shade, high level of habitat disturbance (stream bank erosion, substrate deposition), adjacent mowing, or garden waste depositing.

Table 1. Evaluation characteristics and definition of the vitality classes (r: relative to, * in the survey period: leaf fall before October, ** in the survey period: change of leaf color before September).

Tabelle 1. Bewertungsmerkmale und Definition der Vitalitätsklassen (in Relation zu, * im Erhebungszeitraum: Blattfall vor Oktober, ** im Erhebungszeitraum: Veränderung der Blattfarbe vor September).

Evaluation characteristics	Vitality class		
	High	Medium	Low
Crown dimension and density (r: age, habitus)	Wide, densely branched	Moderately wide and loose	crown wood poorly developed
Leaf abundance (r: age, habitus)	Numerous leaves	Moderate number of leaves	Few leaves
Leaf fall (r: leaf abundance, season*)	Only few leaves dropped	Significant number of leaves dropped	majority of leaves dropped
Annual growth (r: age)	Vigorous sprouting, intense growth	Moderate sprouting	Poor sprouting, hardly any growth
Physiological condition (r: leaf abundance)	Hardly any withered or dry leaves	Numerous withered or dry leaves	Mostly withered and/or dry leaves
Leaf color (r: age, leaf abundance, season**)	Hardly any leaves change color too early	Numerous leaves change color too early	Most leaves change color too early
Growth height (r: age, canopy height, habitus)	Strong longitudinal growth at insufficient light. The zone of high light intensity (canopy) has already been reached or will be reached soon	Moderate longitudinal growth in zones with insufficient light. Not certain whether the high-light zone will be reached. It is not certain whether the vine is vigorous enough to reach the light-rich zone	Low height and hardly any longitudinal growth in insufficient light. Not vigorous enough to reach the high-light zone. Vine does not appear vigorous enough to ascent to the light
Stress/diseases (r: leaf abundance, power)	Signs of stress/disease may be present but not accompanied by any of the above-mentioned low-vitality indicators		Clear signs of stress/disease, accompanied by one of the above-mentioned low-vitality indicators

2.4 Further definitions and analysis

Stem diameter was measured in Ketsch in 2018, using a standard protocol (Schnitzer 2002, Gerwing et al. 2006).

Vine age was unknown and could not be determined non-destructively. To provide evidence for age-related differences among spontaneous specimens, four stem size classes were defined based on the maximum stem diameter (D): 1) small individuals (1 cm ≤ D < 3 cm); 2) medium individuals (3 cm ≤ D < 5 cm); 3) large individuals (5 cm ≤ D < 8 cm); 4) very large individuals (D ≥ 8 cm). For multi-stem growth forms, classification was based on the largest stem diameter. For oval stem cross-sections, the geometric mean was taken (Gerwing et al. 2006).

Plantings were grouped into seven age cohorts (Table 3). Individuals with unknown planting years were not included. Note that because multi-year individuals were transplanted, plant age was higher than cohort age.

Table 2. Evaluation characteristics and definition of the climbing condition classes.

Tabelle 2. Bewertungsmerkmale und Einstufung der Kletterbedingungen.

Evaluation parameter	Climbing condition classes		
	Good	Medium	Poor
Availability	Host tree is present		No suitable host tree, relative to the growth vigor and size of the vine, is currently accessible.
Host tree vitality	Host tree is alive,		Host tree is dead OR ...
	Firm,		Host tree has been logged OR collapsed (does not apply to case *, see last trait)
	Healthy and vital,	Host tree is stressed and/or moderately vital,	Host tree is very weakened OR diseased (e.g., fungal infection)
	Host tree has maximally reached a middle age according to species-specific duration of life ...		Host tree is over-aged according to species-specific duration of life
		OR host tree has reached an older age, but is vital	
Host tree species	Not elm (*Ulmus spp.*) or ash (*Fraxinus spp.*)	Healthy elm or ash	Diseased and weakened elm or ash
Other threats to the vine caused by the host tree	None	Potential threats evident	Acute threats evident
Alternative host tree	Alternative is not necessary since all traits are "good" OR ...	Present climbing conditions are medium to poor due to the host tree (see table row vitality/species/other threats). An accessible and suitable alternative host is available relative to growth vigor of the vine OR ...	Present climbing conditions are poor due to the host tree (see table row vitality/species/other threats) No suitable host tree, relative to the growth vigor and size of the vine, is currently available
	Since there are multiple hosts and one or more of them can fail without risk to the vine	… present climbing conditions are medium due to the host tree. An accessible and suitable alternative host is not available relative to growth vigor and size of the vine	
Liana competition	Host tree(s) only sparsely covered with other lianas		Host tree(s) heavily covered with other lianas
Vine attachment to the host tree	Vine is firmly anchored on the host tree	Vine fell down completely OR has been pulled down OR collapsed with host tree AND ...	
		*Vine starts to ascend to light-rich zones again OR it will do so in relation to its growth vigor in the near future	Vine lies on shady ground and has not yet recovered

Table 3. Age cohorts of plantings (coh.) with year of planting, location (L), and number of living individuals (no.).

Tabelle 3. Alterskohorten von Anpflanzungen (coh.) mit Pflanzjahr, Lokalität (L) und Zahl der lebenden Reben (no.).

Coh.	1974–1980		1990/95		2000		2007/08		2012/13		2015		2016	
Age [y]	38–43	no.	23–28	no.	18	no.	11–10	no.	5–6	no.	3	no.	2	no.
L	Mannheim (1974)	23	Hördt (1990)	10	Mannheim	22	Eggenstein-Leopoldshafen (2007)	2	Römerberg (2012)	19	Au am Rhein	34	Stockstadt am Rhein	230
	Römerberg (1976)	3	Otterstadt (1990)	5			Philippsburg (2008)	9	Leimersheim (2012/13)	13	Mannheim	15		
	Hördt (1978/80)	11	Ketsch (1990/ 1995)	1					Lingenfeld (2012/13)	6	Plittersdorf	33		
									Hördt (2013)	1				
									Plittersdorf (2013)	1				
									Stockstadt am Rhein (2013)	18				
Sum		37		16		22		11		58		82		230
Total		456												

In our analysis, we distinguished two origins of vines: "Spontaneous" *V. * sylvestris* originated from the native population and established itself via natural reproduction, whereas "planted" individuals were introduced. The origin of two individuals in Mannheim was unknown. An individual was considered "established" when the light exposure level and vitality class were high.

During the last survey, the sex of most spontaneous individuals was determined genetically and morphologically if flowers or fruits could be observed (Ledesma-Krist et al. 2013). The sex of clonally propagated individuals was known in all plantings from 2012 onward if the sex of the original genotype was known. For the remaining introduced individuals, flowers or fruits were observed, and sex was determined morphologically and genetically, if possible (Ledesma-Krist et al. 2013). We included some new, previously not recorded individuals that were found during 2013–2017. If fruits were absent and sex could not be determined genetically, it was classified as "unknown". For species identification and parentage analysis, 67 microsatellite markers were used, including published ones (Sefc et al. 1999, Merdinoglu et al. 2005, Castellarin et al. 2006, Laucou et al. 2011, Fechter et al. 2012) and some unpublished ones from the *Vitis* Microsatellite Consortium, which are evenly distributed over the 19 chromosomes of the vine (for a detailed description of the methodology, see Werling et al. (2019) and Niederl et al. (2021). All included individuals were genetically determined as *V. * sylvestris*.

Field data were compared with the results of previous surveys (Ledesma-Krist, unpublished data). The vitality of *V. * sylvestris* individuals planted in 2012 was surveyed at three locations (Römerberg, Leimersheim, Lingenfeld) on a three-level scale (high/medium/low).

3. Results

3.1 Status of the *Vitis vinifera* subsp. *sylvestris* population in Germany

Overall, 1075 *Vitis vinifera* subsp. *sylvestris* individuals were detected. Of these, 503 were dead or presumed dead – including 2 spontaneous ones and 501 (262 “dead,” 239 “presumed dead”) planted individuals (Table 4). Total survival rate was 53% (98% for spontaneous and 49% for planted ones) since the last survey in 2008–2013 and considering the reintroduction projects during 2012–2016. As of 2018, 572 individuals were alive. Overall, 48 individuals (20 spontaneous, 26 planted, 2 with unknown origin) were just considered “alive”, and no further assessment was possible as we had no data on stem size, age, or origin. The sex ratio of the total population was 1:0.9 (0.4 unknown). *Vitis* * *sylvestris* seedlins were observed in two locations (Ketsch and Mannheim). In Ketsch, four adult and one subadult individuals had died from 2009 to 2017 (Ledesma-Krist et al. 2013, Werling et al. 2019), and several adult individuals were in critical condition in 2018. Only 81% of the spontaneous individuals could be considered established, including 70% of the spontaneous individuals with a stem diameter of 1 to 3 cm. Those with stem diameters above 3 cm were several decades old. Table 5 shows the numbers of the dead and living individuals at the different locations in 2018.

Table 4. Vine status of individuals in absolute (abs.) and relative (rel. %) values.

Tabelle 4. Rebenstatus in absoluten (abs.) und relativen (rel. %) Zahlen.

Vine status	Spontaneous		Planted		Origin unknown		Total population	
	abs.	rel. (%)	abs.	rel. (%)	abs.	rel. (%)	abs.	rel. (%)
Dead	2	2	262	27	0	0	264	25
Presumed dead	0	0	239	24	0	0	239	22
Alive	88	98	482	49	2	100	572	53
Sum	90	100	983	100	2	100	1075	100

3.1.1 Spontaneous *Vitis vinifera* subsp. *sylvestris* individuals

Spontaneous individuals experienced a slow but steady decline. Among the 88 living spontaneous individuals, vitality could only be assessed for 80, as 8 individuals were either inaccessible in the field or could not be clearly distinguished from neighboring individuals. Of those whose vitality was assessed, only 13 (16%) fell into the “low” or “medium” vitality classes. In contrast, 67 individuals (84%) were considered established, with high vitality. The distribution of stem size classes for these high-vitality individuals was as follows (absolute/relative %): unknown (11/73%), small (7/70%), medium (16/89%), large (17/77%), and very large (16/89%).

Criteria for vitality, light exposure levels, climbing conditions, and other local threats were applied on the 68 individuals for which stem data were available, which were grouped according to the stem size classes. Here, other local threats mainly include anthropogenic activities such as mowing, cutting, or garden waste depositing and environmental factors such as shading, competition with neophytes, high levels of habitat disturbance (stream bank erosion, substrate deposition), and browsing by deer and boars. Individuals with high vitality (59 ind./87%) were dominant, irrespective of the stem size class (Fig. 3a). In size classes

Table 5. Numbers of living and dead individuals at the different locations in 2018.

Tabelle 5. Lebende und tote Individuen an den einzelnen Standorten in 2018.

Site	No. of living individuals		No. of dead individuals		Sum
	Abs.	Rel. (%)	Abs.	Rel. (%)	
Au am Rhein	35	83	7	17	42
Eggenstein-Leopoldshafen	2	22	7	78	9
Hördt	37	71	15	29	52
Karlsruhe	0	0	7	100	7
Ketsch	84	93	6	7	90
Stockstadt am Rhein	248	43	323	57	571
Leimersheim	13	45	16	55	29
Lingenfeld	9	50	9	50	18
Mannheim	65	68	30	32	95
Maximiliansau	3	100	0	0	3
Otterstadt	7	100	0	0	7
Phillipsburg	11	44	14	56	25
Plittersdorf	34	55	28	45	62
Römerberg	22	35	41	65	63
Speyer	2	100	0	0	2
Sum	572	53	503	47	1075

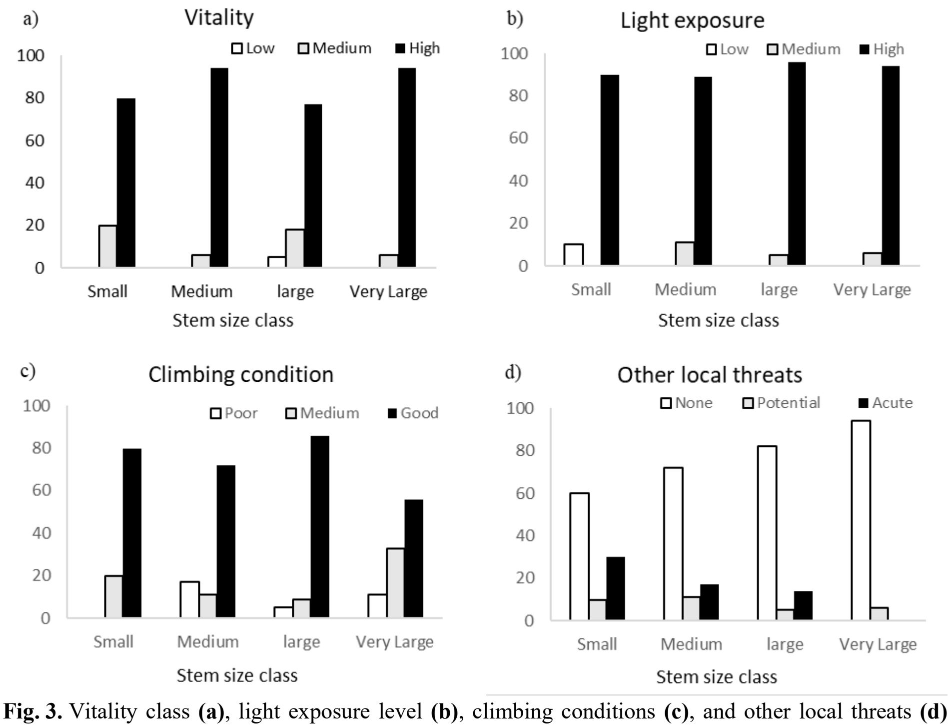

Fig. 3. Vitality class **(a)**, light exposure level **(b)**, climbing conditions **(c)**, and other local threats **(d)** (%) of spontaneous individuals depending on the stem size class, in percentages.

Abb. 3. Vitalitätsklasse **(a)**, Lichtexposition **(b)**, Kletterbedingungen **(c)** und Gefährdungspotenzial **(d)** (%) von spontan aufgekommenen Reben in Abhängigkeit von der Stammgrößenklasse, in Prozent.

Fig. 4. Spontaneous seedling of *Vitis vinifera* subsp. *sylvestris* with cotyledons and mature leaves (Photo: M. Niederl, June 2019).

Abb. 4. Spontan aufgekommener *Vitis vinifera* subsp. *sylvestris* Keimling mit Keim- und Folgeblättern (Foto: M. Niederl, June 2019).

"small" and "large", there was a significant proportion of individuals with medium vitality (80 and 77 ind./20% and 18%, respectively) (for more information, see Supplement E1). For all size classes, light exposure was mainly high (9–17 ind./89%–96%) (Figure 3b). For small and large stems, the climbing conditions were good (72%–86%), whereas only for 56% of the very large stems, the climbing conditions were good (Fig. 3c). The percentages of sites with other potential and acute threats were highest for small and medium individuals and lower for large and very large individuals (Fig. 3d). Figure 4 shows a spontaneous seedling growing in an alluvial forest.

The sex ratio of spontaneous individuals was 1:0.7:0.3 (female: male: unknown sex). In Ketsch, 17 out of 39 female *V. * sylvestris* (44%) produced fruit in 2017. Of these, 36 (92%) were exposed to high light levels and 32 (82%) also showed high vitality and were therefore considered established.

3.1.2 Planted *Vitis vinifera* subsp. *sylvestris* individuals

The losses for older plantings (1974–1995) since the last surveys in 2008–2013 were 4%–11%. For plantings from 2000, the losses amounted to 29%, whereas for plantings from 2007/08, they were 72% since the last survey (Fig. 5a). In younger plantings, 41%–65% of the individuals died in the first 2–7 years. The overall sex ratio was 1:0.9 (unknown: 0.4). According to the sex ratio of clonally propagated *V. * sylvestris* planted since 2012, equal numbers of male and female individuals survived (Figure 5b). Among the 19 individuals planted since 2012 that had already achieved a high light exposure level, male individuals predominated (15 individuals, 79%). Vitality did not differ between sexes. Among 172 female individuals planted since 2012, only one that was planted in 2012 fruited. Overall, 5 individuals from 1990, 5 from 2000, 2 from 1980, and 16 from 1974–1976 produced fruits. For all fruiting individuals, the light exposure level was high.

Overall, of the 456 planted individuals, 16% were considered established (see Table 6).

Table 6. Established planted vines in absolute and relative values according to the planting year. The table only contains surviving plants that could be assigned to a specific cohort.

Tabelle 6. Etablierte gepflanzte Reben in absoluten und relativen Zahlen, abhängig vom Pflanzjahr. Die Tabelle enthält nur überlebende Pflanzen, die einer spezifischen Kohorte zugeordnet werden konnten.

Cohort	Sum alive	Established absolute	Established relative (%)
1974–1980	37	31	84
1990–95	16	8	50
2000	22	13	59
2007–08	11	1	9
2012–13	58	7	12
2015	82	13	16
2016	230	0	0
Total	456	73	16

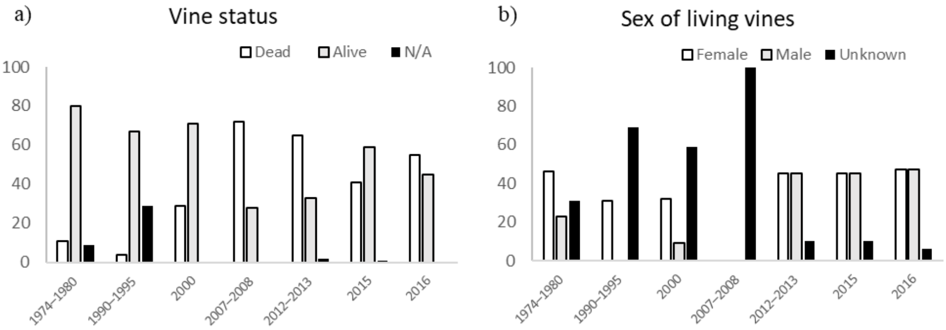

Fig. 5. Vine status **(a)** and sex of living individuals **(b)** in percentages, depending on the planting year. N/A: not applicable.

Abb. 5. Rebenstatus **(a)** und Geschlecht der lebenden Reben **(b)** in Prozent, abhängig vom Pflanzjahr. N/A: nicht zutreffend.

Vitality was high for 45% of the individuals and low for 42%. In the 2007/08 and 2016 cohorts, vitality was mainly low (61%–64%), whereas in the remaining cohorts, vitality was mostly high (Fig. 6a). In 17% and 75% of the planted individuals, the light exposure level was high and low, respectively. For all *V.* * *sylvestris* planted in 2016, the light exposure level was low, whereas for individuals planted in 2000 or earlier, light exposure was mainly high 59%–87%) (Fig. 6b). On average, 79% of all planted individuals had good climbing conditions, i.e., suitable morphological structures in close vicinity (Fig. 6c). Young plantings were often acutely threatened by various local factors (54% of the 2016, 47% of the 2012/13 cohort) (Fig. 6d). For more information, see Supplement E2).

3.2 Success of the reintroduction program in 2012

For the 2012 plantings in Leimersheim, Lingenfeld, and Römerberg, changes in vitality over time were observed (Supplement E3). In the year of planting, vitality was mainly high (90%–100%). In 2013, the proportion of highly vital individuals was lower (70%–79%), but there was no mortality. However, by 2018, at the time of the last monitoring, 30%–65% of

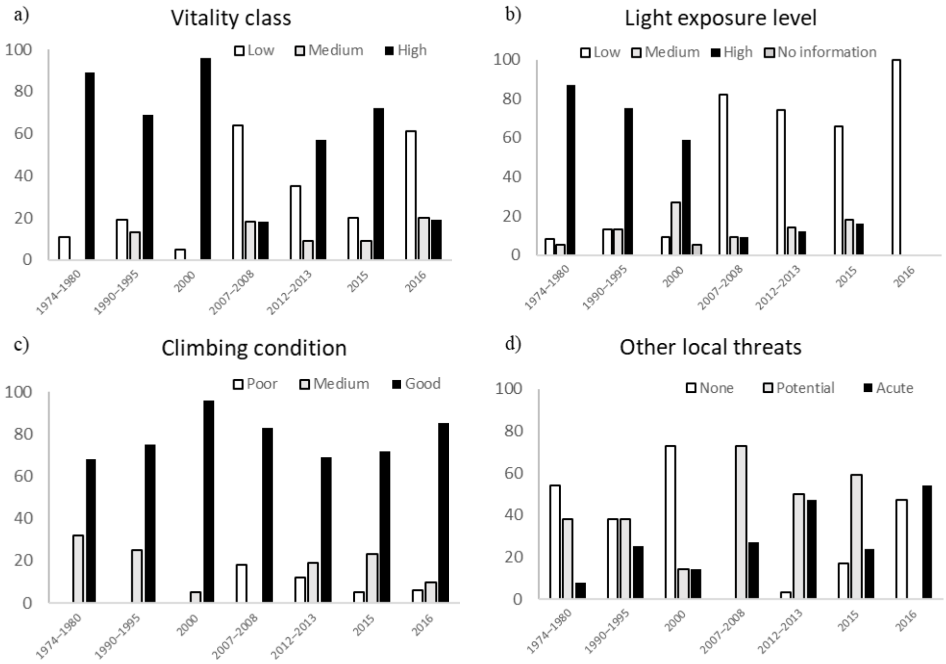

Fig. 6. Vitality class **(a)**, light exposure level **(b)**, climbing conditions **(c)**, and other potential **(d)** (%) of planted *Vitis vinifera* subsp. *sylvestris* individuals depending on the planting year, in percentages.

Abb. 6. Vitalitätsklasse **(a)**, Lichtexposition **(b)**, Kletterbedingungen **(c)** und Gefährdungspotenzial **(d)** (%) der gepflanzten *Vitis vinifera* subsp. *sylvestris* Individuen in Abhängigkeit vom Pflanzjahr, in Prozent.

the individuals planted in 2012 had died, whereas 23%–50% showed high vitality. Individual vitality generally declined over time from 2012 to 2018. All individuals with medium vitality in 2013 had died by 2018, and only 18 individuals showed high vitality at all time points. For more information, see Supplement E3.

4. Discussion

4.1 Current status of the German *Vitis vinifera* subsp. *sylvestris* populations

Our findings suggest that in Germany, *Vitis vinifera* subsp. *sylvestris* is close to extinct-tion, as already indicated by Arnold et al. (1998). However, to make an accurate statement regarding the risk status of this species, the various risk criteria need to be determined in detail (Ludwig et al. 2009), which was beyond the scope of this study. We observed differences in the ways local threats affected spontaneous and planted individuals. Only 36% of the planted individuals were not affected by additional threats compared to 79% of the spontaneous individuals. In Ketsch, where most of the spontaneous individuals occurred, this rare species has been receiving considerable attention by several generations of foresters (Schumann 1974, Ledesma-Krist et al. 2013) and a long-term interest by scientists (Scheu 1937, Schumann 1974, Kortekamp & Schröder 2010, Ledesma-Krist et al. 2013, Werling et al. 2019, Zdunić et al. 2020). This has improved its management and led to a significant improvement of the endangerment situation in Ketsch and Mannheim.

Several individuals are at risk of being cut during land management activities and are therefore acutely threatened. Even though outreach activities have created considerable awareness among foresters and farmers in Ketsch regarding the sensitivity of the species, mowing or pruning of an adjacent area still bears an acute risk. This can be seen in the occurrence of numerous grapevines with a small stem diameter, which have been cut off one or more times. Large individuals are additionally threatened by host tree dynamics since their host trees are old, and the vines themselves can cause breakage damage to the host tree (Putz 1984) by their increasing weight. This dynamic can lead to slight damages up to the complete loss of individuals. To avoid such losses, given the specific requirements of *V.* * *sylvestris*, i.e., suitable morphological structures for climbing, host tree selection is a crucial factor. Priority should be given to selecting tree species that are disease-resistant, have sturdy trunks and branches to provide reliable climbing support, have a long lifespan, and are well-adapted to riparian floodplain forests. Suitable tree species are *Populus* spp., *Salix* spp., *Quercus* spp., or *Fraxinus* spp. Further, only robust and healthy individuals of sufficient size should be planted, with planting sites clearly marked and documented to facilitate ongoing monitoring. Where relevant, host trees should be safeguarded against pruning or felling, which requires close collaboration with forestry departments. To meet the habitat requirements of the species and facilitate hydrochory, which is a possible dispersal mode of *V.* * *sylvestris* and enables it to colonize new habitats far from the parent plant, individuals should generally be planted in floodplains (Werling et al. 2020).

The sex ratio of the spontaneous individuals was 1:0.7:0.3 (female: male: unknown sex). However, since males can only be determined by flower observation during a short period, we assume that we did not accurately determine all males. Female individuals, in contrast, are reliably identified by their fruits, even in winter. The spontaneous individuals were mostly large enough to produce grapes, at least in some years. Thus, the sex ratio of the spontaneous population in Germany is close to 1:1, which is in line with Ledesma-Krist et al. (2013). When clone-propagated individuals were planted at a 1:1 sex ratio (Ledesma-Krist et al. 2013, Angersbach et al. 2018, Kowarsch et al. 2019), the current sex ratio is 1:0.9:0.4 (female: male: unknown sex); because of the considerable number of unknowns, we assume that the sex ratio is also 1:1. In most locations, both sexes occurred, making sexual reproduction theoretically possible. This can also be confirmed by the observation of fruiting females. However, at the site in Maximiliansau, all individuals were male, precluding any sexual reproduction.

We observed a strong spatial fragmentation of *V.* * *sylvestris* stands within the floodplain. Cross-fertilization between most locations is unlikely as the distances to be overcome usually largely exceed the distance of effective pollen transport. According to previous studies, above a distance of 70 m between pollinator and female, the probability of pollination decreases dramatically (Di Vecchi-Staraz et al. 2009, Arnold et al. 2010, Ledesma-Krist et al. 2013). Therefore, the distance between female and male individuals should not exceed 100 m (Kowarsch et al. 2019). For the Ketsch site, genetic screening of seedlings via the use of microsatellite markers (as described above) revealed a maximum pollination distance of 1026 m (Werling et al. 2019), but most locations are even further apart from each other, and 9 of the 14 recent stands have a minimum distance of 2–38 km to the nearest stand (mean 8.8 km, median 6 km) (Werling et al. 2019). For this site, autochory, namely dispersal in the immediate vicinity via clonal growth, was observed.

As of 2018, the number of adult spontaneous individuals was decreasing, and only a few planted ones have reached reproductive age so far. Most likely, this is the result of the high age of most of the spontaneous individuals, which might have been already over 100 years old. Further, land use changes might have played a role as some of the host trees might have been removed or cut back, resulting in the death of *V.* * *sylvestris* individuals. Regarding the planted individuals, most of them would have been too young to reproduce, and for others, the habitat conditions might not have been suitable anymore. This can easily happen when sites are becoming overgrown, smothering young individuals. Successful spontaneous germination, which rarely leads to establishment in this species, was evidenced at two locations in 2017–2018 and at three additional sites in 2022. However, the resulting seedlings were only 5–10 years old, with a maximum height of 1.3 m, and had not yet reached the reproductive age. The total German adult population, estimated at 140–250 individuals, most likely is too small to be viable in the long term, especially with constraints on spontaneous germination and establishment success. Generally, in the absence of neighboring adult individuals, seed rain is not sufficient to facilitate rejuvenation of the population, and the seedlings often die within the first few years. This, in turn, impedes the establishment of a viable seed bank. *Vitis* * *sylvestris* population growth is therefore restricted due to low seedling establishment, along with rare spontaneous germination. Although the germination conditions in frequently flooded sites are generally good, suitable natural germination niches are scarce in the anthropogenically influenced Upper Rhine alluvial landscapes. *Vitis* * *sylvestris* depends on active morphodynamic processes for germinating (Ledesma-Krist et al. 2013, Werling et al. 2019). As a liana, it is a pioneer species that colonizes forest edges, treefall gaps (Schnitzer 2002, Londré & Schnitzer 2006), and sedimentation areas in active floodplains (Schnitzler & Heuzé 2006, Arnold et al. 2010). Its seeds germinate under a wide range of conditions (Orsenigo et al. 2017, Werling et al. 2019) and maintain their germination capacity *in situ* for numerous years (Wendel 1981, Haywood 1994, Meadows et al. 2006). However, only open to semi-shaded areas have sufficient light for seedling establishment. In the past, such vegetation-poor pioneer areas were created periodically by substrate and stream bed relocations during floods. The topography of Ketsch indicates past high morphodynamics due to numerous parallel natural channel embankments. However, similar habitat dynamics are unlikely to be restored on a sufficient scale, especially along a heavily used waterway such as the Upper Rhine. Habitat quality therefore remains insufficient, and consequently, *V.* * *sylvestris* will hardly be able to rebuild a self-sustaining population in Germany, especially without adequate protection and management strategies.

In this context, the importance of adapted management measures should not be underestimated since several risk factors are anthropogenic and/or could have been avoided by adequate planting site selection or subsequently reduced by additional management efforts. Based on our findings, 40% of the planted individuals are acutely threatened by mowing or cutting, heavy shading, extreme hydromorphological dynamics, host tree damage and diseases (such as ash dieback), competition with tall herbaceous species, or direct damage due to wild boars and deer. Increased planting efforts along unmaintained old river arm edges since 2012 are a response to the high risk of cutting along meadows, trails, and forest edges (Ledesma-Krist et al. 2013), but the hydromorphological forces were often underestimated. Future restoration programs should therefore consider these factors.

4.2 Success of *Vitis vinifera* subsp. *sylvestris* reintroduction in Germany

When assessing reintroduction success, the determining factors can be divided into those that affect establishment and those that affect population dispersal or persistence (Armstrong & Seddon 2008). The requirement for significant results from monitoring projects is that the study period is adapted to the species′ generation time (Godefroid et al. 2011). This is especially true for slow-establishing and late-reproducing species such as *V.* * *sylvestris*, as shown by our survey of plantings older than 40 years. In a study encompassing 249 reintroduction projects of different plant species, Godefroid et al. (2011) showed that success, measured by survival, flowering, and fruiting rates, is generally low (on average, 52% survival, 19% flowering, and 16% fruiting in the first 4 years) and decreases over time.
The reintroduction of *V.* * *sylvestris* in Germany began in 1967 with the planting of over 200 individuals (Ledesma-Krist et al. 2013), including approximately 100 near Mannheim. Despite fencing, in the first 6 years, the losses were over 90% (written communication from Dr. Fritz Schumann to Prof. Dr. Neubauer, Botanical Institute of Justus Liebig University, Giessen, on April 29, 1974). The oldest known surviving plantings date back to a later planting of 174 seedlings in 1974 in Mannheim (23 surviving individuals), with a survival rate of 13% after 44 years. These few individuals are largely established, with fruiting female individuals and seedlings in close proximity. The number of reproducing individuals in this location could be increased by reintroduction. If the seedlings originate from individuals introduced in 1974, this reintroduction attempt must be considered successful, despite high losses. However, the low genetic diversity among them might be problematic since all are of the same Ketsch genotype (fruits from only one plant were used for sowing) and thus at least half-siblings (Ledesma-Krist et al. 2013). The increase in the genetic diversity among the Mannheim population therefore depends on the future success of later plantings and on the introduction of genetically distinct individuals. For the sites at Philippsburg and Römerberg, we found no evidence of successful seedling establishment, despite the occurrence of adult individuals. In Hördt, Lingenfeld, and Otterstadt, seedlings were found in 2022 (pers. observation).

We observed the lowest losses in plantings from 2000 and before, most likely because weak individuals had probably already died and were not included in this study. In addition, the proportion of robust, established individuals increases with planting age once the critical establishment phase is passed.

A substantial proportion of planted individuals with a minimum age of 18 years showed high vitality. For the time series, the large proportion of highly vital individuals planted in 2012 indicates suitable planting material and methods. In particular, bare-rooted seedlings were planted that originated from an *ex-situ* collection (Botanical Garden Karlsruhe). All of these individuals survived the summer flood in 2013, although planted in lower areas that were inundated during the flood (Werling et al. 2019). In contrast, those with low and medium vitality did not recover and ultimately died. Without any protective measures, 16% of the spontaneous and 56% of the planted *V.* * *sylvestris* individuals are expected to share this fate in the next few years.

Remarkably, 3 years after planting, the light exposure level of several individuals planted in 2015 was already high, most likely as a result of the small host trees (small-sized shrubs). This suggests that in reintroduction programs, vines should preferably be planted on lower woody plants, which may facilitate access to taller trees. With increasing planting age, the proportion of individuals with high light exposure level increased, but there is a risk of setback due to host tree dynamics or damage.

To assess reintroduction success, it is crucial to define the time point at which an individual can be considered "established". In the case of *V. * sylvestris*, the critical period for establishment seems to be the first 5–10 years. As of 2018, 18-year-old plantings showed a large proportion of established individuals (59%), and after approximately 40 years, most of the surviving planted individuals can be considered established. This long establishment duration is in line with previous findings (Ladwig & Meiners 2010) and sets the time frame for monitoring the success of *V. * sylvestris* introduction projects. Whilst survival rate and vitality were similar for both females and males, initial growth (at least considering the individuals planted since 2012) was more pronounced for males. Most likely, female vines initially invest more in belowground biomass and root development, which lengthens the duration of their establishment phase. Fruiting depends strongly on the climatic and nutritional conditions of the previous year (Guilpart et al. 2014, Keller & Koblet 1995). As the root serves as a nutrient reservoir in winter (Winkler & Williams 1945), it can be assumed that fruiting females require a better water supply and a larger nutrient stock and, therefore, a better developed root system.

Several hundred *V. * sylvestris* hybrids were accidentally planted in different reintroduction campaigns (Ledesma-Krist et al. 2013). Although a large proportion has already been removed, some naturalized rootstocks and wild grapevine-hybrids still exist in the floodplains of the Upper Rhine. Some of these are robust, vigorous, and fruit abundantly (pers. observation, 2018–2022). The high germination capacity of *Vitis* (see Section 4.1) leads to a risk of regeneration from seed even after the removal of a neophytic parent plant. Hybridization seriously threatens *V. * sylvestris* populations (Arrigo & Arnold 2007, Schröder et al. 2015) as the hybrids are habitat competitors that are more vigorous due to disease resistance, high adaptability, and high invasive potential (Arrigo & Arnold 2007).

A general problem of reintroduction projects is that success can only be evaluated after a long time period up to many decades, depending on a species' generation time (Godefroid et al. 2011). Such projects are usually financed by public sources, and the common project duration of a few years does not correspond with the need for long-term monitoring (Armstrong & Seddon 2008, Godefroid et al. 2011). In addition, it is important to share and disseminate the knowledge gained in the scientific community, regardless of project success, rather than producing grey literature (Hodder & Bullock 1997, Fischer & Lindenmayer 2000, Sheean et al. 2012, IUCN SSC 2013).

So far, one remarkable success of the reintroduction efforts in Germany is an increase by 482 individuals. Overall, 16% of 456 living planted individuals can be considered established. Thus, the interim success is limited in relation to the extensive reintroduction efforts but still higher compared to that achieved in the neighboring French Rhine floodplains. There, 91 *V. * sylvestris* individuals were planted in Erstein and Offendorf in 1992 (Arnold et al. 2005), and only 14 individuals survived the first 10 years (Arnold et al. 2005), with a survival rate of 15%. The low number of planted individuals can be justified by the high expenditure. Reintroduction with seedlings requires an established *ex-situ* collection for the provision of high-quality seedlings, which is cost- and labor-intensive. In addition, a developed infrastructure and cooperation partners are crucial to guarantee the success of reintroduction measures. Although in our case, reintroduction has been somewhat successful, it needs to be ensured that the introduced plants can establish themselves and reproduce, which further requires stringent monitoring and protection measures.

4.3 Implications for management strategies

In our study sites, *Vitis* * *sylvestris* was largely threatened by anthropogenic factors such as mowing or cutting and by environmental factors such as heavy shading, extreme hydromorphological dynamics, host tree diseases (ash dieback), competition with tall herbaceous species, and browsing. This calls for specific management strategies to promote spontaneous germination and facilitate the growth of already established seedlings. Although germination can be promoted via regular measures such as cutting back shrubs alongside meadow margins, trails and forest edges, which is accompanied by substrate disturbance (Krotz et al. 2019, Werling et al. 2019), such management needs to be consistent and adapted to the specific requirements of the species. Currently, excluding mowing in these areas appears to be the most appropriate strategy as this allows natural succession to take place. In addition, at least in the first 5 years after germination, the removal of tall and rapidly spreading neophytes (such as *Solidago*, *Impatiens*, or *Fallopia* species) is essential to improve light conditions and nutrient availability. When establishing new plantings, adequate site selection and marking, single-trunk protection, pre-maintenance, the selection of suitable species as supporting trees, and protection from browsing by wild deer or boar are crucial measures to guarantee the successful establishment of *V.* * *sylvestris*.

5. Conclusion

After 50 years of reintroducing *Vitis vinifera* subsp. *sylvestris* in Germany, success is only moderate. Its long establishment period, late reproductive age, dioecy, hybridization with *Vitis* cultivars, and the absence of species-focused site management strategies largely limit the success of reintroduction efforts.

Ex-situ propagation and reintroduction are important keystones for the conservation of this species but must be accompanied by other measures to reach the conservation goals. Effective management involves facilitating the establishment of both planted and naturally occurring individuals by optimizing light and climbing conditions. This includes protecting the sites from the felling or cutting of host trees and from mowing or cutting in adjacent areas. Additionally, promoting spontaneous germination can be achieved by creating suitable germination niches. To maintain the genetic integrity of the population, it is essential to conduct genetic testing and remove any hybrids and neophytic grapevines. During reintroduction, vines should preferably be planted on lower woody plants to facilitate access to taller trees and shorten the critical establishment phase. As planted individuals are most vulnerable in the first 5–10 years, frequent monitoring is crucial.

As a species adapted to natural disturbances, *V.* * *sylvestris* requires a functional floodplain ecosystem in which geomorphodynamic processes occur together with natural successsion. The highly specific habitat requirements of *V.* * *sylvestris* of ecotones between open, early successional states and advanced, complex forest structures used to be amply met in pristine fluvial landscapes. However, the loss of these dynamic, patchy landscapes with their abundant habitat boundaries has largely destroyed the niche of this species. Thus, restoring functionally intact, dynamic fluvial landscapes on the Upper Rhine and beyond remains an indispensable goal for the survival of *V.* * *sylvestris* and other riparian species and habitats.

As rebuilding a self-sustaining population does not seem to be possible at present, focus must be placed on the generation of several subpopulations that preserve the remaining genetic diversity. If established and, thus, reproducing individuals are present in sufficient numbers in terms of individual number, sex ratio, and pollination distances, spontaneous reproduction and establishment can be promoted in a second phase of supporting measures. These activities must be monitored and calibrated periodically to ensure the survival of *V. * sylvestris* in Germany.

In 2007, the species was assigned by the IUCN Red List of Threatened Species to the "Least Concern" category, with the lowest level of extinction risk (Kyratsis et al. 2011). However, this assessment might have been influenced by the scarcity of information regarding the actual situation of European subpopulations, which did not seem to be well quantified. Indeed, the present study supports a different view. The risk factors that have led to the massive decline of the species still exist. Cross-fertilization is largely inhibited by spatial fragmentation, habitat quality has been irreversibly altered, and more reproducing individuals have died than have been gained through spontaneous germination or introduction in the period from the last survey up to now. In light of this, we suggest reclassifying the status of the German *V. * sylvestris* population to "critically endangered".

Erweiterte deutsche Zusammenfassung

Einleitung – Wiederansiedlungen sind mittlerweile Standard in der Naturschutzökologie (Maunder 1992, Berger 1993). Angesichts der hochkomplexen Wechselwirkungen zwischen Pflanzen und anderen Organismen sind Wiederansiedlungen jedoch mit verschiedenen Risiken verbunden (Drayton & Primack 2012). Sie erfordern daher eine sorgfältige Planung und ein genaues Risikomanagement, insbesondere in Bezug auf die Auswahl der Ausgangspopulation (Hufford & Mazer 2003, McKay et al. 2005) und der optimalen Standorte (Giorgi & Francisco 2000, Millar et al. 2007). *Vitis vinifera* subsp. *sylvestris*, als die einzige einheimische Art der Familie Vitaceae in Europa (Núñez & Walker 1989), ist eine der seltensten Pflanzentaxa Deutschlands (Angersbach et al. 2018, Ledesma-Krist et al. 2018) und in weiten Teilen Mitteleuropas gefährdet. Sie wächst in Auwäldern und in Überschwemmungsgebieten, wo sie als Liane oft Höhen von über 20 m erreicht. Der Wandel in der Waldbewirtschaftung sowie die Veränderung der Auenlandschaft durch Flussregulierung, Entwässerung, den Bau von Staustufen und Kiesabbau haben zu großflächigen Verlusten von *V. * sylvestris* und ihren natürlichen Lebensräumen geführt (Arnold et al. 2010, Ledesma-Krist et al. 2013). Darüber hinaus ist der langfristige Bestand dieser Art durch die geringe Populationsgröße, die genetische Isolierung, die Hybridisierung mit Kulturreben, Krankheiten ihrer typischen Stützbäume (Ulmenkrankheit, Eschensterben) und das Fehlen einer erfolgreichen sexuellen Fortpflanzung bedroht. Die kleinen Restbestände entlang des Oberrheins sind aufgrund des speziellen Genpools von hoher Bedeutung (Ledesma-Krist et al. 2013), was deren Erhaltung besonders dringlich macht. Obwohl seit 1967 lokale Wiederansiedlungen durchgeführt werden, sind der aktuelle Populationsstatus und der Erfolg dieser Wiederansiedlungen bis dato unbekannt, stellen aber eine wesentliche Basis für die zukünftige Erhaltung dieser Art dar. In diesem Kontext haben wir uns mit den folgenden Fragen beschäftigt: (1) Wie ist der aktuelle Status der Population von *V. * sylvestris* in Deutschland? (2) Wie erfolgreich sind die Wiederansiedlungsmaßnahmen bislang verlaufen?

Methoden – In der vorliegenden Studie wurden von 2017 bis 2018 alle bekannten Vorkommen (spontan aufgekommene und gepflanzte Individuen) von *Vitis vinifera* subsp. *sylvestris* in Deutschland erfasst. Die Standorte liegen vor allem in Natura 2000 und FFH Gebieten, die noch periodisch überflutet werden. Für die Beurteilung der Etablierungschancen wurden die Vitalität der Pflanzen, die Wachstumsbedingungen und lokale Gefährdungsfaktoren erhoben. Darüber hinaus wurden Zeitreihen von Vitalitätsdaten (2012, 2013 und 2018) für Lokalitäten der Wiederansiedlung in Leimersheim, Lingenfeld und Römerberg analysiert. Im Weiteren wurde der Stammdurchmesser bestimmt, und die Pflanzen wurden in vier Größenklassen eingeteilt, um Rückschlüsse auf ihr Alter zu ziehen.

Ergebnisse und Diskussion – Insgesamt wurden 1075 *Vitis vinifera* subsp. *sylvestris* Individuen nachgewiesen. Davon waren 503 abgestorben oder vermutlich abgestorben – darunter 2 spontane und 501 gepflanzte Individuen. Die Gesamtüberlebensrate betrug 53 % (98 % für spontane und 49 % für ausgepflanzte Exemplare) seit der letzten Erhebung 2008–2013 und unter Berücksichtigung der Wiederansiedlungsprojekte in den Jahren 2012–2016. Im Jahr 2018 waren noch 572 vitale Individuen vorhanden. Für die spontan aufgekommenen Individuen wurde ein langsamer, aber kontinuierlicher Bestandsrückgang verzeichnet. Bei der jüngsten Erhebung im Jahr 2018 fanden wir 482 Individuen aus früheren Wiederansiedlungen (1974 bis 2016); 55 % der seit 2012 gepflanzten Individuen waren in der Zwischenzeit abgestorben. Nur 16 % von 456 Reben, von denen Vitalitätsdaten erhoben werden konnten und das Pflanzjahr bekannt war, wiesen eine hohe Vitalität und ein hohes Reproduktionspotential auf und konnten somit als etabliert angesehen werden. Die restlichen 84 % wurden überwiegend im Jahr 2016 gepflanzt, hatten die Baumkrone noch nicht erreicht und wiesen eine niedrige bis mittlere Vitalität auf. Die Zahl der erwachsenen, sich fortpflanzenden Individuen war rückläufig. Im Jahr 2007 wurde die Art in der Roten List der Bedrohten Arten der IUCN in die Kategorie „Least Concern" (geringste Gefährdung) eingestuft (Kyratsis et al. 2011). Allerdings beruht diese Einschätzung sehr wahrscheinlich auf mangelnden Informationen über die tatsächliche Situation der europäischen Teilpopulationen, und die vorliegende Studie unterstützt eine andere Perspektive. Basierend auf unseren Ergebnissen, ist *V. * sylvestris* in Deutschland vom Aussterben bedroht, und vor diesem Hintergrund schlagen wir vor, den Status dieser Art für Deutschland auf „Critically Endangered" (vom Aussterben bedroht) neu einzustufen. Die Risikofaktoren, die zum massiven Rückgang der Art geführt haben, sind auch 2018 noch wirksam. Insbesondere sind die artspezifischen Lebensraumansprüche in den massiv degradierten Oberrhein-Auen weitestgehend nicht mehr erfüllt und müssen im Rahmen von Renaturierungsmaßnahmen wiederhergestellt werden, damit sich diese Art wieder ausbreiten kann. Hierbei ist die Schaffung einer natürlichen Überflutungsdynamik auf ausgewählten Flächen zu nennen. Momentan ist die Wiederansiedlung von *V. * sylvestris* vor allem durch die begrenzte Verfügbarkeit geeigneter Habitate erschwert. Hinzu kommen die lange Etablierungszeit, das späte Reproduktionsalter, die Zweihäusigkeit und die Hybridisierung mit anderen Vitis-Kultursorten, verwilderten Vitis-Arten und Rebstockunterlagen. Die Kombination dieser Faktoren erfordert geeignete Naturschutz- und forstwirtschaftliche Strategien, um diese Art zu schützen und die Population langfristig zu sichern. Hierfür bedarf es spezifischer Managementmaßnahmen, die darauf abzielen, die spontane Vermehrung durch Keimung zu fördern und bereits etablierte Pflanzen zu unterstützen. Der Erfolg der Wiederansiedlung, die Effektivität der Schutzmaßnahmen und der Zustand der Population müssen regelmäßig überwacht werden.

Acknowledgements

This study is an outcome of the project "Oberrhein VITAL", funded by Stiftung Naturschutzfonds Baden-Württemberg via earmarked proceeds of the GlücksSpirale. The authors would like to thank Norbert Kowarsch, Ute Werling, Norbert Krotz, Franco Röckel, Matthias Jensen, Ernst Heene, and Katrin Back for assisting with field work. We acknowledge Jochen Dümas, Norbert Kowarsch, Peter Vogel, Ernst Heene, Katrin Back, Manuel Karopka, and Heinz Zoller for providing data on *Vitis* sites and reintroduction efforts. We thank the two anonymous reviewers for their valuable comments and questions that helped clarify the ideas presented in this paper.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Vitality classes, light exposure levels, climbing conditions, and other local threats of spontaneous individuals according to stem size classes.
Anhang E1. Vitalitätsklassen, Lichtexposition, Kletterbedingungen (C) und Gefährdungspotenzial (D). für spontan auftretende Reben in Abhängigkeit von der Stammgrößenklasse.

Supplement E2. Vitality classes (2018), light exposure levels, climbing conditions, and other local threats of planted individuals by age cohorts.
Anhang E2. Vitalitätsklassen (2018), Lichtexposition, Kletterbedingungen und Gefährdungspotenzial für gepflanzte Regen in Abhängigkeit von der Altersklasse.

Supplement E3. Time series: changes in vitality class in 2012-plantings in Leimersheim, Lingenfeld, and Römerberg.
Anhang E3. Zeitreihen: Veränderungen in Vitalitätsklassen der Anpflanzungen von 2012 in Leimersheim, Lingenfeld und Römerberg.

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Supplement E1. Vitality classes, light exposure levels, climbing conditions, and other local threats of spontaneous individuals according to stem size classes; med. = medium.

Anhang E1. Vitalitätsklassen, Lichtexposition, Kletterbedingungen (C) und Gefährdungspotenzial (D) für spontan auftretende Reben in Abhängigkeit von der Stammgrößenklasse; med. = mittel.

		Vitality classes						**Light exposure levels**					
		abs.			rel. (%)			abs.			rel. (%)		
Stem size class	Sum	high	med.	low	high	med.	low	high	med.	low	high	med.	low
Small	10	8	2	0	80	20	0	9	0	1	90	0	10
Medium	18	17	1	0	94	6	0	16	2	0	89	11	0
Large	22	17	4	1	77	18	5	21	1	0	96	5	0
Very large	18	17	1	0	94	6	0	17	1	0	94	6	0
Total	68	59	8	1	86	12	2	63	4	1	92	6	2
		Climbing condition classes						**Other local threats**					
		abs.			rel. (%)			abs.			rel. (%)		
Stem size class	Sum	good	med.	poor	good	med.	poor	none	potential	acute	none	potential	acute
Small	10	8	2	0	80	20	0	6	1	3	60	10	30
Medium	18	13	2	3	72	11	17	13	2	3	72	11	17
Large	22	19	2	1	86	9	5	18	1	3	82	5	14
Very large	18	10	6	2	56	33	11	17	1	0	94	6	0
Total	68	50	12	6	74	18	9	54	5	9	79	7	13

Niederl et al.: Wild grapevine (*Vitis vinifera* subsp. *sylvestris*) in Germany: Is reintroduction a viable approach? – Tuexenia 45 (2025).

Supplement E2. Vitality classes (2018), light exposure levels, climbing conditions, and other local threats of planted individuals by age cohorts; med. = medium, n = no information.

Anhang E2. Vitalitätsklassen (2018), Lichtexposition, Kletterbedingungen und Gefährdungspotenzial für gepflanzte Regen in Abhängigkeit von der Altersklasse; med. = mittel, n = keine Information.

		Vitality classes						**Light exposure levels**							
		abs.			rel. (%)			abs.				rel. (%)			
Cohort	sum	high	med	low	high	med	low	high	med	low	n	high	med	low	n
1974-80	37	33	0	4	89	0	11	32	2	3	0	87	5	8	0
1990/95	16	11	2	3	68	13	19	12	2	2	0	74	13	13	0
2000	22	21	0	1	95	0	5	13	6	2	1	59	27	9	5
2007/08	11	2	2	7	18	18	64	1	1	9	0	9	9	82	0
2012/13	58	33	5	20	56	9	35	7	8	43	0	12	14	74	0
2015	82	59	7	16	71	9	20	13	15	54	0	16	18	66	0
2016	230	44	45	141	19	20	61	0	0	230	0	0	0	100	0
Total	456	203	61	192	45	13	42	78	34	343	1	17	8	75	0

		Climbing condition classes						**Other local threats**					
		abs.			rel. (%)			abs.			rel. (%)		
Cohort	sum	good	med	poor	good	med	poor	none	potential	acute	none	potential	acute
1974-80	37	25	12	0	68	32	0	20	14	3	54	38	8
1990/95	16	12	4	0	75	25	0	6	6	4	38	37	25
2000	22	21	1	0	96	5	0	16	3	3	72	14	14
2007/08	11	9	0	2	83	0	18	0	8	3	0	73	27
2012/13	58	40	11	7	69	19	12	2	29	27	3	50	47
2015	82	59	19	4	72	23	5	14	48	20	17	59	24
2016	230	195	22	13	85	10	6	107	0	123	47	0	53
Total	456	361	69	26	79	15	6	165	108	183	36	24	40

Supplement E3. Time series: changes in vitality class in 2012-plantings in Leimersheim, Lingenfeld, and Römerberg; med. = medium, ns = vitality class not specified. Data from 2012 and 2013: Ledesma-Krist 2013, unpublished.

Anhang E3. Zeitreihen: Veränderungen in Vitalitätsklassen der Anpflanzungen von 2012 in Leimersheim, Lingenfeld und Römerberg; med. = mittel, ns = Vitalitätsklasse nicht angegeben. Daten für 2012 und 2013: Ledesma-Krist 2013, unveröffentlicht.

	Vitality classes											
	abs.											
	2012			2013			2018					
Location	high	med.	low	high	med.	low	high	med.	low	dead	ns	Sum
Leimersheim	9	1	0	7	2	1	5	1	0	4	0	10
Lingenfeld	10	0	0	7	0	3	3	0	2	3	2	10
Römerberg	41	2	0	34	4	5	10	1	4	28	0	43
	rel. (%)											
	2012			2013			2018					
Location	high	med.	low	high	med.	low	high	med.	low	dead	ns	
Leimersheim	90	10	0	70	20	10	50	10	0	40	0	
Lingenfeld	100	0	0	70	0	30	30	0	20	30	20	
Römerberg	95	5	0	79	9	12	23	2	9	66	0	