Path-finding algorithm as a dispersal assessment method for invasive species with human-vectored long-distance dispersal event

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Abstract

Aim: An assessment method that can precisely represent human-vectored long-distance dispersals (HVLDD) is currently in need for the effective management of invasive species. Here, we focussed on HVLDD happening along roads and proposed a path-finding algorithm as a more precise dispersal assessment tool than the most widely used Euclidean distance method by using pine wilt disease (PWD) as a case study.

Location: Busan Metropolitan City, Republic of Korea.

Methods: A path-finding algorithm, which calculates distances by considering the spatial distribution of road networks, was tested for its effectiveness in estimating dispersal distances of HVLDD events. To this end, annual HVLDD cases were classified from entire PWD occurrence data from 2016 to 2019, and their dispersal distances were calculated using the path-finding algorithm and the Euclidean distance method. We constructed potential dispersal ranges based on the occurrence points in 2016, 2017 and 2018 using the respective year’s mean dispersal distance for both methods, and their performances in accounting for each subsequent year’s HVLDD cases were compared to determine which method calculated more precise distances. The information on which road class contributed more to dispersal occurrences and distances was analysed as well using the proposed algorithm.

Results: The potential dispersal ranges of the path-finding algorithm accounted for more future anthropogenic infection cases than the ones that used the Euclidean distance method, validating its higher functionality. It also revealed that most HVLDDs started and ended on small roads, and large roads constituted the majority of the total dispersal length.

Main conclusions: The path-finding algorithm has proven to be a more effective dispersal assessment method for HVLDD events. It can help design effective control strategies. Thus, we encourage using the path-finding algorithm for the dispersal assessment of invasive species that move along road networks, and for the development of more powerful HVLDD prediction models.
INTRODUCTION

Among general traits of invasive species that make them successful invaders—high dispersal ability, fast growth, rapid reproduction and generalist feeder (Stohlgren & Schnase, 2005), high dispersal ability is the main factor that leads to their broad expansion by initiating new populations in unvisited sites (Travis & Dytham, 2002). Dispersal of invasive species often consists of two components: short-distance dispersal (SDD) and long-distance dispersal (LDD). Even though SDD accounts for the majority of dispersal cases and LDD rarely happens (Smith et al., 2018; Trakhtenbrot et al., 2005), LDD is the key factor that contributes to the high dispersal ability of invasive species. It has a disproportionately high influence on species expansion rate as it results in further and faster dispersal than SDD (David et al., 2014; Jordano, 2017).

With the growth of international and intercity trade, humans have started to serve as a generalized LDD vector of invasive species (Gippet et al., 2019; Nathan, 2006). The introduction of invasive species to new distant sites by anthropogenic factors is referred to as human-vectorized long-distance dispersal (HVLDD). HVLDD occurs via various forms, such as the attachment of seeds to clothes and vehicles, and translocation of species via road networks, skylakes and maritime routes (Bullock et al., 2018). In this manner, many exotic and invasive species have been introduced to new regions where they cannot reach on their own at global and regional scales (Gippet et al., 2019; Turner et al., 2021).

Invasive species inflict substantial ecological and economic damage and disrupt the fundamental structure of the ecosystem (Davis & Thompson, 2000; Ehrenfeld, 2010). Therefore, it is imperative to control their dispersal to minimize further damage. Detailed knowledge of the dispersal patterns of species can assist in adopting more effective management strategies. Hence, a large number of studies have been conducted to fully understand how invasive species disperse by analysing their dispersal patterns (Chuong et al., 2016; McQuaid & Phillips, 2000; Rauschert et al., 2017; Robinet et al., 2009; Suarez et al., 2001). However, anthropogenic dispersals have mostly been neglected in studies because of their low occurrence ratio despite of their significance (Auffret et al., 2014).

Generally, dispersal patterns are analysed by investigating the dispersal distances of every dispersal event (Westcott et al., 2008; Etherington et al., 2014; Pierre et al., 2017). They are typically represented using descriptive statistics or as a dispersal kernel, which shows the probability of dispersal over a range of distances (Nathan, 2008; Lemke et al., 2019; Rogers et al., 2019). In this respect, the distance measuring method becomes the key factor that determines the accuracy of the identified dispersal pattern. To date, most of the research have used linear distance from dispersal source to destination to estimate dispersal distances (Hereafter referred to as Euclidean distance method; Cayuela et al., 2019; Nathan et al., 2002; Pyšek & Hulme, 2005). However, it could often be misleading for landscape-scaled dispersal events especially when the dispersal pathway and its structure in the matrix are explicitly known. The Euclidean distance disregards the existence of dispersal pathway and measures the dispersal distance by linearly connecting the source and destination locations. This simplistic view toward the landscape would result in an inaccurate estimation of dispersal distances and, ultimately, dispersal patterns (Lookingbill et al., 2010; Murphy & Lovett-Doust, 2004; Szabó et al., 2012). Therefore, there is a need to develop a more suitable method for assessing HVLDD patterns (Auffret et al., 2014; Nathan et al., 2003).

A growing body of research has addressed that the matrix constituting strongly influences species movement among patches (Adriaensen et al., 2003; Bakker & Van Vuren, 2004; Brown et al., 2017; Ricketts, 2001; Schadt et al., 2002). For precise estimation of dispersal patterns, the focus should be placed on incorporating how the moving entities—either individuals or their vectors—actually move in the matrix in distance measurement (Trakhtenbrot et al., 2005). Integrating the spatial dynamics of the moving entities into dispersal assessment results in a better understanding of dispersal patterns and even future prediction (Auffret et al., 2014; Buchan & Padilla, 1999).

The objective of the present study is to develop a novel method that can precisely estimate the dispersal patterns of HVLDD events of invasive species. In this study, we focussed on the anthropogenic dispersal that occurs by cars, regardless of whether it happened via attachment or transportation. Other modes of HVLDD are beyond the scope of this study. Then, vehicles moving on roads are the vectors that transport the invasive species, and the road network is their dispersal pathway (Bullock et al., 2018; Hodkinson & Thompson, 1997). To fully imitate how vehicles move on a road network, we proposed a path-finding algorithm as a precise way to quantify the pattern of the HVLDD. Unlike the Euclidean distance method, the proposed algorithm is advantageous as it considers the spatial distribution of roads in the matrix and calculates the path distance following the road network.

Here, we attempted to validate the path-finding algorithm as a more precise and effective method for investigating HVLDD along roads. To this end, the path-finding algorithm was compared with the Euclidean distance method by using pinewood nematodes (PWN; Bursaphelenchus xylophilus) in Busan Metropolitan City, the Republic of Korea (ROK) as a case study. We set two criteria for the comparison: functionality and applicability. Functionality refers to the ability to estimate more accurate dispersal patterns. To determine which method achieves more precise patterns, we constructed future dispersal ranges using each dispersal pattern result and compared their performances in explaining future HVLDD points, based on a
real dataset. Applicability identifies whether the method can offer additional information other than dispersal patterns that can assist in making more powerful management strategies. To check higher applicability of the path-finding algorithm, we analysed the most frequently used sequence of road classes and which class contributed the most to the total dispersal distance. Based on these two results, we discussed whether the path-finding algorithm is suitable for assessing dispersal patterns of HVLDD events of invasive species.

2 | METHODS

2.1 | Study species and study area

Pine wilt disease (PWD) is a pine tree illness caused by the PWN, which is native to North America (Kiritani & Morimoto, 2004). Currently, PWN are established internationally and are the most lethal forest pests in southern Europe and Asia; they can affect multiple species in several genera including *Pinus*, *Abies* and *Larix* (David et al., 2014; Hirata et al., 2017; Rodrigues, 2008). In its native region (North America), the nematodes are only secondary pathogens that do not fatally damage the host tree. However, they have inflicted substantial ecosystem loss in non-native sites by causing the deaths of millions of indigenous pine trees via tracheid cavitation (Akbulut & Stamps, 2012; David et al., 2014).

PWN require pine sawyers, primarily from the genus *Monochamus*, as their dispersal vector (Linit, 1988). The nematodes are transmitted to healthy pine trees through feeding and oviposition wounds made by nematode-infected beetles (Linit, 1990). In addition, pine sawyers in the breeding season (summer) tend to lay their eggs under the bark of dead or weakened trees, indicating the increased chance to oviposit on the trees that are already infected with the nematodes (Akbulut & Stamps, 2012). When these eggs reach the pupal stage after the overwintering period, PWN enter the insects for transmission to new tree hosts (Akbulut & Stamps, 2012). This leads to an increase in the population of nematode-infected pine sawyers in the spring of the subsequent year.

The dispersal dynamics of PWD comprise SDD and LDD. SDD, which accounts for the majority of dispersal cases, happens through beetle jumps or flies. As beetles use their wings to move, they remain within a certain range from the dispersal source in accordance with their flying capacity. In contrast, LDD is rather a passive dispersal event of pine sawyers because they are moved to another region by an anthropogenic factor—vehicles. Many studies have clearly stated that the HVLDD of PWD occurs through human activities and movements (Choi et al., 2017; Robinet et al., 2009; Sousa et al., 2011; Yoshimura et al., 1999). It is known that HVLDD has two typical modes: log transportation and beetle hitchhiking (de la Fuente et al., 2018; Robinet et al., 2011). As for log transportation, it happens when logs containing nematode-infected pupae are displaced to another region, and the pupae emerge as adult beetles. It can also happen when adult pine sawyers are transported together within log packaging. In addition, the beetle hitchhiking occurs when beetles accidentally land on or get inside a vehicle that is about to depart soon and get off in distant sites. In any case, vehicles are the vectors that move PWN inhabiting pine sawyers via road networks.

Even though the role of anthropogenic factors in the LDD of PWD has become evident, the efforts on understanding the HVLDD patterns have been lacking. Most studies have simply ended up emphasizing the importance of understanding the effect of anthropogenic factors on PWD dispersal. Furthermore, existing studies that measured dispersal patterns of PWD have only used the Euclidean distance method (Choi et al., 2017; Park et al., 2018). Linear distances are meaningful in the estimation of short-distance dispersal (SDD) events that occur within a forest patch by a beetle fly. However, this does not hold true for HVLDD events of PWD because it is explicitly known that dispersals happen through road networks and are highly likely to be nonlinear (Murphy & Lovett-Doust, 2004).

To investigate the performance of the path-finding algorithm as an assessment method, we selected Busan Metropolitan City, the Republic of Korea as our study area (Figure 1a). Busan was the first invasion of the PWN occurred in the ROK in 1988 (Choi et al., 2017). As more than 30 years have passed since the first outbreak of PWD, active HVLDD events have occurred in the region. Cases of PWD infection in distant forests have constantly been reported. In this sense, Busan Metropolitan City provided a great opportunity to survey the dispersal patterns of HVLDD events on a regional scale. In this region, PWN are carried by a beetle from the genus *Monochamus* (*M. alternatus*) and can infect multiple species of the genus *Pinus* (Kwon et al., 2018).

2.2 | Data

The PWD occurrence points in Busan were obtained from the National PWD Occurrence Point Dataset for four consecutive years from 2016 to 2019. The national data were provided by the National Institute of Forest Science, and they were created based on regular field (in situ) monitoring and laboratory analysis. Approximately 30 PWD observation teams—with at least one forestry professional in each team—monitored Busan forests for four years. Forest areas were classified into three categories: areas with and without a recent history of infection, and areas with high conservation value. As for the forests that have been infected with PWD within a year, the surrounding area within a 2-km radius from every infection point was intensively monitored with regular visits by foot. Highly valuable pine forests that need protection were also monitored in a similar way. Forests that have been free from PWD, far from infected sites, and have low conservation values at the same time were monitored following roads based on the established fact that long-distance dispersals of PWD happen through road networks. Along with these monitoring efforts, aerial inspections and reports of citizens were also used to locate the possible infected stands. When the suspected trees were found, an observation team surveyed the area and sampled branches of the vegetation. Those samples were then sent to the laboratory.
to confirm their PWD infection. The location of trees that were diagnosed as infected from laboratory analysis was recorded as occurrence points. The annual data included the PWD locations that occurred from the summer of the corresponding year to the spring of the following year.

The path-finding algorithm is only suitable for estimating the dispersal distance of HVLDD events. Therefore, only occurrence points that happened through HVLDD events (hereafter, HVLDD points) should be included in the analysis. To this end, LDD points were classified from entire PWD points. We reviewed several studies that estimated the maximum flying capacity of the vector beetle to find the optimum threshold value that distinguishes SDD from LDD. However, there has been no scholarly consensus on the distance that the beetles can naturally disperse to. Furthermore, many studies have measured the dispersal capacity by including anthropogenic dispersal cases in their analysis. Therefore, we decided to use 2 km as the flying capacity of vector beetle based on the composite distribution kernel results of Takasu et al. (2000) who used the mark and recapture data provided by Shibata (1986) and Fujioka (1993). This is also supported by another dispersal distance study conducted in the ROK, which reported that the average dispersal distance of M. alternatus was 0.38 km, and only 1% of beetles had dispersal distance >2 km (Choi et al., 2017). We assumed that this 1% represents HVLDD events considering the high coverage rate of forests in ROK (64%) and low motivation of beetles to fly when they have a sufficient food supply (Zhang et al., 2020).

Classifying LDD using a 2-km threshold value was not sufficient, and the data needed further filtering. This is because when a vector settles in a new habitat after transportation by anthropogenic factors, it can cause several infection cases by making intermittent flights between multiple trees during summer. Leaving these SDD events in the analysis data could result in inaccurate identification of SDD events as HVLDD events, which could result in an erroneous dispersal pattern. This was what happened in Tae-jong Mountain in our study area, where the cliff-sided pine forests were found largely infested with PWD. The region has been overlooked by observation teams because of its inaccessible geographical features. The region was lately discovered in 2018, even though the spread started several years prior. This led to an abrupt recording of approximately 250 occurrence points in 2018 as HVLDD events due to active SDD cases during the undocumented 2–3 years. Therefore, data correction that filters out SDD should be performed. To do this, we clustered the classified HVLDD points using 100 m as a threshold value as most natural PWD dispersal in a forest (87.9%) remains within 100 m (Ma et al., 2018). Consequently, low-grade roads only included cul-de-sac roads, forest roads and one-lane local roads, whereas

![Figure 1](image-url)
high-grade roads included local roads with at least two lanes and the rest of the upper-ranked roads (Figure 1a). 

Topology errors in road networks can cause serious connection problems in the analysis. Therefore, a topology-cleaning procedure was conducted before the implementation of the path-finding algorithm. Three types of topology errors (undershoot, overshoot and missing intersection) were cleaned using topology-cleaning tools in GRASS 7.8.3 (Lu et al., 2018; Maraş et al., 2010).

2.3 | Path-finding algorithm: convenient path algorithm

Choosing the most suitable path-finding algorithm for HVLDD pattern analysis is important because different algorithms produce different routes. Assuming that every road has the same level of importance in networks is highly inappropriate considering that road traffic volume and road size can affect the occurrence probability of HVLDD events. To prevent the generation of paths that find the shortest route with little consideration of the abovementioned factors, we decided to choose an algorithm among hierarchical-based path-finding algorithms.

A convenient path algorithm proposed by Park et al. (2001) was used. This reflects the reality in which drivers prefer a shorter yet more convenient route (Sung et al., 2006). A convenient path is calculated by minimizing the use of low-grade roads, such as forest roads, and maximizing high-grade roads while using maximally two road-level transition points (Shapiro et al., 1992). In the original algorithm, a parameter defined the extent to which the driver can tolerate the difference between the linear shortest path and the convenient path. However, in the present study, we assumed that the drivers prioritized finding large roads unless the general shortest path between the origin and destination only used low-grade roads.

To measure the dispersal distances from the dispersal source to destination points (s and d in Figure 1b), dispersal entry and exit points on road networks must be identified first. They were designated by finding the nearest road vertices from s and d respectively. Depending on the road classes on which the entry and exit points are located, the dispersal could start and end in either low-grade or high-grade roads. There are six possible combinations of road classes used for dispersals, which are hereafter referred to as route types. However, a type that has a high-low-high combination was disregarded in the analysis due to its improbability considering that the entire high-grade road networks are interconnected with each other. This resulted in five dispersal route types considered in the analysis (Figure 1c).

Regardless of route type, the dispersal route from entry to exit was generated by minimizing the length of the low-grade roads. This was done by finding the nearest transition point from low- to high-grade roads on both sides (entry–u and exit–v in Figure 1b), thus minimizing the total length of the low-grade roads. For example, in route type 4, where dispersal starts and ends on low-grade roads, drivers find the shortest path to the nearest transition point to the high-grade road (u). Similarly, they select the latest transition point (v) when entering the low-grade roads to reach the destination. This ultimately maximizes the dispersal distance on large roads, thereby minimizing the travel distance on small roads. The shortest paths in each component were calculated using the Dijkstra algorithm ( Cormen et al., 2001).

2.4 | Human-vector long-distance dispersal assessment

Without the knowledge of the true origin of dispersal events, dispersal sources should be determined a priori. Generally, every occurrence point from the previous year is regarded as a potential source, and the point that is nearest to each destination point is selected as a dispersal source (Choi et al., 2017; Suarez et al., 2001). For this reason, applying the path-finding algorithm and the Euclidean distance method to the same data produces disparate patterns owing to the difference in how they measure the dispersal distances. The Euclidean distance method selects a source point that is linearly nearest to each HVLDD point. In contrast, the path-finding algorithm uses path distance as a standard, considering the road structure. This leads to the different source points being selected for the same HVLDD points and ultimately much more different dispersal pattern results.

When finding dispersal sources, we regarded occurrence points from all the available previous years as potential dispersal sources for PWD to account for the presence of asymptomatic trees. Asymptomatic trees do not show any symptoms even when infested with the nematodes and remain latent for up to two to three years ( Futai, 2003). Due to these characteristics, they evade annual control measures even though they occur adjacent to symptomatic trees. To prevent misclassification of asymptomatic trees that became symptomatic after several years as LDD invasions, occurrence points from all available previous years were accumulated and used as potential dispersal sources. For example, to analyse the dispersal patterns of 2018 and 2019, occurrence points from 2016 to 2017 and from 2016 to 2018 were accumulated and used as source candidates.

We compared the HVLDD patterns obtained using the path-finding algorithm and Euclidean distance method for the three years of dispersal events: 2016–2017, 2017–2018 and 2018–2019. To determine which method more precisely estimated the dispersal distances and, ultimately, patterns, we compared the functionality of the two methods. To calculate the functionality, three potential dispersal ranges were constructed based on the occurrence points in 2016, 2017 and 2018 using the mean dispersal distance of the respective years calculated in the prior step for each method. Thereafter, the number of actual HVLDD points of the subsequent year that fell within the range was calculated every year. This number of predicted points was used as an indicator for each method's
functionality and interpreted as an amount of the future HVLDD events that each method was able to account for. By comparing the percentage of how much each algorithm was able to explain among the entire HVLDD events, we determined which method was superior in evaluating HVLDD patterns. It is worth noting that the mean dispersal distance was selected as a representative value of the entire dispersal patterns. If we have used a bigger value, the number of unpredicted points would have been reduced, but still, the presence of unpredicted points would be inevitable. Therefore, the difference in the amount of HVLDD events that can be explained between the two methods was used as a ground for decision, not the exact number of points each algorithm was able or not able to predict.

The Euclidean distance method and path-finding algorithm treat landscape matrix differently, resulting in different characteristics when future dispersal ranges are calculated. The Euclidean distance method treats the space around the occurrence point as a homogeneous environment where every direction has equal importance. Consequently, a perfectly circular dispersal range is created. In contrast, the path-finding algorithm assumes a heterogeneous landscape by considering a dispersal pathway, the road network, embedded in the matrix. This results in an amorphous dispersal range. Therefore, dispersal ranges of the Euclidean distance method were computed simply by buffering every dispersal source with the mean dispersal distance. In contrast, for the path-finding algorithm, every road connected within the mean dispersal distance from source points was selected and then buffered using the maximum flying distance of vector beetles from roads after anthropogenic dispersal events. Distances from HVLDD points to the nearest roads were measured, and the maximum value was used as a buffer distance value. The general maximum dispersal ability of 2 km used in HVLDD classification was not used for this case as the flying ability of vectors directly after the anthropogenic introduction event would include distinct characteristics, due to travel stress and environmental changes. Furthermore, the 2-km value was based on the dispersal distances between the source tree and the sink tree, not between the roads and the infected tree.

Additional information about dispersals that assessment tools can provide other than dispersal distances can aid in designing more effective management plans. In this respect, our second objective, applicability, is also an important supplementary factor that must be examined to determine a more desirable assessment method. The path-finding algorithm can provide us with information that is not available in the Euclidean distance method because it exploits the hierarchical structure of the road network. Along with the total dispersal distance, the algorithm also stores the route type used for the dispersal. Based on this information, we analysed which route type was most favourably used in HVLDD dispersal. A more in-depth analysis of the contribution of each road class to the total dispersal distance was also conducted using route types included both high- and low-grade road classes: route types 2, 3 and 4.

All data preparation and analysis were performed using the “igraph” package version 1.2.5 (Csardi & Nepusz, 2006) and “tidygraph” package version 1.2.0 (Pedersen, 2020) in R version 3.6.1 (R Core Team, 2019).

3 | RESULTS

3.1 | Pine wilt disease occurrences in Busan Metropolitan City

Between 2016 and 2019, the total number of PWD occurrences in Busan Metropolitan City gradually decreased (Figure 2). The number of outbreaks in 2016 exceeded 10,000 cases, which was the highest occurrence during the study period. In 2017, it decreased sharply to 5654. Thereafter, a consistent decrease was observed, with 3880 cases in 2018 and 1732 in 2019.

![Figure 2](image-url)

FIGURE 2  (a) The occurrence number of entire pine wilt disease (PWD) cases (yellow; left y-axis) and PWD points classified as long-distance dispersal (LDD) cases (blue; right y-axis) for four consecutive years; (b) the locations of LDD events of each year
Although the total number of occurrence points gradually reduced by up to one-tenth for four years, the number of HVLDD cases showed a different pattern (Figure 2). Among a total of 33 HVLDD cases during the three years of dispersal, 12 LDD events occurred each year in 2017 and 2018. However, in 2019, the number of HVLDD cases decreased to nine. Annual LDD cases accounted for less than 1% of the total spread of the respective years.

### 3.2 Human-vectored long-distance dispersal assessment results

The path-finding algorithm recorded a greater dispersal distance than the Euclidean distance method for all 33 dispersal cases. In 2017, the Euclidean distance method recorded dispersals as moving 2312 m on average (Table 1). The path-finding algorithm had an average dispersal distance of 3929 m in the same year, which is approximately 1.7 times more. A similar trend was also observed for dispersal cases in 2018 and 2019, with the proposed algorithm showing a much greater mean dispersal distance of approximately 1.4 and 1.7 times the value obtained using the Euclidean distance method respectively. Generally, the Euclidean distance method measured the annual dispersal distance as 3.1 km, while the path-finding algorithm estimated it as 4.8 km, with a difference of 1.749 m.

#### 3.2.1 Functionality

To construct the future dispersal ranges of the path-finding algorithm, 383 m was used for the maximum flying distance of vector beetles from roads after anthropogenic introduction events. This figure was calculated based on the 33 HVLDD points and their distance from road networks.

The comparison between the future dispersal ranges of the two methods showed that the path-finding algorithm had a higher performance for all three years, and thus, it estimated much more accurate dispersal patterns (Table 2). In 2017, the future dispersal range obtained using the Euclidean distance method accurately forecasted six HVLDD cases, whereas the path-finding algorithm successfully predicted eight cases. Likewise, the proposed algorithm successfully forecasted more dispersal events than the Euclidean distance method in 2018 and 2019 (one and four more than those predicted by the Euclidean distance method respectively). The HVLDD cases that were exclusively predicted using the path-finding algorithm were located outside the dispersal range of the Euclidean distance but within the range of the path-finding algorithm (Figure 3).

#### 3.2.2 Applicability

Among the five different dispersal routes, route types 3, 4 and 5 accounted for almost all HVLDD cases with 9, 12 and 10 occurrences respectively (Figure 4a). Two cases were recorded using route type 2, whereas no dispersal event took place along route type 1. Route type 1 contrasted with route type 5 in that they both used only one road class for the entire dispersal process, but route type 5 showed a much higher occurrence frequency.

When the dispersal distance of each route type was estimated, route type 5 showed a maximum dispersal distance up to 6.5 km while dispersal cases of route types 2 and 3 showed similar maximum distances with less than 6 km (Figure 4b). Route type 4 showed the furthest dispersal distance, with a maximum distance of up to 7.7 km. The analysis of the contribution of each road class to the

| Year | 2017 | 2018 | 2019 | All |
|------|------|------|------|-----|
|      | ED   | PF   | ED   | PF  |
| Minimum | 2009 | 2822 | 2464 | 3379 |
| 1st quarter | 2053 | 3111 | 2721 | 3890 |
| Median | 2320 | 3493 | 3754 | 5431 |
| Mean | 2312 | 3929 | 3930 | 5574 |
| 3rd quarter | 2486 | 4961 | 5404 | 7207 |
| Maximum | 2790 | 5280 | 5708 | 7699 |
| SD | 259 | 935 | 1302 | 1669 |

**TABLE 1** Dispersal patterns of human-vectored long-distance dispersal events of pine wilt diseases for three years of dispersal events. Distances were calculated using the Euclidean distance method (ED) and path-finding algorithm (PF), and their basic descriptive statistical values are presented. SD row shows the standard deviation values of calculated dispersal distances for the corresponding year and method (unit: metre)

| Year | 2017 | 2018 | 2019 |
|------|------|------|------|
| ED   | 6 (50%) | 7 (58%) | 4 (44%) |
| PF   | 8 (67%) | 8 (67%) | 8 (89%) |

**TABLE 2** The prediction performance of future dispersal ranges predicted using the Euclidean distance method (ED) and path-finding algorithm (PF) for three years. The numerical values indicate the number of HVLDD events that each algorithm was able to predict with its future dispersal ranges using respective mean dispersal distance. The percentage in the parentheses shows how much each algorithm could explain among entire HVLDD points in every year. From 2017 to 2019, HLVDD points happened 12, 12 and 9 times respectively.
total dispersal distances using route types 2 and 3 showed that both high- and low-grade roads increased in length as the total distance increased (Figure 4c). High-grade roads were used for a longer time than low-grade roads in most HVLDD cases. However, the low-grade roads contributed more to the increase in the total dispersal distance, indicated by a steeper slope of the regression line.

4 | DISCUSSION

Understanding the precise dispersal traits of invasive species is imperative for designing suitable control strategies. Although its importance has been recognized for a long period, the rare and stochastic properties of HVLDD events have made it difficult to unveil...
the characteristics of such events. By identifying a factor in the matrix that acts as a dispersal pathway and integrating it into an assessment algorithm, HVLDD can be more precisely understood. In the case of the HVLDD of a PWD, transportation serves as a vector that moves along road networks. Therefore, a path-finding algorithm that simulates the movement of vehicles on roads can be a novel and effective HVLDD assessment method.

PWD in Busan Metropolitan City provided a great opportunity to validate the functionality and applicability of the path-finding algorithm. There were 33 HVLDD cases occurred between 2016 and 2019. Considering the fact that HVLDD occurs at a very low rate every year, 33 cases were considered sufficient to analyse the dispersal patterns and validate the algorithm. The declining trend in the total occurrence of the disease indicates that the strong implementation of control and preventative activities in the city successfully diminished the total number of PWD cases. However, when only HVLDD events were considered, it was observed that they were not managed well. The constant frequency of HVLDD, in contrast to the decreasing trend of the total number of occurrences, signifies that the ratio of HVLDD is, in fact, increasing.

4.1 | Case study: Pine wilt disease

4.1.1 | Human-vectored dispersal assessment results

The path-finding algorithm estimated much further dispersal distance for HVLDD when compared to the Euclidean distance method every year. Longer dispersal distances in the path-finding algorithm's dispersal pattern result can be considered a natural outcome as the Euclidean distance seeks the shortest linear distance between two occurrence points. However, several studies have already demonstrated that overlooking the explanatory factors of LDD in the assessment algorithm leads to an underestimation of the real dispersal magnitude (Koenig et al., 1996; Nathan et al., 2003). This substantiates the path-finding algorithm as a solution to the chronic misjudgment of dispersal capacities of HVLDD events.

Measuring the performance of each algorithm's future dispersal ranges allowed us to compare and determine which method is more effective in estimating dispersal patterns of HVLDD events. The results showed that the proposed algorithm achieves higher performances in all three years by accounting for the larger number of HVLDD points of the following years. Therefore, the proposed algorithm is a more effective dispersal assessment method for HVLDD events than the Euclidean distance method.

The path-finding algorithm's higher performance in explaining future occurrences was, in part, due to its production of amorphous-shaped dispersal ranges along the road network. Unlike the Euclidean distance method, the path-finding algorithm produced unique dispersal ranges with distinct shapes and areas for each source point (Figure 3). The morphology and area of dispersal ranges were largely determined by the spatial distribution of roads surrounding the occurrence point. A larger range was computed if the nearby roads were sprawled out in diverse directions, whereas small and oriented ranges were illustrated for a region with a linear layout of roads in a certain direction. Furthermore, even though the path-finding algorithm's future dispersal range for 2018 was smaller than the Euclidean distance one, it had higher performances in predicting future occurrences. This demonstrates that consideration of how vectors move in the landscape and reflecting this feature in generating potential dispersal ranges can effectively tell the direction of future occurrences.
4.1.2 | Management implications

The frequencies of the dispersal route type demonstrate the class of roads that are used for the beginning and end of HVLDD. Approximately 70% of all HVLDDs used low-grade roads as their entry or exit for dispersal (route types 2, 3 and 4 in Figure 4a). This implies that the start and end of the HVLDD are most likely to occur on small roads such as forest roads. Furthermore, in most cases of route types 2, 3 and 4, high-grade roads constituted the largest part of the total dispersal distance. However, this does not mean that the importance of small roads on dispersal can be neglected; low-grade roads also have the potential to account for the same or even greater part of the total dispersal distance than large roads in a few cases. Considering the fact that the maximum dispersal distance of route type 5 was up to 6.5 km, small roads also contribute considerably to dispersal.

Based on this information, two policy implications are provided. First, control efforts should be prioritized in different regions in the following order: forests adjacent to small roads, forests adjacent to large roads and forests remote from roads. Forests located near small roads should be regarded as the primary management sites because low-grade roads are the regions where most cases of HVLDD occur. Management actions can include removing all PWD-infested stands, including the asymptomatic ones, focussing on the forests adjacent to small roads. Preventative measures, such as sprays and pesticide injections in reachable regions near roads, could be adopted. Second, vehicles and log-transporting trucks moving on high-grade roads should be monitored and regulated. Large roads contributed the most to the total dispersal length. Therefore, installing inspection offices in gateways from small to large roads near the new occurrence sites can effectively reduce the dispersal length and even suppress the occurrence of HVLDD events.

Strict enforcement of the abovementioned regulations can effectively decrease the number of future occurrences and the distances covered by HVLDD. Moreover, the path-finding algorithm can guide the spatial configuration of such policies by predicting future dispersal ranges. This can substantially reduce the management costs and human resources considering the original management methods deal with the entire forest landscape. However, caution should be taken not to exclusively focus on a given range that uses mean dispersal distance as the government should be aware of the extreme HVLDD events.

4.2 | Path-finding algorithm as an HVLDD assessment method of invasive species

The case study successfully demonstrated the superiority of the path-finding algorithm in functionality and applicability compared with the Euclidean distance method. The path-finding algorithm not only provides accurate dispersal patterns of HVLDD but also offers management implications that help establish more cost-effective control policies.

In addition to PWD, the proposed algorithm can be applied to other invasive species that disperse along with human movements, such as the invasive plants that disperse along the road networks with their seeds being attached to moving vehicles (Adhikrai et al., 2020; Mortensen et al., 2009; Lippe & Kowarik, 2007). Analysing their dispersals using the path-finding algorithm will offer dispersal pattern and kernel that have not yet been discovered. Furthermore, they can have direct implications on desirable control and conservation design.

Now that we have validated the path-finding algorithm as an effective assessment method for HVLDD cases that happen along road networks, it can assist in making a much more powerful HVLDD prediction model. Previous studies that predicted the future distribution of PWD have modelled LDD to move in a random direction with a specified distance (NIFS, 2016; Takasu et al., 2000; Togashi & Shigesada, 2006). This is similar to the Euclidean distance method in that they both disregard the presence of dispersal pathways in the landscape matrix. Therefore, a mechanistic dispersal model should integrate the path-finding algorithm for HVLDD prediction instead of simulating it as a random occurrence. This would yield much more accurate prediction results by using road networks as a guide to predict future dispersal events.

Although the path-finding algorithm has many advantages, there are also several limitations compared to the Euclidean distance method. The path-finding algorithm requires topology-cleaned and detailed road network data. This results in a longer computation time than the Euclidean distance method. In addition, the proposed algorithm cannot provide information on SDD events, which accounts for the majority of dispersal cases. In short, the Euclidean distance has strength in its universality and time management. However, its universality can rather result in an inaccurate estimation of dispersal distances. Therefore, researchers should fully consider each method's pros and cons of each method and select one based on their research objectives.

This study had three limitations. First, we investigated dispersal patterns using three years of HVLDD data. When clustering the occurrence points using 100 m each year, possible asymptomatic trees in 2017 could not be removed due to the absence of the previous year. Therefore, the dispersal pattern of 2017 could include dispersal cases that were not HVLDD events. Second, LDD cases can occasionally take place by natural beetle migration events, not by anthropogenic factors. Under extreme environmental conditions with low metabolic reserves in their bodies, beetles are forced to fly over long distances to find a suitable habitat (Kwon et al., 2018; Lukáš et al., 2010). Therefore, there is a possibility that a few natural LDD events were included in our HVLDD dataset. This was the reason why we assumed every classified LDD point as HVLDD point because it is yet impossible to distinguish whether LDD points happened through road-based dispersal and natural migration. Third, dispersal patterns are generally sensitive to the analysis scale (Nathan, 2005). The HVLDD assessment using the path-finding algorithm targeting the national scale would produce different dispersal patterns from our results.
Future studies on dispersal assessment of HVLDD events should be multi-scale; not only regional but also national scale HVLDD movements must be analyzed to draw the generalized dispersal trend of anthropogenic dispersals along roads. As to national scale analysis, considering the spatial locations of the facilities that are likely to be used as dispersal sinks, such as lumber mill for PWN, could also provide another insight into dispersal patterns when analyzed together with the path-finding algorithm. This will provide more diverse and detailed implications for the precautions against the rapid spread of invasive species.

5 | CONCLUSION

To date, the comprehension of HVLDD events remains low. This study established a path-finding algorithm an effective dispersal assessment method for invasive species with HVLDD events that happen along road networks. The algorithm showed its higher efficacy in analyzing dispersal patterns and providing a basis for effective management plans than the Euclidean distance method. Integrating the algorithm into future dispersal simulation models can largely contribute to higher prediction accuracy. In addition, this study once again confirmed the importance of considering the vector movements in the landscape matrix for precise dispersal assessment. Identifying the pathway of a moving entity and reflecting it in the dispersal assessment model is key to the successful estimation of dispersal patterns.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The occurrence points classified as being occurred by human-vector long-distance dispersal events in this study can be obtained from the Dryad Repository: https://doi.org/10.5061/dryad.k98s17m6w. R codes for road network handling and convenient path algorithms, and road network data are available as well.

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BIOSKETCH

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