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# The ecological footprint of outdoor activities: Factors affecting human-vectored seed dispersal on clothing

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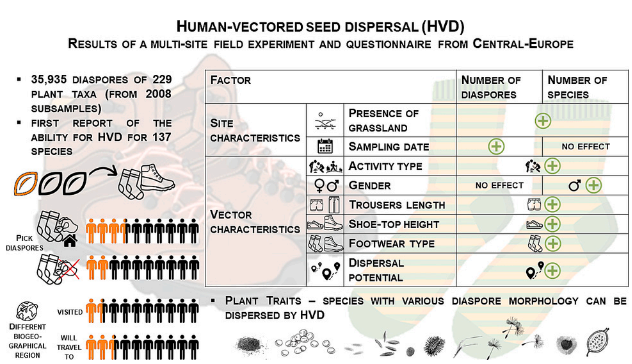
## HIGHLIGHTS

- Large numbers of diaspores and species are dispersed by human-vectored dispersal (HVD).
- Most diaspores belonged to weeds and competitors, and few to specialist species.
- Site and vector characteristics had significant influence on HVD, but considered plant traits did not.
- Most diaspores dispersed in grasslands, in midsummer, during field surveys.
- By choosing proper clothing, the unintended diaspore dispersal can be decreased.

## GRAPHICAL ABSTRACT

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## ABSTRACT

In the Anthropocene, humans are among the most abundant long-distance seed dispersal vectors globally, due to our increasing mobility and the growing global population. However, there are several knowledge gaps related to the process of human-vectored dispersal (HVD) on clothing. In a multi-site field experiment covering various habitat types in three countries of Central-Europe, we involved 88 volunteer participants and collected 251 HVD samples and 2008 subsamples from their socks and shoes. We analysed the number of diaspores and species in the samples. Specifically, we studied the effects of site characteristics (variables related to habitat types and season), vector characteristics (activity type, gender, clothing type, shoe type) and plant characteristics (species pool of the visited habitats and plant traits) on the number of diaspores and array of species dispersed. We assessed the habits of people that could be relevant for HVD with a questionnaire survey. A total of 35,935

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diaspores of 229 plant taxa were identified from the samples, which indicates a huge potential of HVD in dispersing diaspores across habitats and regions. Most diaspores were recorded in grassland habitats, and more diaspores were dispersed during fieldwork than excursions. Clothing type also played a decisive role: there were more diaspores and species when wearing short-top shoes and short trousers than long ones. Even though our study was carried out mainly in natural or semi-natural habitats, a large number of dispersed species were disturbance-tolerants and weeds and only a few were specialists, suggesting the controversial role of HVD in conservation. At the individual level, people can reduce the number of diaspores through their clothing choices and diaspore removal habits, while providing adequate equipment for staff, operating cleaning stations, and increasing awareness of employees are main ways in which unintended diaspore dispersal can be tackled at the institutional level.

## 1. Introduction

The dispersal of plant diaspores is a major driver of several important ecological and evolutionary processes such as gene flow, population dynamics, range expansion, and community diversity (Beckman and Sullivan, 2023). In the Anthropocene, humans are among the most abundant long-distance seed dispersal vectors globally, due to our increasing mobility and the growing global population (Bullock and Pufal, 2020; Valkó et al., 2020). There are two forms of human-vectored dispersal (HVD): intentional HVD (e.g., intentional introduction of plants for agricultural or horticultural purposes, and translocation for conservation purposes) and accidental HVD (e.g., unintended dispersal of seeds attached to clothes, vehicles, pets and livestock, or as contamination in transported materials such as seed stocks or potting soil) (Bullock et al., 2018; Sonkoly et al., 2022). Among accidental HVD types, seed dispersal on clothing can be considered a form of epizoochory. On clothing people can spread diaspores even across continents and can connect otherwise unconnected habitat types and regions worldwide (Ansong and Pickering, 2016; Huiskes et al., 2014; Valkó et al., 2020).

Despite the fact that people can transport numerous diaspores on their clothing, so far only 28 studies have investigated this phenomenon (see reviews by Ansong and Pickering, 2014a; Lukács and Valkó, 2021). This is a disproportionally smaller number of publications compared to the vast literature base (thousands of publications) on anemochory (e.g., reviewed by De Langre, 2008; der Weduwen and Ruxton, 2019), hydrochory (e.g., reviewed by Nilsson et al., 2010; Hyslop and Trowsdale, 2012) and zoochory (e.g., reviewed by Godó et al., 2022; Green et al., 2022). Most studies dealing with HVD on clothing have reported adverse ecological effects of this process, with a special focus on the dispersal of weeds and invasive alien species that cause serious damage in many natural ecosystems of the world (Pickering and Mount, 2010; Huiskes et al., 2014). Therefore, there are several biosecurity measures in the most vulnerable regions, which specifically address the prevention, mitigation, and control of the negative effects of HVD on clothing (Lukács and Valkó, 2021).

Given the above-mentioned potential of HVD on clothing in affecting global biodiversity patterns, it is essential to examine this process comprehensively to understand a typical dispersal process of the Anthropocene and to develop effective prevention and mitigation strategies against the spread of weedy and invasive species. Despite previous studies have investigated this process, there are still several open questions related to HVD on clothing. Experimental studies and field studies used different approaches and focused either on the underlying mechanisms or the results of HVD. Experimental studies on HVD so far focused mainly on the key mechanisms determining attachment or retention potential of diaspores, such as fabric types and diaspore traits, usually studying selected model species (see e.g., Ansong and Pickering, 2016). There is a few research that aimed to quantify the outcome of HVD in real world conditions, that is, the diaspore quantity and species pool dispersed through certain outdoor activities (e.g., on clothing of meadow workers (Auffret and Cousins, 2013), or on clothing and equipment of tourists (Huiskes et al., 2014; Ware et al., 2012)). However, the combination of the two approaches, i.e., the joint evaluation of the underlying mechanisms and results of HVD on clothing is still missing. Also, no studies have jointly evaluated the effect of site characteristics, vector characteristics, and plant traits on the number and species richness of dispersed diaspores. There is a lack of knowledge related to the potential dispersal distances of cloth-dispersed diaspores, as most studies give information on the total number of diaspores found on cloth items at a given time, without differentiating between loosely and firmly attached diaspores. Studies addressing the above-mentioned knowledge gaps would be essential for improving our general understanding of the process of HVD.

In our study, using the data from a multi-site field experiment covering various habitat types in Central-Europe, we analysed potential mechanisms that might affect the outcome of HVD. We expected based on former studies on zoochory in general or HVD in particular, that the number of dispersed diaspores and species depend on the attachment and detachment dynamics that are determined by clothing types and diaspore characteristics (Ansong and Pickering, 2016). Additionally, we studied the effects of other mechanisms, i.e., site characteristics (variables related to habitat types and season), vector characteristics (activity type, gender, clothing type, shoe type) and plant characteristics (species pool of the visited habitats and plant traits) on the number of diaspores and array of species dispersed on human clothing. Since the habits of people can play an important role in the fate of cloth-dispersed diaspores (Ansong and Pickering, 2014b), we complemented our field experiment with a questionnaire survey to assess the habits of people that could be relevant in determining the outcome of HVD on clothing.

## 2. Methods

### 2.1. Collection of samples

We collected HVD samples from the socks and shoes of volunteer participants during various outdoor activities at different sites of Hungary, Romania, and the Czech Republic, in the years 2019 and 2020. The sampling procedure is summarized in Fig. 1. Before starting the field activity, all participants were asked to clean their shoes. We provided all volunteers with a new pair of cotton socks (73 % cotton, 20 % polyester, 6 % nylon, and 1 % elastane) that they wore during their outdoor activity with their own shoes. We asked the volunteers to engage in their planned field activity, i.e., perform their fieldwork or go on field excursion. At least one author of this paper joined them for the entire duration of the outdoor activity to record site characteristics, vector characteristics, and the species pool of the visited habitats, and also to explain the sampling protocol to the participants and facilitate sample collection. At the end of the outdoor activity, we collected the HVD samples: we requested the participants to put the right and left socks in separate labelled paper bags. Additionally, we asked them to pick and sweep diaspores from the right and left shoes into separate labelled paper bags. In the case of shoes, the diaspores attached to the outside and inside of the shoe were collected separately. In total, six samples were collected from one person: left shoe outside, right shoe outside, left shoe inside, right shoe inside, left sock and right sock.

We collected HVD samples between June 2019 and October 2020 in Hungary, Romania, and the Czech Republic. During this period, we

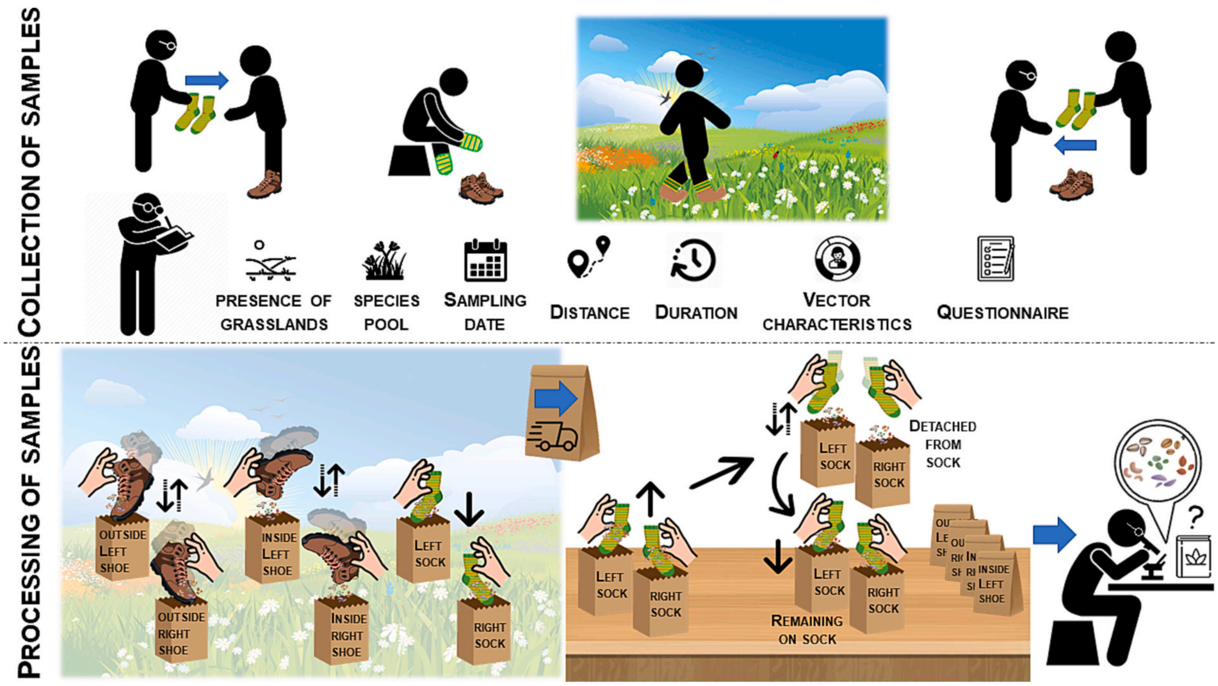


**Fig. 1.** The workflow of sample collection and sample processing.

collected 251 samples from 88 volunteer participants. Different categories of participants were distinguished: professional field biologists (34 persons; 170 samples) (including the authors of this article), biologist students (40 persons; 61 samples), and others (14 persons; 20 samples).

We distinguished two types of activity: field surveys (botanical monitoring, $N = 118$) and excursions (educational field trip or leisure activity, $N = 133$). In the case of field surveys, we usually worked in smaller groups (2–8 participants). In excursions, samples were usually collected by a larger group (>10 participants). In both cases, the members of the groups were moving together.

The sample collection was carried out at 39 locations that were assigned unique site IDs. At each site, we recorded the habitat types that occur (e.g., grassland, forest, wetland, and anthropogenic habitat). Based on the occurrence of the different habitat types, we categorised the landscapes into two broad categories: grassland-dominated landscape and forest-dominated landscape. In the analyses, we used the presence/absence of grasslands as an explanatory variable.

During the time spent outdoors, we recorded a list of vascular plants to characterise the species pool of the visited site and marked on the list those species that were in fruit at the time of sampling (i.e., the part of the species pool that had the opportunity for being dispersed by HVD on cloths), to facilitate the identification of the diaspores in the lab. Furthermore, we recorded the following explanatory variables: sampling date (Julian day), distance walked (km), and time spent outside (hour). The participants walked an average of 4 ± 3.78 km distance and spent 6 ± 2.39 h outside. We took photos of each participant's clothing and shoes to record the types of fabric and shoes worn. As the distance walked and the time spent outdoors showed a positive correlation, we used only the distance in the analyses.

At the end of the sample collection, all volunteers were asked to fill out a questionnaire (Appendix 1). We asked them about how much time they spend in the field per year, which places/locations they visited in the field during the last three times before the sample collection, and where they plan to go within the next week, a month, and in the more distant future. Furthermore, we also asked what they usually do with the diaspores attached to their clothes and shoes.

### 2.2. Processing of samples and identification of diaspores

The collected samples were transported to the laboratory for processing. First, we removed the diaspores attached to the socks. We aimed to distinguish between the diaspores that are loosely or firmly attached, as the level of seed attachment is a good predictor of potential dispersal distances. To simulate vector movement, we shook the socks by hand three times and put the detached diaspores (i.e., those that fell during shaking together with those diaspores that were already detached from the socks and were in the paper bag) in a ziploc bag. This fraction represented diaspores with a low attachment potential and a shorter potential dispersal distance. The diaspores that remained on the socks after shaking were removed with tweezers and placed in a separate ziploc bag (representing the fraction of firmly attached diaspores with a longer potential dispersal distance). We performed this procedure separately for the right and left socks. Finally, there were a total of eight subsamples from one person: left sock detached, left sock attached, left shoe inside, left shoe outside, right sock detached, right sock attached, right shoe inside and right shoe outside (in total 2008 subsamples). We grouped the subsamples into two categories based on the potential dispersal distance: i) short-distance (diaspores collected from the shoe surfaces and the diaspores detached from socks) and ii) long-distance (diaspores collected inside shoes and the diaspores remained attached on socks).

The next step was to identify and count the diaspores. In this process we used the seed atlas of Schermann (1967), species lists, and reference seed specimens collected from the sampling sites, and the reference seed collection at the University of Debrecen (Török et al., 2013, 2016). The diaspores that could not be identified on the basis of morphology (in total 8900 diaspores, approximately 24.8 % of all diaspores) were germinated in a greenhouse from March to November 2021.

### 2.3. Data analysis

Some important dispersal-related traits of the identified species were retrieved from trait databases (Hintze et al., 2013; Király, 2009; Török et al., 2013, 2016; Schermann, 1967, for details, see Appendix 2). To characterise the ecological role of the dispersed species, the species were classified according to Borhidi's social behaviour types (Borhidi, 1995, please see details in Appendix 3). The system classifies plant species, ranging from low (e.g., alien competitors) to high naturalness value (e.g., habitat specialist species) (please see the classification in Appendix 4).

Data handling and statistical data analyses were performed in R (ver. 4.2.0, R Core Team). To assess how the site characteristics and the vector characteristics affect the number of collected diaspores and species present on the clothing, we prepared linear mixed-effects regression models (GLMMs) with negative binomial error term, using the R-package "glmmTMB" (Brooks et al., 2017). The number of diaspores and the number of species were the response variables, and the factors described above were the predictor variables (sampling date (Julian day), presence of grasslands at the collection site, activity type, gender, footwear type, shoe-top height, trousers length, potential dispersal distance).

In all models, we also specified the identity of collector, and ID of collection event, as random grouping variables. In addition, we specified the log-transformed value of the distance covered by the specific collector as an offset, to control for varying sampling efforts. In particular, this was necessary because it can be expected that larger distances covered yield larger numbers of diaspores and species encountered. Variance inflation factors (VIFs) were calculated between all explanatory variables to test for multicollinearity ('faraway' package in R; Faraway, 2014). As the VIF was lower than 1.7 (that is, the rate of multicollinearity was negligible) in each case, we considered all explanatory variables uncorrelated and used them for the statistical analyses.

To study whether certain plant traits (namely: the presence of appendix, diaspore morphology (spherical or elongated), plant height, and seed mass) were associated with footwear types (i.e., dispersed on socks or shoes) or affected potential dispersal distance (i.e., dispersed on short- or long term), we calculated community weighted means (CWMs). For continuous numerical traits (plant height and seed mass) we used the log-transformed average trait values for the present species, weighted by species abundances. For categorical traits (Appendix 2), we summarized the number of seeds belonging to the given group (having versus not having appendix; having spherical versus elongated diaspore morphology). The CWMs of plant height and seed mass were analysed with compound Poisson-Gamma GLMM and Gaussian LMM, respectively. CWMs from categorical traits were analysed with negative binomial GLMMs. In all models, the predictor variables were footwear type and potential dispersal distance. Also, the collector's identity and the collection event ID were specified as random factors in all CWM models.

## 3. Results

### 3.1. Diaspore numbers

A total of 35,935 diaspores of 229 plant taxa were identified from the samples. We identified all diaspores, but for approximately 18 % of all collected diaspores ($N = 6493$), identification was only possible at the family or genus level even after germination. The most common species in the samples were *Achillea collina* (4830 diaspores), *Agrostis stolonifera* (3174 diaspores), *Galium aparine* (2713 diaspores) and *Poa angustifolia* (1960 diaspores). Of the 229 plant species that we identified, we were the first to report the ability for cloth-dispersal for 137 species (Appendix 4).

The species were from 31 families of plants; however, more than half of the species belonged to five families, with 59 species from Poaceae, 29 from Asteraceae, 14 from Fabaceae, 13 from Apiaceae and 13 from Lamiaceae. We identified 6 alien competitors (AC), 10 ruderal competitors (RC), 3 adventive species (A), 2 introduced alien species (I), 46 weeds (W), 64 disturbance-tolerants (DT), 14 natural pioneers (NP), 53 generalists (G), 23 competitors (C) and 8 specialists (S) (Appendix 4). In the complete species list of the vegetation of the visited habitats, 660 species were in fruit at the time of sample collection, of which we registered 35 % of the species in the collected HVD samples (Appendix 4). The largest proportion of HVD dispersed species compared to the species present in the total species pool were ruderal competitors (83.3 % of available species were recorded in HVD samples), weeds (45.5 %), natural pioneers (45.2 %), competitors (44.2 %), and disturbance-tolerants (40.5 %) while the lowest proportion of HVD dispersed species was recorded in specialists (14.0 %) (Fig. 2).

### 3.2. Factors that affect human-vectored dispersal

#### 3.2.1. Site characteristics

The sampling date (Julian day) had a significant effect on the number of cloth-dispersed diaspores and species ($p < 0.001$; Fig. 3A). Considering the visited habitat types, the presence of grassland habitats in the sampling sites significantly increased the number of dispersed diaspores and species ($p < 0.001$) (Fig. 3B).

#### 3.2.2. Vector characteristics

We found that most of the vector characteristics studied, i.e., activity type, shoe top height, and trouser length, had a significant effect on the number and species richness of the dispersed diaspores (Appendix 5). Analysis of activity type revealed that significantly more diaspores can spread by HVD on clothing ($p < 0.05$) during field surveys than during excursions (Fig. 3C). Men tended to disperse more diaspores and species on clothing than women, but the difference was not significant ($p = 0.122$) (Fig. 3D). However, men dispersed significantly more species than women ($p < 0.05$) (Appendix 6). We recorded more diaspores and species on socks than on shoes ($p < 0.001$) (Fig. 3E). The type of clothing also played an important role: there were more diaspores and species when wearing short-top shoes ($p < 0.001$ both for number of diaspores and species) and short trousers than long ones ($p < 0.05$ for number of diaspores, $p = 0.122$ for number of species) (Fig. 3F-G). Finally, we found that more species and diaspores with larger potential dispersal distances (firmly attached to socks or inside shoes) were found ($p < 0.001$) than with species with small potential dispersal distances ($p < 0.001$) (loosely attached to socks or on the surface of shoes) (Fig. 3H). The vector characteristics studied had the same effect on the species richness of the dispersed diaspores as on diaspore number in case of all explanatory variables, except gender (Appendix 6).

#### 3.2.3. Plant traits

The dispersal-related plant traits studied (presence of appendices, diaspore form spherical or elongated, plant height, and diaspore mass) had no significant effect on the number of diaspores on the different types of footwear or on the potential dispersal distances (see details in Appendix 2).

### 3.3. Questionnaire

67 % of the participants spent more than one month in the field per year. Most participants visited sites in the same region or landscape as the sampling sites prior to sampling (previous three weeks), but 17 % visited different biogeographical regions in Europe or in other continents. Future plans for outdoor activities of the participants were also mainly within the same landscape or region as certain sampling sites, but 25 % planned to travel outside the biogeographical region or continent in the coming three weeks. The majority (43 %) of the participants generally pick the diaspores from their clothing on the site, but 35 % remove them at home or do not remove them at all (22 %). The detailed results of the questionnaire survey are given in Appendix 1.

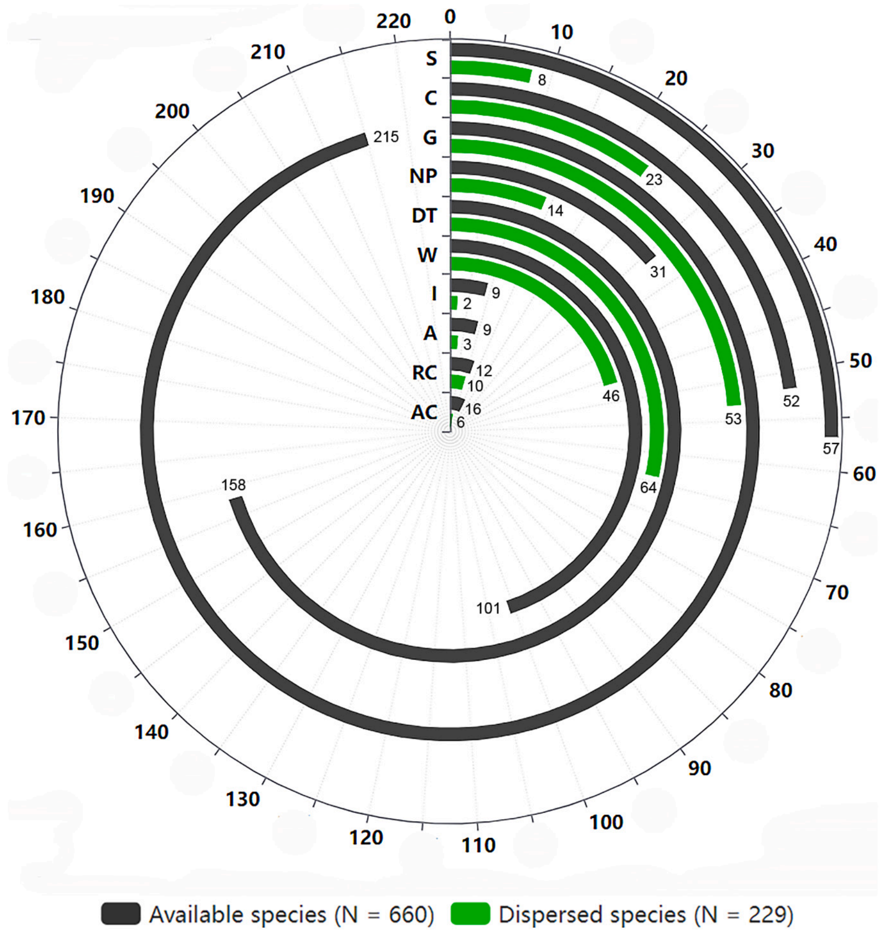


**Fig. 2.** Number of species in the collected HVD samples (green lines) and in the species pool of the vegetation at the collection sites (grey lines). Species are grouped according to their social behaviour type categories, starting from the highest naturalness value (S) following a descending order. Notations: S – specialists, C – competitors, G – generalists, NP – natural pioneers, DT – disturbance-tolerants, W – weeds, I – introduced alien species, A – adventives, RC – ruderal competitors and AC – alien competitors.

## 4. Discussion

### 4.1. Array of species dispersed and ecological importance of HVD

Our study demonstrates that HVD can play an important role in the transfer of diaspores between various habitats and regions, as people can collect large amounts of diaspores during their outdoor activities. In total, we counted 35,935 diaspores and 229 species in our samples. We recorded 137 species, which were previously not registered to be able to spread by clothing (this is approximately 28 % addition to the list of the species known to be dispersed by HVD, Ansong and Pickering, 2014a). The large number of new species is related to the fact that there were no previous studies of HVD on clothing from Central Europe. In the future, more studies on HVD are needed, especially from currently data-deficient regions (e.g., Africa, Asia, many parts of Europe and South America; Mount and Pickering, 2009).

Despite the fact that our study was carried out mainly in habitats with natural or semi-natural vegetation, a large number of dispersed species were disturbance-tolerant and weedy species (see also Ansong and Pickering, 2014a; Mount and Pickering, 2009). This can be partly explained by the ubiquity and high diaspore production rate of these generally r-strategist species. Specialist species of natural habitats were dispersed only in a small proportion, but we recorded diaspores of *Agropyron cristatum*, *Danthonia alpina*, *D. decumbens*, *Festuca ovina*, *Pholiurus pannonicus*, *Silene viscosa*, *Stipa borysthenica*, and *Trifolium angulatum* in the samples. This result suggests that human-vectored dispersal may play a role in diaspore transfer between natural habitats (see also Auffret and Cousins, 2013). The most noxious species (ruderal competitor, adventive competitor, and invasive species) were also represented with a relatively small number of species and diaspores, but several alien species were recorded in the samples, such as *Ambrosia artemisiifolia*, *Conyza canadensis*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Galinsoga parviflora*, and *Solidago gigantea*. These results suggest that HVD on clothing is a controversial phenomenon from a conservation point of view.

### 4.2. Factors influencing HVD

#### 4.2.1. Site characteristics

We found that the number of diaspores and species attached to socks and shoes was highest when grassland habitats were visited during sampling. Grasslands are open habitats that have long co-evolution with large-bodied herbivores that had a great role in epizoochory (Couvreur et al., 2004; Sridhara et al., 2016; Baltzinger et al., 2019), which might explain the greater potential of anthropochory in grasslands. Furthermore, vegetation is denser in grasslands than in forest understory, therefore, seed stock near the ground surface is usually larger than in forests, so there is a greater chance for a diaspore-human encounter in grasslands (Albert et al., 2015). We found >35 thousand diaspores of plant species on clothes after sampling in grassland habitats. The highest

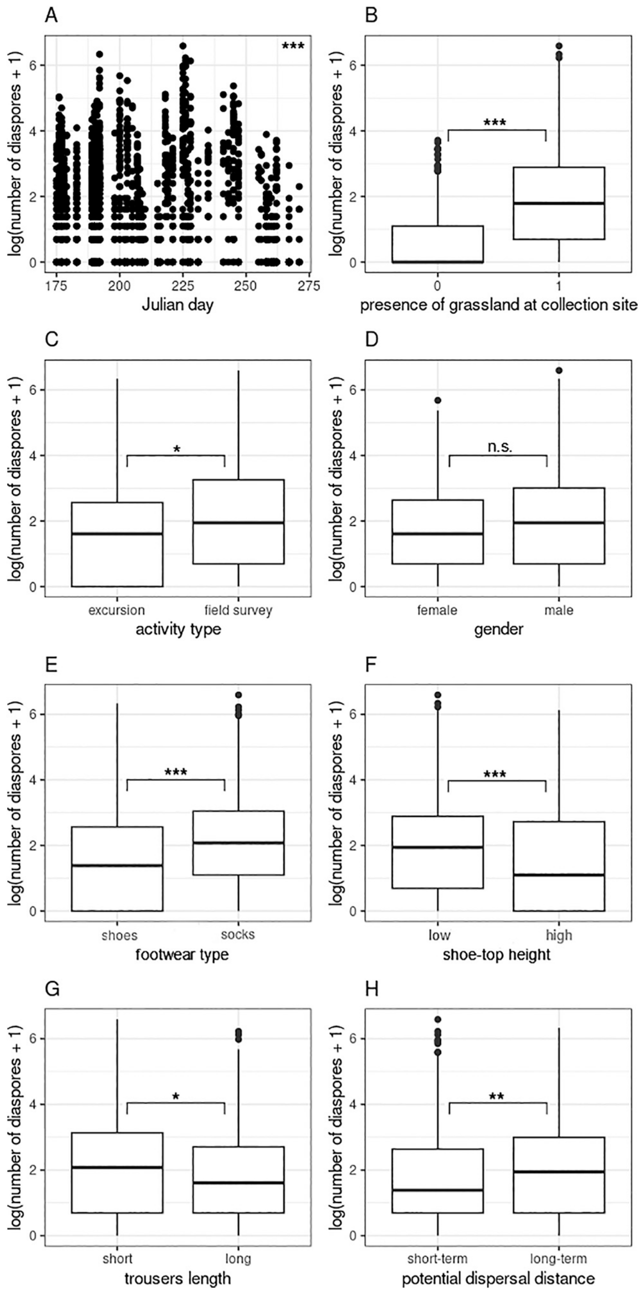


**Fig. 3.** The number of diaspores collected according to (A) sampling date (Julian day), (B) presence of grasslands at collection site, (C) activity type, (D) gender, (E) footwear type, (F) shoe-top height, (G) trousers length, and (H) potential dispersal distance. Asterisks denote significant effects: *** – $p \leq 0.001$, ** – $p < 0.01$, * – $p < 0.05$; n.s. indicates non-significant effects.

number of diaspores collected by a single person in our study in one day was 2172, which can be considered an outstandingly high number compared to previous studies. In previous studies, the largest amounts of dispersed diaspores were also reported from grasslands. Healy (1943) found more than three hundred diaspores of *Nusella trichotoma* on his clothes, after a five-day field work and Faliński (1972) counted similar amounts of diaspores on his clothes after two-day field work. Auffret and Cousins (2013) collected 115 ± 286 diaspores per person per day from the clothing of farmers who work on meadows.

#### 4.2.2. Vector characteristics

We found that activity type had a significant effect on the number and species richness of dispersed diaspores. Our results highlight that people doing field surveys disperse more diaspores than those who perform leisure activities. A potential reason is that field biologists leave the roads and trails more often and are in more direct contact with the vegetation. They often need to go to certain pre-defined spots, and cross dense vegetation patches that are often avoided by hikers. A study in Antarctica (Huiskes et al., 2014) also found that staff at the research station (field scientists, station scientists, field support personnel and station support personnel) dispersed a significantly higher number of diaspores than tourists. These results show that scientists and other personnel who routinely travel to protected areas should be encouraged to conduct the most rigorous assessments of their clothing and gear (see also Huiskes et al., 2014). This message can be effectively communicated to field biologists through research articles and other academic forums, which can greatly support prevention measures.

We found that men dispersed significantly more species and tended to disperse more diaspores than women, but this latter difference was not significant. Additionally, the largest amounts of diaspores per day were collected by men. This might be related to that men are more risk-taking and explorative than women (Byrnes et al., 1999), and therefore they might have a closer contact to dense vegetation.

Clothing type also determined the number of species and diaspores dispersed. We found that significantly more diaspores were attached to people's clothing when they wear short pants and low-top shoes (e.g., sneakers) than if they wear long pants and high-top shoes. Short trousers, which leave the socks, laces, and shoes uncovered, support human-vectored seed dispersal, as these items provide a good adhesion surface and collect a large number of diaspores (Mount and Pickering, 2009). We showed that wearing long trousers can reduce the number of diaspores collected on socks and shoes, which is consistent with the study of Mount and Pickering (2009). It is also important to emphasize the type of fabrics, as different fabric types have different adhesion surfaces. More diaspores can attach for longer periods on clothing made of fleece, wool, and cotton/nylon materials than clothing made of denim, nylon weave, canvas, and drill cotton (Ansong and Pickering, 2016). Our results as well as previous results on the effect of clothing type on the outcome of HVD imply that in this process the role of individual decision is crucial, as it is possible to reduce the spread of diaspores by choosing appropriate clothing. To reduce the spread of harmful species on clothing, it is essential that people who regularly visit natural habitats prefer clothes and fabrics with low adhesion potential.

#### 4.2.3. Plant traits

We expected that dispersal-related plant traits will play a crucial role in HVD. Previously, HVD on clothing was considered mainly as a form of epizoochory, but our results show that clothes can provide a great opportunity for the dispersal of those diaspores that do not have adaptations for epizoochory. Interestingly, we found that even fleshy fruits (e.g., *Ribes aureum*) were capable of dispersal in considerable numbers by shoes. We also found that small diaspores without appendices (e.g., *Achillea collina, Dianthus pontederae*, *Galium verum*, and *Potentilla argentea*) can easily get into shoes or even into the creases of socks and trousers and can disperse over long distances. These results suggest that HVD is a more general phenomenon than previously thought and that a wide range of species can be dispersed this way (Green et al., 2022).

Based on previous studies, we hypothesised that diaspores with attachment structures, and small diaspores have a higher chance for long-distance dispersal (see Ansong et al., 2015; Ansong and Pickering, 2016). However, we did not find a significant difference between the potential dispersal distances explained by plant traits. Notably, we observed some interesting trends that might be worthy of detailed investigations in the future. For example, diaspores with appendages and an elongated shape tended to be more numerous on socks than on shoes. Diaspores with appendices and those with spherical shape tended to have a higher chance for long-distance dispersal, while elongated ones tended to have a higher chance of short-term dispersal. It should be noted that all these trends were nonsignificant, which implies that the role of plant traits in human-vectored dispersal is probably much weaker than site and vector characteristics, and that several plant species are capable of spreading by clothing regardless of their traits. The role of plant traits in HVD is a topic worthy of future investigation. Although we collected a huge HVD dataset, we only had presence/absence data about the species pool of the visited vegetation, which is a limitation of our study. Incorporating the abundance of the species in the vegetation into the models would allow us to make more detailed trait-based analyses and explore the role of plant traits in a more sophisticated way (see also Albert et al., 2015).

### 4.3. Implications for conservation

With our sampling approach, we could distinguish between diaspores that have the potential for short- or long-distance dispersal, and we found that a large number of species can be dispersed over long distances by clothing. This is a crucial point, as in many cases, the long-distance dispersal of diaspores depends on the individual decisions of people regarding choosing the type of clothing and footwear and treatment of the attached diaspores. We found that the process of HVD is dependent on the type of clothes and fabrics; therefore, people can reduce or increase the number of diaspores through their clothing choices (see also Mount and Pickering, 2009; Ansong and Pickering, 2016).

Our questionnaire survey showed that there are several individual decisions where people can reduce the negative environmental consequences of HVD. There are some widespread practices which can lead to the unintended dispersal of diaspores: i) most people remove the diaspores outdoors (this can be a major source of dispersal of unwanted species in natural areas); ii) many people do not remove the diaspores at all from their clothes (these diaspores have the chance to survive the laundry washing (Valkó et al., 2020) and can even establish in anthropogenic habitats that can be a starting point for future invasion processes. To reduce the risk of unintended dispersal, the best option would be to clean clothing indoors, dispose the collected diaspores in a closed bin, and enter nature reserves with diaspore-free clothes and footwear (see also Ansong and Pickering, 2014b).

Our results showed that field biologists and other professionals working outdoors could do the most to reduce the risk of unintended dispersal. Providing adequate equipment for staff, operating cleaning stations, and increasing awareness of employees are main ways in which unintended diaspore dispersal can be tackled at the institutional level.

There are serious concerns about the negative environmental impacts and carbon footprint of long-distance travel (Christensen, 2016), but the importance of these movements in HVD is greatly underestimated considering the ability of cloth-dispersed diaspores for long-distance dispersal. The results of our questionnaire survey showed that 27 % of the participants do not remove diaspores from their clothing; furthermore, 24 % planned to visit other biogeographical regions within and outside Europe in the more distant future. This indicates a great potential of carrying still attached diaspores even to distant biogeographical regions. The transformation of the attitude of people (especially that of field biologists) is crucial to reduce the risk of the long-distance dispersal of diaspores on clothing.

## CRediT authorship contribution statement

**Katalin Lukács:** Conceptualization, Methodology, Investigation, Data curation, Original draft preparation, Reviewing and Editing; **Ágnes Tóth**: Investigation, Reviewing and Editing; **Réka Kiss**: Investigation, Reviewing and Editing; **Balázs Deák:** Conceptualization, Investigation, Reviewing and Editing; **Zoltán Rádai:** Formal analysis, Reviewing and Editing; **Katalin Tóth**: Investigation, Reviewing and Editing; **András Kelemen**: Investigation, Reviewing and Editing; **Alida Anna Hábenczyus**: Investigation, Reviewing and Editing; **Zoltán Bátori**: Investigation, Reviewing and Editing; **Csaba Tölgyesi**: Investigation, Reviewing and Editing; **Tamás Miglécz**: Investigation, Reviewing and Editing; **Laura Godó:** Conceptualization, Investigation, Reviewing and Editing, Visualisation; **Orsolya Valkó:** Conceptualization, Investigation, Data curation, Original draft preparation, Reviewing and Editing, Supervision.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Orsolya Valko reports financial support was provided by Hungarian National Research, Development and Innovation Office. Balazs Deak reports financial support was provided by Hungarian National Research, Development and Innovation Office. Reka Kiss reports financial support was provided by Hungarian National Research, Development and Innovation Office. Zoltan Batori reports financial support was provided by Hungarian National Research, Development and Innovation Office. Zoltan Batori reports financial support was provided by Hungarian Academy of Sciences.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.167675.

## References

Albert, A., Auffret, A.G., Cosyns, E., Cousins, S.A., D'hondt, B., Eichberg, C., Eycott, E.A., Heinken, T., Hoffmann, M., Jaroszewicz, B., Malo, E.J., Mårell, A., Mouissie, M., Pakeman .J., R., Plue, J., Poschlod, P., Provoost, S., Schulze .A., K., Baltzinger, C., 2015. Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. Oikos. 124 (9), 1109–1120. https://doi.org/10.1111/oik.02512.

Ansong, M., Pickering, C., 2014a. Weed seeds on clothing: a global review. J. Environ. Manage. 144, 203–211. https://doi.org/10.1016/j.jenvman.2014.05.026.

Ansong, M., Pickering, C., 2014b. Weed Hygiene: What Do we Do with Seeds we Find on our Clothing? Paper Presented at the 19th Australiasian Weeds Conference-Science, Community and Food Security: The Weed Challenge. Tasmania, Australia.

Ansong, M., Pickering, C., 2016. The effects of seed traits and fabric type on the retention of seed on different types of clothing. Basic Appl. Ecol. 17 (6), 516–526. https://doi.org/10.1016/j.baae.2016.03.002.

Ansong, M., Pickering, C., Arthur, J.M., 2015. Modelling seed retention curves for eight weed species on clothing. Austral Ecol. 40 (7), 765–774. https://doi.org/10.1111/aec.12251.

Auffret, A.G., Cousins, S.A., 2013. Humans as long-distance dispersers of rural plant communities. PloS One 8 (5), e62763. https://doi.org/10.1371/journal.pone.0062763.

Baltzinger, C., Karimi, S., Shukla, U., 2019. Plants on the move: hitch-hiking with ungulates distributes diaspores across landscapes. Front. Ecol. Evol. 7, 38. https://doi.org/10.3389/fevo.2019.00038.

Beckman, N.G., Sullivan, L.L., 2023. The causes and consequences of seed dispersal. Annu. Rev. Ecol. Evol. Syst. https://doi.org/10.1146/annurev-ecolsys-102320-104739.

Borhidi, A., 1995. Social behaviour types, the naturalness and relative indicator values of the higher plants in the Hungarian fora. Acta Bot. Hungar. 39, 97–181.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9 (2), 378–400. https://doi.org/10.3929/ethz-b-000240890.

Bullock, J.M., Pufal, G., 2020. Human-mediated dispersal as a driver of vegetation dynamics: a conceptual synthesis. J. Veg. Sci. 31 (6), 943–953. https://doi.org/10.1111/jvs.12888.

Bullock, J.M., Bonte, D., Pufal, G., da Silva Carvalho, C., Chapman, D.S., García, C., Matthysen, E., Delgado, M.M., 2018. Human-mediated dispersal and the rewiring of spatial networks. Trends Ecol. Evol. 33 (12), 958–970. https://doi.org/10.1016/j.tree.2018.09.008.

Byrnes, J.P., Miller, D.C., Schafer, W.D., 1999. Gender differences in risk taking: A meta-analysis. Psychol. Bull. 125 (3), 367. https://doi.org/10.1037/0033-2909.125.3.367.

Christensen, L., 2016. Environmental impact of long distance travel. Transp. Res. Procedia. 14, 850–859. https://doi.org/10.1016/j.trpro.2016.05.033.

Couvreur, M., Christiaen, B., Verheyen, K., Hermy, M., 2004. Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. Appl. Veg. Sci. 7 (2), 229–236. https://doi.org/10.1111/j.1654-109X.2004.tb00614.x.

De Langre, E., 2008. Effects of wind on plants. Annu. Rev. Fluid Mech. 40, 141–168. https://doi.org/10.1146/annuerv.fluid.40.111406.102135.

der Weduwen, D., Ruxton, G.D., 2019. Secondary dispersal mechanisms of winged seeds: a review. Biol. Rev. 94 (5), 1830–1838. https://doi.org/10.1111/brv.12537.

Faliński, J.B., 1972. Anthropochory in xerothermic grasslands in the light of experimental data. Acta Soc. Bot. Pol. 41 (3), 357–368. https://doi.org/10.5586/asbp.1972.028.

Faraway, J.J., 2014. Linear Models with R. Chapman & Hall, London.

Godó, L., Valkó, O., Borza, S., Deák, B., 2022. A global review on the role of small rodents and lagomorphs (clade Glires) in seed dispersal and plant establishment. Glob. Ecol. Conserv. 33, e01982 https://doi.org/10.1016/j.gecco.2021.e01982.

Green, A.J., Baltzinger, C., Lovas-Kiss, Á., 2022. Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. Oikos. 2022 (2) https://doi.org/10.1111/oik.08327.

Healy, A.J., 1943. Seed dispersal by human activity. Nature. 151 (3822), 140. https://doi.org/10.1038/151140b0.

Hintze, C., Heydel, F., Hoppe, C., Cunze, S., König, A., Tackenberg, O., 2013. D3: the dispersal and diaspore database–baseline data and statistics on seed dispersal. Perspect. Plant Ecol. Evol. Syst. 15 (3), 180–192. https://doi.org/10.1016/j.ppees.2013.02.001.

Huiskes, A.H., Gremmen, N.J., Bergstrom, D.M., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Lee, E.J., Tsujimoto, M., Ware, C., Van de Vijver, B., Chown, S.L., 2014. Aliens in Antarctica: assessing transfer of plant propagules by human visitors to reduce invasion risk. Biol. Conserv. 171, 278–284. https://doi.org/10.1016/j.biocon.2014.01.038.

Hyslop, J., Trowsdale, S., 2012. A review of hydrochory (seed dispersal by water) with implications for riparian rehabilitation. J. Hydrol. N. Z. 137–152. https://www.jstor.org/stable/43945038.

Király, G. (Ed.), 2009. Új magyar füvészkönyv. Magyarország hatásos növényei (New Hungarian Herbal. The Vascular Plants of Hungary. Identification Key) [in Hungarian]. Aggtelek National Park Directorate, Jósvafő.

Lukács, K., Valkó, O., 2021. Human-vectored seed dispersal as a threat to protected areas: prevention, mitigation and policy. Global Ecol. Conserv. 31, e01851 https://doi.org/10.1016/j.gecco.2021.e01851.

Mount, A., Pickering, C.M., 2009. Testing the capacity of clothing to act as a vector for non-native seed in protected areas. J. Environ. Manage. 91 (1), 168–179. https://doi.org/10.1016/j.jenvman.2009.08.002.

Nilsson, C., Brown, R.L., Jansson, R., Merritt, D.M., 2010. The role of hydrochory in structuring riparian and wetland vegetation. Biol. Rev. 85 (4), 837–858. https://doi.org/10.1111/j.1469-185X.2010.00129.x.

Pickering, C., Mount, A., 2010. Do tourists disperse weed seed? A global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. J. Sustain. Tour. 18 (2), 239–256. https://doi.org/10.1080/09669580903406613.

R Core Team, R, 2013. R: A Language and Environment for Statistical Computing.

Schermann, S., 1967. Magismeret I–II. Akadémiai Kiadó, Budapest, p. 1074.

Sonkoly, J., Takács, A., Molnár, A., Török, P., 2022. Trade of commercial potting substrates: a largely overlooked means of the long-distance dispersal of plants. Sci. Total Environ. 825, 154093 https://doi.org/10.1016/j.scitotenv.2022.154093.

Sridhara, S., McConkey, K., Prasad, S., Corlett, R.T., 2016. Frugivory and seed dispersal by large herbivores of Asia. Ecol. Large Herb. South Southeast Asia. 121–150. https://doi.org/10.1007/978-94-017-7570-0_5.

Török, P., Miglécz, T., Valkó, O., Tóth, K., Kelemen, A., Albert, Á.-J., Matus, G., Molnár, V.A., Ruprecht, E., Papp, L., Deák, B., Horváth, O., Takács, A., Hüse, B., Tóthmérész, B., 2013. New thousand-seed weight records of the Pannonian flora and their application in analysing social behaviour types. Acta Bot. Hung. 55 (3–4), 429–472. https://doi.org/10.1556/abot.55.2013.3-4.17.

Török, P., Tóth, E., Tóth, K., Valkó, O., Deák, B., Kelbert, B., Bálint, P., Radócz, Sz, Kelemen, A., Sonkoly, J., Miglécz, T., Matus, G., Takács, A., Molnár, V.A., Süveges, K., Papp, L., Papp Jr., L., Tóth, Z., Baktay, B., Málnási Csizmadia, G., Oláh, I., Peti, E., Schellenberger, J., Szalkovszki, O., Kiss, R., Tóthmérész, B., 2016. New measurements of thousand-seed weights of species in the Pannonian flora. Acta Bot. Hung. 58 (1–2), 187–198. https://doi.org/10.1556/034.58.2016.1-2.10.

Valkó, O., Lukács, K., Deák, B., Kiss, R., Miglécz, T., Tóth, K., Tóth, Á., Godó, L., Radócz, S., Sonkoly, J., Kelemen, A., Tóthmérész, B., 2020. Laundry washing increases dispersal efficiency of cloth-dispersed propagules. NeoBiota. 61, 1. https://doi.org/10.3897/neobiota.60.53730.

Ware, C., Bergstrom, D.M., Müller, E., Alsos, I.G., 2012. Humans introduce viable seeds to the Arctic on footwear. Biol. Invasions 14, 567–577. https://doi.org/10.1007/s10530-011-0098-4.