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PERSPECTIVES AND PARADIGMS

Natural and human dimensions of a quasi-wild species: the case of kudzu

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Abstract The human dimensions of biotic invasion are generally poorly understood, even among the most familiar invasive species. Kudzu (*Pueraria montana* (Lour.) Merr.) is a prominent invasive plant and an example of quasi-wild species, which has experienced repeated introduction, cultivation, and escape back to the wild. Here, we review a large body of primary scientific and historic records spanning thousands of years to characterize the complex relationships among kudzu, its natural enemies, and humans, and provide a synthesis and conceptual model relevant to the ecology and management of quasi-wild invasive species. We documented over 350, mostly insect, natural enemy species and their impacts on kudzu in its native East Asian range. These natural enemies play a minor role in limiting kudzu in its native range, rarely generating severe impacts on populations of wild kudzu. We identified a number of significant influences of humans including dispersal, diverse cultural selection, and facilitation through disturbances, which catalyzed the expansion and exuberance of kudzu. On the other hand, harvest by humans appears to be the major control mechanism in its native areas. Humans thus have a complex relationship with kudzu. They have acted as both friend and foe, affecting the distribution and abundance of kudzu in ways that vary across its range and over time. Our conceptual model of kudzu emphasizes the importance of multiple human dimensions in shaping the biogeography of a species and illustrates how kudzu and other quasi-wild species are more likely to be successful invaders.

Keywords Control mechanisms · Human domestication · Invasive species · Natural enemy · *Pueraria montana* · Utilization

The study was conducted before Quan Dong joined USGS.

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Introduction

Humans have extensively modified the earth's ecosystems (Vitousek et al. 1997). Along with land cover and climate change, a major aspect of human domination has been the significant reduction of natural barriers between biotic regions, leading to an explosion of species having a "neo-disjunct" distribution. Such species may behave in novel ways in their introduced range, taking on aggressive characteristics that were not observed in their native range, often to the detriment of the adopted ecosystems.

Several hypotheses are often invoked to explain this newfound exuberance, chief among them, those related to a release from natural enemies. The enemy release hypothesis (Williamson 1996) states that an exotic species grows with increased vigor and expands its abundance upon experiencing less regulation in new areas that lack consumers or pathogens. This and the related evolution of increased competitive abilities hypothesis (Blossey and Notzold 1995) are widely considered contributing factors in the spread of many invasive species (Elton 1958; Keane and Crawley 2002). Note that these explanations imply that the natural enemy is a non-human species.

Another recurring explanation for the invasion of some exotic species is related to disturbance. Changes in disturbance regimes, generally through increased disturbance by humans and associated domesticates, are often cited to explain the success of many invasive species (i.e., the anthropogenic disturbance hypothesis; see Sher and Hyatt 1999; Levine et al. 2004). It is thus understandable that human activities are generally assumed to favor the introduction and proliferation of exotic species. This leads to a view of humans as "friends" of exotic invaders, with the "foes" of invaders being non-human consumers, competitors, and parasites.

However, the human dimensions of biological invasions are complex and defy simple characterizations. For example, while human domestication may contribute much to the invasion success, harvest by humans may drive local populations to extinction. Just as human dimensions are integral parts of most ecosystems (Vitousek et al. 1997; Palmer et al. 2004), they are integral parts and perhaps the most responsible factors of biological invasions. Nevertheless, outside of ecosystem disturbance and propagule pressure, other human dimensions have largely been ignored in the ecological studies of species introduction and biological invasion.

The friend or foe question is critical in understanding the successful invasion, historical control, and potential future control of kudzu. Kudzu, *Pueraria montana* (Lour.) Merr., is a clonal, leguminous vine. First introduced into the United States from Japan in 1876, kudzu was widely planted as an ornamental, for erosion control, as a source of starch, cloth, and paper products, and as fodder for livestock, especially in the first half of the 1900s (Forseth and Innis 2004; Simberloff 2011). As both technology and the economy evolved, kudzu transformed from a desired plant to a weed (Kinbacher 2000). By the 1950s, the noxiousness of this plant was recognized (Britton et al. 2002). Today, kudzu, sometimes known as "the vine that ate the South," is a federally-listed noxious weed species (US Department of Agriculture, Agricultural Research Service 1971), covering 3 million ha and spreading at a rate of 50,000 ha per year (Southeast Exotic Pest Plant Council 2001; Pappert et al. 2000; Forseth and Innis 2004). Its invasive status extends beyond the US, being listed as one of the 100 world's worst alien species (Lowe et al. 2000).

While the history and ecology of kudzu have been studied intensively in the United States (e.g., Hoots and Baldwin 1996; Mitich 2000; Forseth and Innis 2004), information of great value to ecologists and land managers on kudzu in its native areas is lacking. Note that in its native China, Japan, and other East Asian countries, kudzu is not considered a noxious weed. In its US range, kudzu appears to flourish in areas where natural habitats have been disturbed by human activities, such as roadsides and forest edges, and in abandoned agricultural lands and logged forest patches (Forseth and Teramura 1986; US Congress 1993). In China, measurable amounts of human disturbance have been present for more than 10,000 years, with a dramatic escalation in recent decades. Nevertheless, kudzu has never been considered a noxious species in China and eastern Asia, even in disturbed areas. This raises the question of what limits kudzu in its native range.

In this article, we summarize the heterotrophic organisms that affect kudzu in China and neighboring countries. Also, we review the long historical record of kudzu, including its utilization, introduction, acclimatization, and cultivation. Based on this

information, we hypothesize that human use is a major controlling factor of kudzu in eastern Asia and discuss the dual role of humans as both friends and foes of kudzu. More generally, we hypothesize that species such as kudzu, having experienced repeated introduction, cultivation, and escape back to wild, are more likely than other species to become invasive in human dominated landscapes.

Kudzu in its native range

Distribution and habitats

Kudzu is distributed in eastern Asia, including eastern and southern China, the Korean peninsula, and Japan, and southwards to northern Myanmar, northern Laos, and northern Vietnam (Fig. 1). It is widely introduced and naturalized elsewhere in south and southeast Asia, Africa, Oceania, the tropical Americas, and the United States, and is also found in less abundance in southern Europe and southwest Asia. In the United States, kudzu can be found throughout much of the East, from New York in the north, south to Florida, and west to Texas (Fig. 1). The most extensive infestations occur in the southern states of Mississippi, Alabama, and Georgia (Southeast Exotic Pest Plant Council 2001; Britton et al. 2002).

The occurrence and invasiveness of kudzu are most likely limited by climate, light availability, and local biotic factors (Winberry and Jones 1973; Munger 2002). Kudzu is most prolific in areas where winters are mild (4–16°C), summer temperatures rise above 27°C, the growing season is long, and annual precipitation exceeds 1,000 mm. It especially thrives in open areas of regions experiencing abundant sunny weather during the growing season. Kudzu grows on a variety of soil types, but performs best on deep, well-drained, loamy soils. Kudzu is a nitrogen-fixing plant, and thus competitive on nitrogen-deficient sites. Seeds mature in fall and foliage is generally killed by the first frost, after which plants are dormant until spring. The composition of the particular local native plant community seems to have little influence on susceptibility to kudzu invasion. Even core areas of otherwise undisturbed forest can eventually succumb, as kudzu advances from established populations slowly along a forest perimeter (Winberry and Jones 1973; Munger 2002).

Natural enemies

Kudzu has many natural enemies in its native lands, with records tracing back more than 1,000 years. For example, a medical book, 'Lei Gong Pao Jiu Lun' (anonymous, *Master Lei's Discourse on Drug Processing*, written between 420 and 479 CE) documented the occurrence of bean blister beetle (*Epicauta gornami* Marseul) and lesser blister beetle [*Mylabris cichorii* (L.)] in kudzu (cited by Zhang and

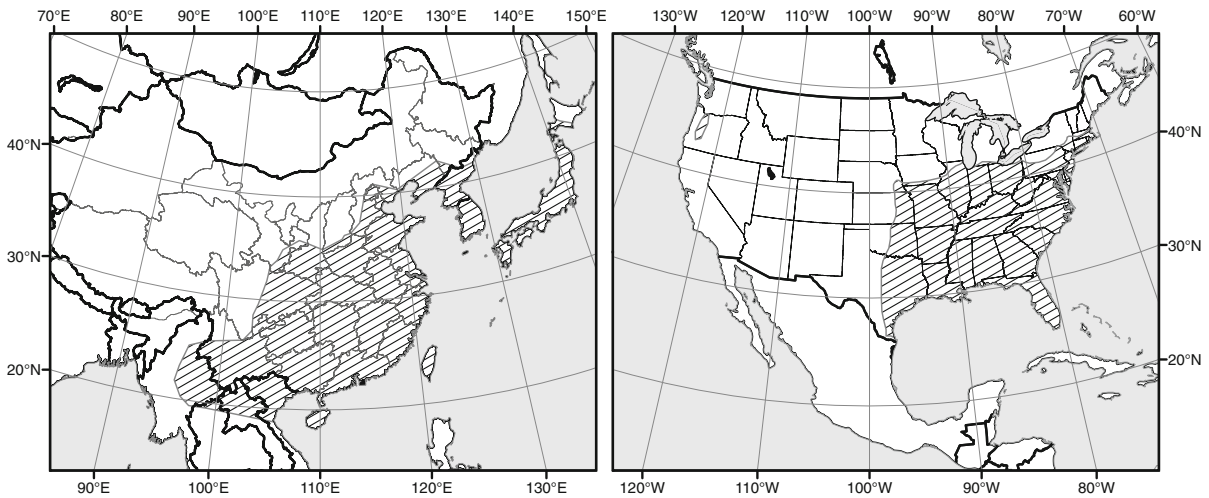

Fig. 1 The distribution of kudzu in its native range, eastern Asia (*left*), and in its naturalized range of the United States (*right* following Follak 2011)

Zhao 1996). In the Liang Period, Tao Hong Jing (502–549 CE) observed pregnant bean blister beetle occurring in kudzu flowers from June to July (cited by Li 1590).

Arthropod

Over 350 species consume or infect kudzu (Tables 1, 2, Online Resource Tables 3–6). Among them, 290 species are arthropod, including 285 insect species (belonging to 209 genera, 51 families and 7 orders), and 5 mite species (belonging to 5 genera, 1 family and 1 order), and have been identified and documented consuming kudzu in the wild (Table 1, Online Resource Table 3). These species may consume different parts of the plant. In China, approximately 185 species eat leaves, buds, and young shoots (Fig. 2, Online Resource Table 4). Some 50 species consume stems, 31 forage on flowers, and 13 eat fruits and seeds. Only one species, a mole cricket, is known to eat roots (Online Resource Table 4). Most of these species only cause minor damage to kudzu tissues and produce no observable impact on growth and survival when compared to adjacent, uninfected kudzu plants in the same habitats (personal observations by Z. Li; Everest et al. 1999). Twenty insect species were found to cause intermediate damage to plant tissue and have minor impact on growth.

Only 10 species were locally reported to have caused severe damages to plant organs and to significantly impact growth (Zhang 1995; Cai et al. 2001; Li et al. 2003a, Online Resource Table 4). However, severe damage from these species was confined to starch kudzu cultivated in a monoculture. Furthermore, while most cause damage to leaves, only *Sagra femorat purpurea* Lichtenstein and *Aponsila montana* (Distant) mainly damage stems, which are of greater demographic consequence.

Table 1 The arthropods and nematodes that feed on living kudzu plant

Taxa	Number of orders	Number of families	Number of genera	Number of species (incl. subspecies)
Arthropods				
Insects	7	51	209	285
Mites	1	1	5	5
Nematodes	1	1	2	6

Table 2 The bacteria and fungi infecting living kudzu plant

Taxa	Number of orders	Number of families	Number of genera	Number of species
Bacteria	1	1	1	1
Fungi	11	12	22	26

Fig. 2 A hawkmoth (Sphingidae) caterpillar feeding on kudzu leaves. Over 350 species consume or infect kudzu. Most of them are insects. *Photo by* Quan Dong

Damage by an insect species varies in degree between different kudzu populations. For example, *Aponsila montana* (Distant) was associated with severe damage in Ziyun, Guizhou province (Zhang 1995), but only minor damage near Guangzhou, Guangdong Province (Li et al. 2003a). Other than the little known species, *Coptosoma pinfa* (Yang), these 9 species are generalists living on a variety of hosts over a wide geographic range. There is no evidence that they controlled the abundance and distribution of wild kudzu. Furthermore, these herbivorous species attract a variety of predators, including wasps, spiders, ants, rove beetles, and lady beetles, which aggregate as their prey abundance increases (Shimoda et al. 1997; Li et al. 2003b, 2004a, b), further limiting the effectiveness of herbivores in controlling kudzu.

Nematodes

Nematodes, including 5 species of *Meloidogyne*, and *Rotylenchulus reniformis* (Linford et Oliveira), also damage kudzu (Table 2, Online Resource Table 5), usually at root tips. Note that these nematode species are agricultural pests that can also damage wild plants. They are quarantined or otherwise forbidden

to be imported in many countries, including the United States. Other invertebrates that may damage kudzu include slugs and snails, e. g. *Laeochaica subsimilis* (Deshayea). They often appear on the leaves of kudzu, but seem to cause little damage (personal observations).

Fungi and bacteria

Fungi and bacteria can infect, cause disease, and severely affect growth and survival in cultivated kudzu. For example, *Myrothecium verrucaria* (Alb. et Schw.) Ditm. has been shown in greenhouse and field experiments to cause 90% mortality to kudzu plants (Boyette et al. 1999). Twenty-six species of fungi, according to the system of Ainsworth et al. (1973), belonging to 22 genera in 12 families of 11 different orders, have been observed causing damage (Table 2, Online Resource Table 6). One bacterium species, *Pseudomonas savastanoi* pv. *phaseolicola* (Burkholder) Gardan et al. can cause kudzu leaf spot disease (Goto and Hyodo 1987; Zidack and Backman 1996). Nevertheless, reports showing control of wild kudzu by microorganisms are lacking. For example, *Synchytrium minutum* (Pat.) Gäum. (*S. puerariae* Miyabe) often infected about 10% of cultivated starch kudzu ('*Pueraria thomsonii* Benth.') near Guangzhou, causing imitation rust disease. The infection rates varied, occasionally reaching 20–30% there in cultivation (Yan et al. 1999), whereas, the disease is rarely observed in the wild. We monitored three wild populations in Wanzhou, Chongqinq, China for 3 years, and found scattered infections of *S. minutum* affecting only a few stems and leaves in each case. Note that these microorganisms are not host-specific, but infect economically important crops (Tai 1979; Abbas et al. 2001).

Mammals

Some mammals consume kudzu, occasionally causing severe damage and affecting growth and survival. Wild pig, *Sus scrofa* L., itself considered a pest species in many locations, and hares, *Lepus* spp., eat leaves and new shoots of kudzu, and wild pigs sometimes dig kudzu roots (Verdcourt 1979). However, we know of no cases where the consumption of kudzu by wild mammals has contributed to its control.

Overall, while it is clear that kudzu has numerous natural enemies, few of them cause severe damage, and there is very little evidence of their ability to control the abundance and distribution of wild populations of kudzu. Perhaps the key reason for this has to do with the lack of enemies affecting the perennial root, which may grow up to 3.7 m in depth and 30 cm in diameter (Miller and Edwards 1983; Miller 1988) and contains defensive chemical compounds. Because single factors, such as natural enemies and plant community, do not seem to limit kudzu alone, it appears that multiple agents working in tandem control kudzu in undisturbed areas.

Anthropogenic influences: a brief historical account of kudzu in China

Significantly missing from the tables and above discussion is our own species, *Homo sapiens* L., which is associated with numerous positive and negative interactions with kudzu. First, humans transport and introduce kudzu to new locations and thus expand its distribution. Second, humans cultivate kudzu for a variety of purposes. Cultural selection of heritable traits for various purposes and for different local conditions is likely to increase the genetic diversity and competitiveness of kudzu. Third, anthropogenic disturbance facilitates exuberance of kudzu. These influences have contributed to kudzu's success in invasion and expansion. On the other hand, human beings are also the most important control agent of kudzu, especially in China, where harvest has been pervasive.

Long history

The history of kudzu utilization is extremely long. We found records of kudzu in both archaeological studies and in ancient literature. For example, an archaeological study by a team from Nanjing Museum, China, found pieces of textile called "ko-pu" (meaning kudzu cloth) at a site of new stone-age remains, in Caoxie Mountain, Wu County, Jiangsu province, in 1972. Carbon^{14} dating of the surrounding wood (Nanjing Museum 1978, Wang Zunguo, personal communication) suggested that the ko-pu was made more than 6,000 years ago, making it the earliest record of textile created from kudzu fiber. While archaeological records offer solid evidence of

Fig. 3 Various products (tablets, powder, capsules, extract, gel, tincture) sold at supermarkets, drug stores, and gift stores. Kudzu has been used for >6,000 years and is still been used commercially

kudzu use and distribution, literature records about kudzu, found sporadically throughout most Chinese dynasties, reveal more multifarious stories.

Diverse uses

Kudzu has been harvested for at least three major purposes: (a) fiber, (b) food, and, (c) medicine.

Together with ramie (*Boehmeria nivea* (L.) Gaud.) and silk, kudzu fiber was one of the three major textile materials in China from the Zhou dynasty (1046 BCE–770 BCE) until the early twentieth century. People used fibers from kudzu bark to make cloth garments, shoes, and hats. By the nineteenth century, the quality of kudzu textile had reached a very high level, as complicated and laborious techniques were developed to process it (Wu 1848). In addition to textiles, fiber from kudzu bark was used to make paper, artifacts, carpet, and furniture.

People also used different parts of kudzu as food ingredients. The buds and young flowers were cooked and served as vegetables in the Zhou dynasty (Zhu 1406). The flour extracted from the root of wild kudzu was used as a substitute for grain, first during periods of famine, and then regularly before 540 CE (Zhu 1406; Li 1590). Consumption had increased so that kudzu was cultivated widely and strains called "starch kudzu" were developed.

Kudzu has long been a frequently used ingredient of traditional Chinese medicine for treating a variety of illnesses. As early as 200 CE, kudzu was documented as a medical ingredient in *Shen-Nung Pen-Tsao Ching* (Divine Farmer's Materia Medica) (Li 1590). In the middle of the 3rd century, kudzu was used in medicine treating typhoid (Li 1590; Kimura 1932). Later, kudzu was included in medicine to treat diabetes, bleeding in the upper digestive track, and hangover (Li 1590; Fan et al. 1998). Today, different organs of kudzu are still used in medicine and nutritional supplements (Fig. 3). It is known that the root and stem of kudzu are rich in flavonoids, isoflavonoid, and isoflavone, which have a variety of applications (Foster and Duke 1990; Keung and Vallee 1998; Chen et al. 2004). These include treatment of hangovers and alcoholism, gastrointestinal disorders, cancer, and cardiovascular disorders. Note that wild kudzu is the major source for medical use because of its richer concentration of these chemical compounds compared with cultivated kudzu (Fan et al. 1998).

Kudzu is used in other areas of East and Southeast Asia in a similar way. These native regions share many cultural and agricultural traditions. Humans consume a large amount of kudzu every year. For example, family mills of kudzu starch appeared at least as early as seventeenth century in Japan, with large scale production by the 1930s (Kimura 1932). Today, the consumption of kudzu starch in Japan is ranked second only to China. Japan imports kudzu starch from China in addition to its own harvest to produce bread, noodles, ice cream, drinks, jelly, and other popular products (Fan et al. 1998; Huang et al. 2001). Medicinal uses in Korea, Japan and Indo-China also continue to remain very common (Perry and Metzger 1980). Kudzu has been a valuable plant resource, rather than a noxious weed, in these regions.

Diversity and variants

Kudzu *Pueraria montana* (Lour.) Merr. (Ma 2008) is a polymorphic species and includes many geographical races, ecotypes, and cultivars. Considerable variation exists in the taxonomic classification of kudzu, including subspecies and varieties (Van der Maesen 1985; Van der Maesen and Almeida 1988; Wu 1995). Being difficult to distinguish, we generally

do not think these should be recognized taxonomically. Nevertheless, starch kudzu (Thomson's kudzu), usually under the name of *P. thomsonii* Benth., *P. lobata* var. *thomsonii* (Benth.) van der Maesen, *P. lobata* subsp. *thomsonii* (Benth.) Ohashi et Tateishi or *P. montana* var. *chinensis* (Ohwi) van der Maesen et Almeida, should be represented as a cultivar group of kudzu. Partly due to the great variation in morphology, debate continues on the taxonomic status of kudzu and its varieties.

Kudzu's high level of variation seems to be contingent upon diverse human uses, cultivation, and introduction to a variety of regions in Asia. Human economic activities could have imposed artificial selection on the heritable life history traits of kudzu, including the size and shape of different organs. Cultivation and reintroduction of cultivated strains into the wild likely have contributed to the genetic and morphological diversity of wild kudzu, causing taxonomic confusion. For example, the two cultivars of starch kudzu, 'Da Ge' and 'Ma Ge' in Guangzhou, have been known to escape cultivation (How 1954). In addition to the spatial and morphological variability, genetic diversity is also high within populations (Pappert et al. 2000). A high level of genetic and phenotypic diversity may facilitate the success of invasion.

Harvest and control

Human harvest seems to be a major demographic factor controlling wild kudzu and may have prevented it from dominating human-disturbed areas in China. For example, a very common harvesting practice, the removal of bark and roots, leads to severe damage and may cause death of kudzu plants. In contrast, natural enemies cause much less harm to the plant, as most of them damage leaves, which fall in winter anyway. It takes 3–4 years of frequent removal of >80% of vegetative growth to kill even young kudzu plants (Everest et al. 1999).

The intensity of harvest on wild kudzu was likely high through most of history, due to a high level of consumption. Several lines of evidence suggest that the scale of cloth production was often large. First, in Chinese literature, ordinary people are also called "Ge Yi", literally meaning kudzu clothes, because these people wore clothes made of kudzu fiber. This suggests that kudzu textiles were common, inexpensive, and durable, due to large-scale, high-quality production. Mechanical processing techniques were invented and widely used about 7,000 years ago. Numerous archaeological studies found machine-made textiles in many places of the middle and lower ranches of Yangtze River and in Huabei plain, north China (Jiang 2002). Secondly, *ShiJin* (The Book of Songs), one of the most famous and earliest poetry books, documented that kudzu-related commerce occurred at a very large scale from the early Zhou dynasty to the middle of the era of the Spring and Autumn period (770 BCE–476 BCE) (Pan 2001). Offices were even set up to administer kudzu affairs in the Zhou dynasty (Wu 1848). The production of kudzu textiles declined after the introduction of upland cotton (*Gossypium hirsutum* L.) in 1898 and the introduction of modern textile machinery from the US.

Root removal and resultant mortality of kudzu were likely to be at an extremely high level during famine, as people sought almost anything edible to avert starvation. Famines occurred frequently in China, and millions and millions of people died. Mallory (1926) reported that 1828 famines occurred between the years 108 BCE and 1911 CE, or one nearly every year in some provinces. Human consumption of kudzu during famines no doubt reduced the abundance of kudzu to extremely low levels and might have driven many local populations to extinction.

Today, the tuberous roots of wild kudzu are still harvested for food and medicinal purposes at a commercial scale (Fig. 3). Flour made from wild kudzu can be purchased in many supermarkets and gift stores as health food in China and Japan. In many areas of China, kudzu is harvested two or three times a year to feed domestic animals (Sun 2001). People bury the side-roots and sprouts in soil after harvesting the tuberous roots, in order to allow kudzu to regrow.

Further evidence of human control of kudzu comes from our observations that kudzu has flourished after the discontinuation of harvest in various sites. In 1998, China initiated the Natural Forest Conservation Project. Deforestation and the harvest of kudzu were halted in most areas covered by the project, and kudzu subsequently flourished in many sites. For example, kudzu became conspicuously more abundant near Lungman Village, Xingshan county, Hubei province during 1999–2002 (personal observation, Fig 4). Similar situations also have occurred in some

Fig. 4 Kudzu covered trees and shrubs in Lungman Village, Xingshan county, Hubei. *Photo by* Quan Dong

natural reserves, such as the Maoer Mountain National Natural Reserve, Guangxi. Kudzu invasion may impact the recovery of natural vegetation in some of these sites.

Cultivation, introduction, and habitat creation

Various human activities have facilitated the spread of kudzu. While the historical details are unclear, there is a long history of cultivation, introduction, and habitat creation.

Kudzu was probably first cultivated to make cloth. It played an interesting and important role in the recovery of the Yue kingdom after their 494 BCE defeat at the hands of the Wu kingdom. After humiliating enslavement by the Wu, Guo Jian, the Yue king, was released and he began to promote growing kudzu among his people. The women of Yue then made kudzu cloth to develop their economy and as a tribute to the King of Wu. This made the Yue prosperous and led to the hegemony of Guo Jian about twenty years later ("Yue Jue Shu", cited by Pan 2001).

Kudzu was also cultivated for food. An starch kudzu was raised from cultivation in the middle of Jiangxi province, China, recorded by Su Song in 1062 CE (cited by Li 1590). Its root is less fibrous and can be directly used for cooking (Li 1590). The production of starch kudzu increased to a large scale, only to decline after sweet potato, *Ipomoea batatas* (L.) Lam., and potato, *Solanum tuberosum* L., were introduced into China in 1594 CE and in the early seventeenth century, respectively. Today, starch kudzu is still cultivated in scattered areas of southern China. Use of both wild and starch kudzu continues as a health food and domestic animal feed, the latter motivated by its high protein content.

Widespread farming of both wild and cultivar strains introduced kudzu to new areas and promoted its escape into the wild. In the long history of Asia and particularly China, agricultural lands were abandoned repeatedly as famine, wars, natural disasters, and epidemics broke out and human population fluctuated drastically. This land use cycle may have been an important mechanism for the abundance and expansion of kudzu, providing many opportunities for introduction and reintroduction. Repeated introductions from different native locations would increase the intra-species diversity thus enhancing the species' invasiveness (Cox 2004). Recent introduction and escape have been documented in the United States and other countries far from the native areas (e.g., Miller and Edwards 1983). The records of cultivated strains, such as *P. montana* var. *chinensis*, also documented the link between the earlier introductions and cultivation and the escape and establishment of wild populations in new areas, including Hainan island (Wu 1994), Taiwan (Wu et al. 2003), north Vietnam (Gagnepain 1916), and probably Sikkim and Bhutan (Grierson and Long 1987), northeast India (Banker 1876) and southeast Tibet (Li and Ni 1985) in the Himalayas.

Discussion and conclusion

Who are enemies and who are friends? This is an important question for both managers and ecologists to consider. The answer to this question can provide critical insights about the invasion success, the historical control, and potential future control of kudzu and other invasive species. We have identified many natural enemies of kudzu, which could offer potential agents of biological control in some cases. However, we stop short of suggesting any potentially effective biological control agent, because most natural enemies we have identified seem of little consequence to kudzu in the wild at large spatial scales.

We contend that, just as kudzu is both friend and foe of humans, humans are both the primary friend

and foe of kudzu. A conceptual model can illustrate the control mechanisms of kudzu abundance and distribution and the dual role of humans (Fig. 5). This model suggests: in its native areas, the human controls are strong, whereas natural biotic controls are numerous and weak. In contrast, several of those dominant mechanisms are missing in the introduced areas (Fig. 5). Some human dimensions in our model have been ignored in the previous studies of biological invasion.

While the case of kudzu provides a vivid illustration, the dual role of human control via multiple mechanisms is clearly not exclusive to kudzu. Our model may generate insights into understanding similar invasive species, for example, Japanese honeysuckle (*Lonicera japonica* Thunb.), Chinese tallow (*Triadica sebifera* (L.) Small), and Chinese tamarisk (*Tamarix chinensis* Lour.). These plant species have been harvested and planted in their native ranges for medicinal material, seed oil, firewood, or other economic purposes.

Introduced species extend from entirely wild species to totally domestic species that have lost the ability to survive in the wild. Kudzu represents a wild species with cultured strains, best described as a *quasi-wild species*. This kind of species is closely associated with human activities and has very high potential to become invasive and noxious, especially in human dominated landscapes. Some fishes have also experienced cultural selection through repeated cultivation, introduction, and reintroduction in native areas, including bighead carp (*Aristichthys nobilis* Richardson), silver carp (*Hypophthalmichthys molistrix* Valenciennes), grass carp (*Ctenopharyngodon idellus* Valenciennes), common carp (*Cyprinus carpio* L.), largemouth bass (*Micropterus salmonoides* Lacépède), mosquitofish (*Gambusia affinis* Baird et Girard), rainbow trout (*Oncorhynchus mykiss* Walbaum), and tilapia (*Oreochromis mossambicus* Peters). Their invasions to new ranges are often extremely successful (Heidinger 1976; Fuller et al. 1999; Chick and Pegg 2001; Garcia-Berthou et al. 2005). Many of the plants, fish, and mammals listed as the world's 100 worst invasive alien species can also be seen as quasi-wild species (Lowe et al. 2000). We suspect that, like kudzu, some strains of these species may have been culturally selected through cultivation, introduction, and escapes, and thus have developed fast growth rates, greater adaptability to harsh environments, and even resistance to natural enemies through their long histories. Some of these strains may be particularly well suited for frequently disturbed landscapes. We hypothesize that *species having experienced repeated introduction, cultivation, and escape back to wild are more likely to invade successfully*.

In the management of biological invasion, it is critical to integrate the ecological and human dimensions of coupled social-ecological systems (Fig. 5). However, human dimensions and their relationships with quasi-wild species can be very dynamic, making integrated management a great challenge. In particular, the roles of humans as friends or foes may switch over time and space. Biological invasion is often contingent upon cultural evolution and changing social values: Economic species may become noxious species, and vice versa. For example, the appeal of kudzu has undergone a boom and bust cycle in the United States. In the first half of last century, millions of dollars were spent to promote kudzu, and millions of dollars were contributed into the economy from kudzu production and use. Later, kudzu's status changed dramatically from "king", replacing cotton, to "green menace". It imposed hundreds of millions of dollars of economic costs annually, with perhaps millions more spent to control kudzu in recent years (Westbrooks 1998; Simberloff 2011). Social, economic, and technological transitions certainly played a key role in the transformation of kudzu from desired plant to weed (Kinbacher 2000). Failure to develop a commercially profitable harvest during the cultural transition might be a key to the kudzu problem. One of the best strategies to control this kind of invasive species may be to promote commercially profitable harvest (e.g., biofuel). Maintenance, tolerance, and promotion of cultural diversity in society may contribute to the control of invasive species as well.

In China, kudzu has been an important economic plant for more than 6,000 years and contributed much to the economy (even contributing to the dominance of a kingdom). During this long history, kudzu has not presented a major problem, perhaps because of the slow pace of ecosystem disturbance and relatively extensive utilization, such as the large-scale removal of roots and bark, which has never occurred in the United States. However, China is changing at an unprecedented scale, and the economic importance of

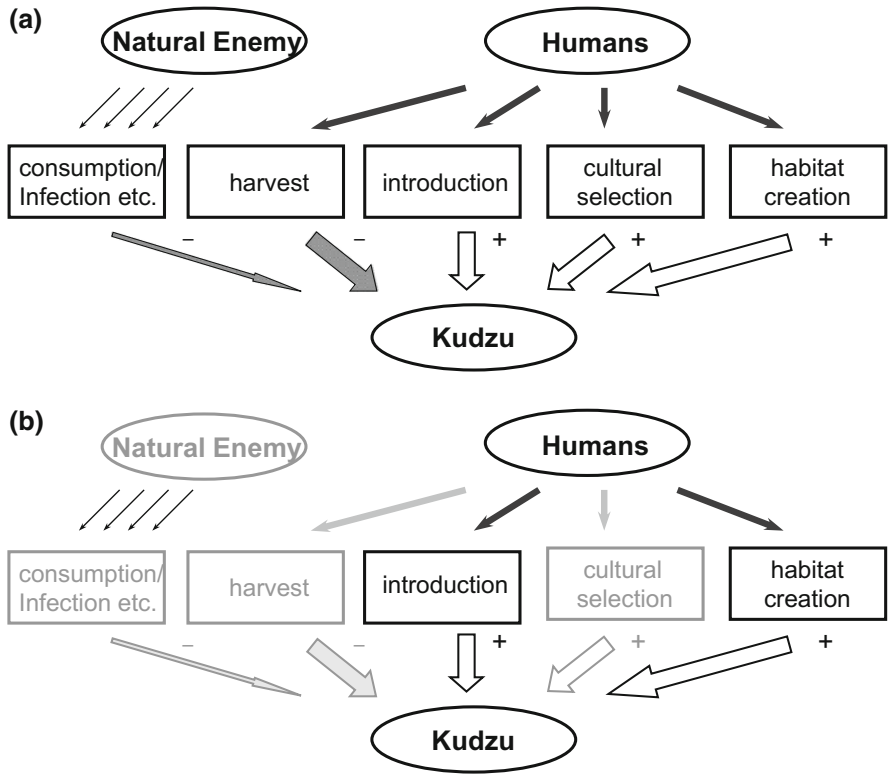

Fig. 5 The mechanisms that influence the abundance and distribution of kudzu: the human and natural dimensions. – and + indicate negative and positive influences. **a** In its native areas, human dimensions are strong, and natural biotic controls are numerous and weak. **b** In its introduced range in USA, several dominant mechanisms are missing (in *grey*)

kudzu appears to be declining as these rapid social, cultural, and economic changes alter the status of kudzu in society. This may lead to a transformation of kudzu in China from friend to foe of humans. Reports of rapid expansion of kudzu in many localities may be an early indication of this. Note that kudzu cultivation had led to local expansions and invasions into new habitats in China before (Guo and Ricklefs 2010). In some other countries of East Asia, similar situations may also take place.

In short, through the long history of human domestication of species and domination of the Earth's surface, humans have facilitated and controlled biological invasion via multiple mechanisms. Thus, it is important to understand both the natural and cultural histories of a species in its native areas before promoting or introducing the species for large scale economic use. For effective control and management, it is as important to understand the ecology and population dynamics of the invasive species as it is its relationships with humans (Guo 2006). If a species, such as kudzu, has a history of repeated cultivation and (re)-introduction and thus a demonstrated ability to adapt to a variety of conditions, it may have a high potential to become a successful invader. It is possible that plants introduced to exotic regions such as the United States have been domesticated by humans for fast growth and maximum production and are not from natural populations in native habitats. Great caution should be exercised in considering introduction of such plants. It is also critical to keep in mind that human activities make important contributions to the noxiousness of invasive species. High rates of habitat alteration, disturbance after industrialization, transportation, and dynamic agricultural and silvicultural practices contributed much to the success of quasi-wild exotic species. The example of kudzu provides vivid illustration of the complex and changing relationships between invasive species and humans over time and space. Similar dynamic relationships exist for many other species. A broader perspective of the human dimensions and the role of quasi wild species may contribute much to the science and management of biotic invasions.

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