Roles of Human Activity in Biological Invasion Threatening Forest Biodiversity

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Abstract

Humans move many species from their native ranges to places all over Earth, both deliberately and inadvertently. Where those species establish new, self-maintaining populations, this movement leads to human-caused biological invasion. Human-caused biological invasions have become so widespread as to threaten Earth's biota. Biological invasions thus represent an important component of anthropogenic global change.

In Japan, Pinewood Nematode (PWN), *Bursapherenchus xylophilus*, is one of the most serious exotic invaders that caused damage to forests. The major pine species in Japan, *Pinus densiflora* and *P. thunbergii*, have suffered heavy mortality for several decades. Recent genetic studies of the systematics of PWN found that PWN in Japan had possibly been introduced from the USA and that PWN in Asian countries was derived from the same strain. The spreads of the PWN show a typical pattern of biological invasion described by stratified diffusion: i.e. combination of diffusions with long-distance dispersals. In Ishikawa, most of the Japanese black pine plantations in the coastal area were badly damaged by PWN.

Another serious pest that kills living tree cropped up in Japan. Deciduous oak dieback has spread into new west coastal areas for these ten years. An unidentified ambrosia fungus, genus *Raffaelea*, is the causal agent in oak dieback. A symbiotic ambrosia beetle, *Platypus quercivorus* is the vector of this fungus. The beetles realized the highest reproductive success on *Quercus crispula* but showed the least preference for this species, and the mortality of infested trees were highest. Spread of oak dieback showed concentric pattern at a regional level and a pattern of stratified diffusion at a local level. From these results, we speculate that the *Raffaelea* sp. and *P. quercivorus* were not exotic pests but invasive ones that had been introduced from other warmer regions of Japan. Only *Q. crispula* have suffered great mortality because of a lack of coevolutionary processes among tree-fungus-insect. We suggest that future global warming will accelerate the overlapping of the *P. quercivorus* and *Q. crispula* distributions and that oak dieback on *Q. crispula* in Japan will become more prevalent. Tree composition in the deciduous broad-leaved forest in Japan will be greatly altered, which results in the decreased biodiversity in forests.

1. Introduction

Humans move many species from their native ranges to places all over Earth, both deliberately and inadvertently. Where those species establish new, self-maintaining populations, this movement leads to human-caused biological invasion. Human-caused biological invasions have become so widespread as to threaten Earth's biota. Biological invasions thus represent an important component of anthropogenic global change. Biological invasion have caused forest decline in many places in the world: the chestnut blight, gypsy moth in the North America, the Dutch elm disease in Europe. In the North America, it is believed that the decreased biodiversity in deciduous broad-leaved forests by the lost of chestnut trees by the chestnut blight promoted and accelerated the gypsy moth outbreak. In Japan, pine tree mortality caused by the pinewood nematode (PWN), *B. xylophilus* and deciduous oak dieback caused by the unidentified ambrosia fungus belonging to the genus *Raffaelea* have been prevalent. Both are thought no to be native pests. In this paper, we discuss the roles of human activity in the spreads of these invasive pests in relation to their spreading pattern.

2. Spreading Pattern of Invasive Species

2.1 Diffusion: Muskrats in Europe

The muskrat, which is a species native to North America, was brought to Europe for fur breeding. In 1905, five muskrats escaped from a farm located near Prague in Czech. They started to spread and reproduce, inhabiting the entire European continent in the short period of 50 years. Figure 1 gives the contours the range of spread [1, 25]. Such a pattern of concentric circles is one of the typical patterns of biological invasion, especially for species that cannot fly or those of which dispersal ability is limited.

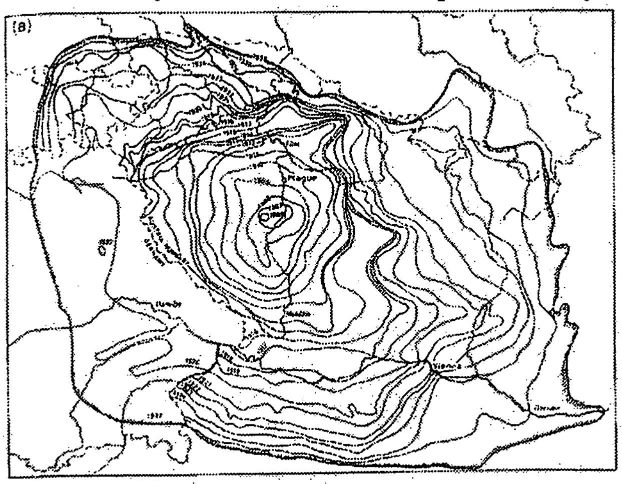

Fig. 1 Range expansion of muskrat in Europe from 1905 to 1927. [1].

2.2 Stratified Diffusion: House Finch in North America

The House Finch was not native in the North America but was introduced from Europe [18]. The House Finch was released in 1940s in western Long Island, New York. Figure 2 illustrates the winter range expansion for several selected time intervals. The spatial change of the invaded area indicates that the House Finch range expansion involved two dispersal processes: neighborhood diffusion and jump dispersal. From the boundary of the central core area, the range reveals a gradual extension. On the other hand, a small satellite area separated from the core range was occasionally generated by jump dispersals of a small outlaying population. The sizes of these satellite areas increase in successive years, until they are absorbed by the main part of the range. This pattern of range expansion, a combination of two dispersal processes, neighborhood diffusion and jump dispersal, is called stratified diffusion, which is also the typical spreading pattern of invasive species. The jump distance from the nearest border of the core range to a satellite area is determined by the dispersal ability of the species.

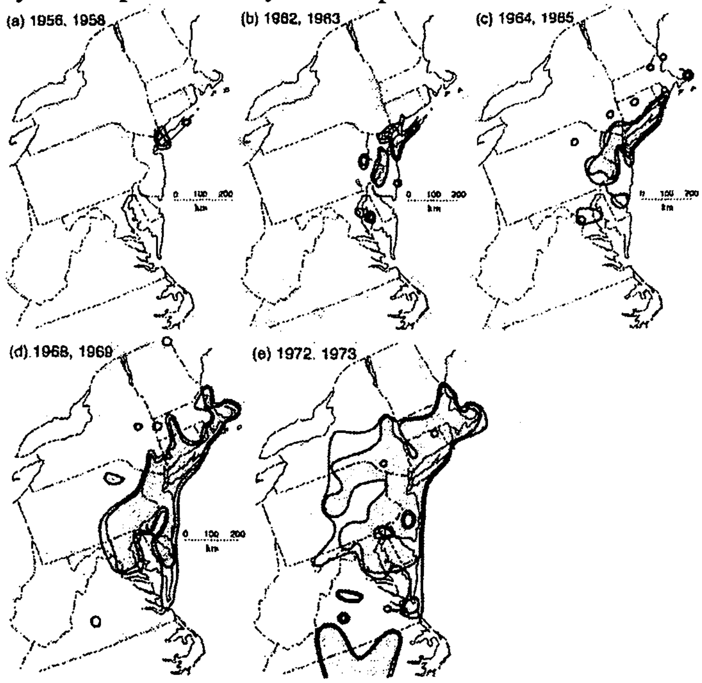

Fig. 2 Expansion of winter range of the House Finch in eastern North America for several selected time intervals [21].

3. Pine Wilt Disease

3.1 Pine Wilt Disease Caused by Pinewood Nematode

The major pine species in Japan, *P. densiflora* and *P. thunbergii*, have suffered heavy mortality for several decades [14]. In the early 1970's, the causal disease agent was found to be the pinewood nematode (PWN), *B. xylophilus* [15]. The Japanese pine sawyer (JPS), *Monochamus alternatus* (Coleoptera: Cerambycidae) is the principle vector insect in Japan. The existence of the nematode was reported in the United States, where only exotic pine plantings were severely damaged suggesting that the nematode was native in US. Recent genetic studies of the systematics of PWN found that PWN in Japan had possibly been introduced from the USA and that PWN in Asian countries was derived from the same strain [7].

3.2 Spreading Pattern of PWD at a Nation Level

Severe pine damage that was recorded at Nagasaki City in Kyushu Island from 1905 is speculated to be the first record of PWD in Japan [14]. However, because PWN was proved to be the causal disease agent of PWD in early 1970s, the detailed data of expanding range of PWD were not available before 1970. In Tohoku district northern part of the main island of Japan, the PWN invasion was recorded minutely at municipality level because PWN first invaded there in 1975, which is after PWN was proved to be the causal agent of PWD. In the Tohoku district, northern part of the main island of Japan, pine wilt disease (PWD) was first found in Ishinomaki in Miyagi Prefecture 1975 (Fig. 3a), which is >200 km apart from the nearest edge of its expanding front. The distance is much greater than the dispersal ability of JPS, a vector of PWN: Annual rate of range expansion by neighborhood diffusion is reported to be several kilometers. According to the probability function vs. distance of JPS dispersal [26], >95% of JPS dispersals were <2km. It is believed that pine logs infested by PWN were introduced to the place by human transportation. At present, PWD has invaded the northern part of Akita Prefecture and the middle part of Iwate Prefecture, but it has not been found in Aomori Prefecture, the northernmost prefecture in the main island of Japan. Recently, rate of expansion is slowing down because PWD is expanding into cooler regions. It is well known that emperature limits PWD expansion in various pathways. Therefore, we speculate that future global warming will help expansion of PWD to cooler regions, such as Hokkaido.

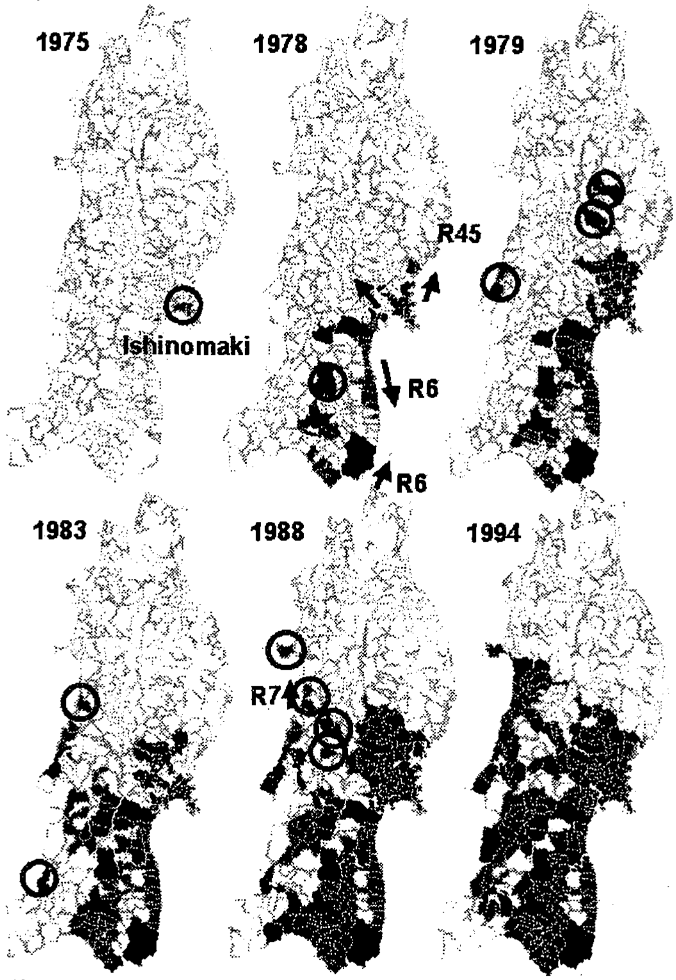

Fig. 3 Range expansion of the pine wilt disease caused by pinewood nematode in Tohoku Distrikut in northern Japan for several selected time intervals. A circle indicate new satellite populations separated from the core range.

In Tohoku District, the PWD spreads showed a typical pattern of stratified diffusion, a combination of jump dispersals and neighborhood diffusion (Fig. 3). Regarding neighborhood diffusion, PWD spread along big roads, which indicates that human transportation may also play roles in PWD at smaller scales. In the late 1970s, PWD spread from Ishinomaki along Routes 6 and 46. In 1978, new invasion started in the southern edge of Tohoku District, which is supposed to be caused by neighborhood diffusion of southern populations in Kanto District. In 1977, 1979, 1983, 1984, 1985, 1986, 1988, new satellite population separated from the core range was generated by jump dispersals, which is supposed to be caused by human activity because the distance from the nearest border of the core range to a satellite area is greater than the dispersal ability of JPS.

4. Oak Dieback

4.1 Oak Dieback in the West Coastal Area of the Main Island of Japan

Deciduous oak dieback in Japan has been known since the 1930s but in the last 10 years epidemics have intensified and spread into new west coastal areas [6]. An unidentified ambrosia fungus, genus *Raffaelea*, is the causal agent in oak dieback [Takanori KUBONO Pers. Comm.]. A symbiotic ambrosia beetle, *Platypus quercivorus* (Murayama) (Col.: Platypodidae) is the vector of this fungus. Although related beetles generally attack stressed trees, *P. quercivorus* attacks and kills vigorous trees. This is the first example of an ambrosia fungus carried by an ambrosia beetle that kills vigorous trees [4]. Although 45 species among 27 genera in 17 families of woody plants have been recorded as host plants of *P. quercivorus* [5, 19, 20, 22], woody plants belonging to the Fagaceae family are considered as an essential host of *P. quercivorus* because the beetle attack density was high on trees of the Fagaceae family but low on trees belonging to other families [5, 22]. There are many records of *P. quercivorus* outbreaks in evergreen oak stands in Japan, but few evergreen oak trees were killed by this beetle even though many entry holes were found on the trunk surface [17, 22, 23, 24]. In Ishikawa, the mortality was ca. 40% for *Quercus crispula* but low for other concurrent Fagaceae species even though each species received a similar number of beetle attacks [10, 11]. Trees other than *Q. crispula* proved to be resistant to *Raffaelea* sp. The beetles showed the least preference for *Q. crispula* but they had their highest reproductive success in this species [11, 13]. Since these beetles can realize a higher reproduction rate on *Q. crispula*, the beetles can spread more rapidly in stands with a high composition of *Q. crispula* [11]. This situation, similar to an exotic pest introduced into a new environment, results in higher insect performance than on the original host. Among the Fagaceae species found in our research plots in Ishikawa, *Q. cripsula* is distributed in the coolest places [16]. Platypodids are abundant in tropical and subtropical regions [8, 9]. *Platypus quercivorus* is also distributed in S to SE Asia, Taiwan, and the Japanese Archipelago [19, 20]. Japan is the northernmost region of the *P. quercivorus* distribution. Oak dieback occurs in the northern/high margins of the *P. quercivorus* distribution and in the southern/low margins of *Q. crispula* distribution. Oaks other than *Q. cripsula* are resistant to *Raffaelea* sp. probably because a stable relationship has been formed among these tree species, the fungus, and the insect in a long evolutionary process. *Quercus crispula* was probably left out of the coevolution [11]. *P. quercivorus* was native in Japan but does not seem to be native in the places where the oak dieback is prevalent. The insect was probably introduced from the Kyushu Island, southernmost main island of Japan, and/or foreign countries by transportation of logs. We speculate that future global warming will accelerate the overlapping of the *P. quercivorus* and *Q. crispula* distributions, and that the dieback of *Q. crispula* will become more prevalent.

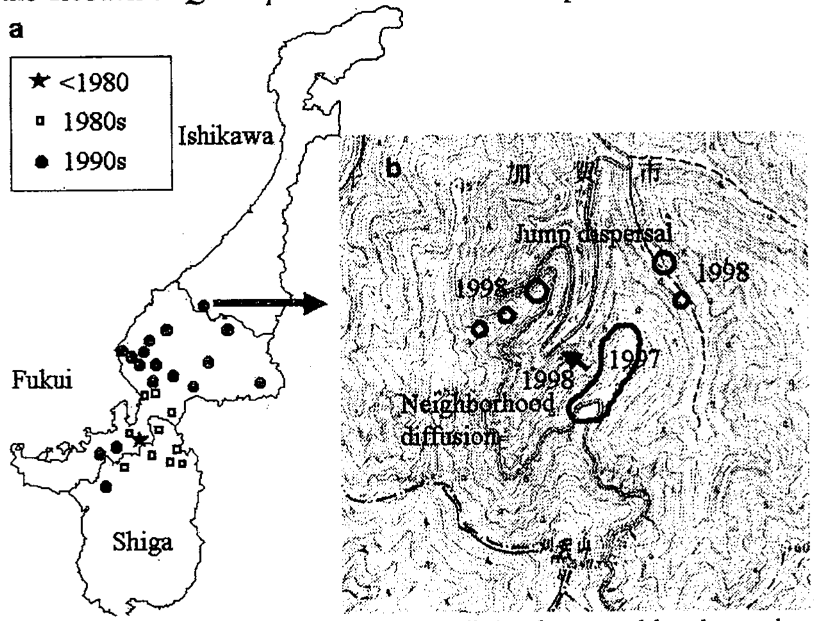

Fig. 4 Range expansion of the oak dieback caused by the ambrosia fungus-ambrosia beetle relationship.
a: a nation-level expansion focused on the part of Ishikawa, Fukui and Shiga Prefectures.
b: a local-level expansion in Mt. Kariyasu located on the border of Ishikawa and Fukui (modified figures in Kamata *et al.* [12]).

4.2 Spreading Pattern of Oak Dieback at Three Different Scales

Kamata *et al.* [12] summarized the spreading pattern of the oak dieback (Fig. 4). At a nation level, the spreading pattern of the range of oak dieback expanded concentrically from the source population (Fig. 4a), which is a similar pattern as shown in the section 2.1 in this paper. At a local level, oak dieback spread by a combination of jump dispersal and neighborhood diffusion. It first spread along a mountain ridge because *P. quercivorus* aggregates near mountain ridge or upper edge facing roads (Fig. 4b). These spreading patterns of diffusion and stratified diffusion support the hypothesis that the pathogen is not native in these places. At a stand level, the incidence of the dieback spread downwards along slopes from the ridge

4.3 Human Activity and the Spreads of Oak Dieback

In Fig. 3a, the source populations were likely to be introduced to the places by transportation of infested logs by human. However, transportation by human does not seem to contribute to a nationwide-scale of range expansion from the source populations because a nationwide-scale of oak-dieback expansion showed a pattern of concentric circles rather than stratified diffusion. On the other hand, regarding a local-level analysis, a pattern of stratified diffusion was recognized. At this local scale, jump dispersal is mainly caused by insect flight.

Because adult beetles tend to move upward along slopes and show positive phototaxis, the highest concentration of flying beetles usually occurs at the forest edge or at the edge of forest gaps [2, 3]. Recently, the Japanese Forestry Agency promoted cutting and clearing the understory of natural broad-leaved forests, which makes the inner forest brighter. Igeta et al.

[3] pointed out the possibility that *P. quercivorus* will become highly concentrated in the brighter treated stands and attack healthy trees there.

5. Conclusions

In Ishikawa, two invasive forest pests, PWD and oak dieback, are epidemic and threaten biodiversity in forests. Human activities are responsible for the epidemics. Transportation of infested logs was crucial for invasion of the source populations and greatly helped their range expansion. In addition to this, silvicultural treatment such as cutting and clearing the understory sometimes promoted the forest damage by these pests. We speculate that future global warming will accelerate expansion of both PWD and oak dieback to cooler regions.

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