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HUMAN-MEDIATED SEED DISPERSAL
IN THE SWISS ALPS

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Master Thesis of Science in Behaviour, Evolution and Conservation, specialization « Geosciences, Ecology and Environment »

par

Marie BOLE-FEYSOT

Directeur : Prof. Antoine Guisan

Superviseuse : Dr. Sabine Rumpf

Expert : Anonyme

Département d'Ecologie et d'Evolution

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Abstract

English

Due to global warming, mountaintops are becoming increasingly suitable for low-elevation plant species. Compared to natural seed dispersal, human-mediated seed dispersal is quicker and targeted towards summits. This study aimed at assessing human-mediated seed dispersal in mountains. I sampled the footwear of 132 hikers for vascular plant seeds in the Swiss Alps and asked them to answer a survey concerning their habits as hikers. Material collected on shoes was sorted, and seeds were germinated under alpine conditions. To assess whether hikers impact summit vegetation, I analysed vascular plant records from 2010 and 2020 and summit frequentation for 2020. Results show an 11% increase in plant species richness on summits, but there was no relationship between human summit frequentation and the number of new species on these summits. I collected an average of 0.88 seeds per person, with hooky seeds and balloon-shaped seeds being more frequent than expected by chance. Lastly, seed dispersal on footwear was unintentional and people were ready to clean their shoes more often to reduce seed transport. Altogether, my findings indicate that hikers are selective seed-dispersal vectors in mountains. With growing interest in mountain activities, managing human-mediated seed dispersal might prove crucial to preserve alpine ecosystems.

French

Sous l’effet du réchauffement climatique, les conditions de vie sur les sommets montagneux deviennent propices aux espèces de plantes de basse altitude. Contrairement à la dispersion naturelle des graines, la dispersion par l'homme est plus rapide et ciblée vers les sommets. Cette étude vise à évaluer la dispersion des graines par l'homme en montagne. J'ai collecté les graines de plantes vasculaires transportées par les randonneurs sur leurs chaussures et leur ai demandé de répondre à un questionnaire concernant leurs habitudes en tant que promeneurs. Le matériel recueilli sur les chaussures a été trié et le potentiel de germination des graines dans des conditions alpines a été estimé. Pour évaluer si les randonneurs ont un impact sur la végétation des sommets, j'ai analysé des relevés de plantes vasculaires datant de 2010 et 2020, et j’ai estimé la fréquentation des sommets en 2020. Les résultats montrent une augmentation de 11% de la richesse d’espèces de plantes vasculaires sur les sommets, sans qu’il n’y ait de relation entre la fréquentation humaine et le nombre de nouvelles espèces sur les sommets. En moyenne, j'ai collecté 0,88 graines par personne. Les graines avec un crochet et les graines de forme sphérique étaient plus fréquentes qu’attendu par chance. Enfin, la dispersion de graines pas le biais des chaussures était non-intentionnelle et les participants étaient prêts à nettoyer leurs chaussures plus souvent pour réduire le transport de graines. Dans l'ensemble, mes résultats indiquent que les randonneurs sont des vecteurs sélectifs de dispersion des graines. Avec l'augmentation des activités touristiques en montagne, la gestion de la dispersion des graines par l'homme pourrait s'avérer cruciale pour préserver les écosystèmes alpins.

List of abbreviations

m.a.s.l. = meters above sea level

Table of content

List of Figures and Tables

Introduction

Ecosystems are threatened worldwide by ongoing climate change (Parmesan & Yohe, 2003; Wiens, 2016). Among others, global warming modifies living conditions in several environments, resulting in massive species redistributions (Bakkenes *et al.*, 2002; Haller *et al.*, 2013; Lenoir & Svenning, 2015). Plants are particularly sensitive to global warming because their dispersal is random. In Europe, more than 675 plant species are expected to become vulnerable by 2080 (Thuiller *et al.*, 2005). Mountain ecosystems are vulnerable because they experience higher warming rates than the global average (Fischlin *et al.*, 2007; Gobiet *et al.*, 2014; Pepin *et al.*, 2015). Low elevation habitats that were previously suitable are now becoming unsuitable for some species due to increased competition from newly colonizing species (Alexander *et al.*, 2015). To follow the conditions they are adapted to, species shift upward in elevation, a phenomenon known as upward range shift (Chen *et al.*, 2011; Lenoir *et al.*, 2008; Rumpf *et al.*, 2018b). If temperature was the only driver of range shifts, all species from the same environment should be shifting at the same rate. However, shift rates vary greatly among species (Chen *et al.*, 2011; Rumpf *et al.*, 2018b), suggesting that another phenomenon must be considered.

Each plant species has its own dispersal capacity because different dispersal vectors can result in a wide range of dispersal distances, and this is potentially responsible for the variability in range shifts (Engler *et al.*, 2009, Lenoir & Svenning, 2015). Dispersal is the movement of a reproductive plant propagule (hereafter called “seed”) away from the mother plant. During dispersal, seeds can travel long distances and provide plants with the capacity to geographically track changing environments (Tucker *et al.*, 2021). While most of natural dispersal vectors randomly disperse seeds in the environment, human-mediated seed dispersal in mountains is not random since hikers mainly walk from valleys to mountaintops and remain on trails (Bullock & Pufal, 2020; Pickering & Mount, 2010; Vittoz & Engler, 2007; Wichmann *et al.*, 2009). Hence, seeds are likely to be transported from low to high elevations, making humans possibly responsible for the observed upward range shift of some species. In addition, humans disperse seeds over greater distances than natural processes (Vittoz & Engler, 2007). Wichmann *et al.* (2009) showed that, while over half of the seeds detach from footwear within five meters, seeds are regularly still attached on shoes after five kilometers. In comparison, wind disperses seeds within approximately 250 meters. Overall, dispersal rates are significantly higher in areas with a high anthropogenic activity (Johnson *et al*., 2020). Under the hypothesis that people disperse the seeds of new species towards summits, highly frequented summits are expected to have more new species than less frequented summits. In addition, I expect certain seed morphologies to favor attachment on shoes and hence increase the probability of dispersal towards summits. Finally, only the seeds able to germinate and to survive during seedling stage under harsh mountain conditions have the potential to increase their range towards higher elevations.

The two most comprehensive studies on human-mediated seed dispersal on footwear were conducted in the Arctic (Ware *et al.*, 2012) and New Zealand (McNeill *et al.*, 2011). To the best of my knowledge, no study has assessed human-mediated dispersal and germination rates in the European Alps so far. Yet, the Swiss Alps attract more and more tourists every year (Haller *et al.,* 2013) increasing the probability of seed dispersal by hikers. Previous studies (Bullock & Pufal, 2020; Pickering & Mount, 2010; Ware *et al.,* 2012; Wichmann *et al.,* 2009) defined seed dispersal by humans as unintentional or accidental for it was implicitly assumed that people were not aware that they may transport seeds on their equipment. Yet, this assumption has never been assessed.

The main objectives of this study were to determine whether humans are seed-dispersal vectors in the Swiss Alps and whether vegetation changes are related to human presence. I used vascular plant species occurrences (hereafter called vegetation records) of eight summits in the Swiss Alps to assess changes in vegetation between 2010 and 2020. The frequentation of these summits was estimated based on records from summit books. Lastly, in order to determine what humans transport on their shoes, I collected material from the footwear of 132 hikers encountered in the same mountains and asked them to answer a survey about their habits as hikers. With this dataset, I addressed the following questions: **(1)** How has vascular plant species richness changed on summits between 2010 and 2020? **(2)** Is there a relationship between number of new species on summits and frequentation between 2010 and 2020? **(3)** Do humans transport seeds on their footwear in mountains? **(4)** Do certain seed morphologies favor or impede seed attachment on footwear? **(5)** Can seeds collected on footwear germinate under simulated local summer mountain conditions? and **(6)** How aware are humans of seed dispersal on footwear? A better understanding of human-mediated seed dispersal on footwear will be of great value to conservation programs in alpine ecosystems.

Materials and Methods

Study sites

The study took place in the canton of Grisons, in the Swiss Alps (eastern Switzerland). The Alps are one of the richest biodiversity hotspots in Europe (Agrawala, 2007), the region is of high wilderness quality (Haller *et al*., 2013; Radford *et al*., 2019) and hosts the Swiss National Park in which “nature is withdrawn from all human interventions” (Assemblée fédérale de la Confédération suisse, 1980). Although a clear definition of mountains is difficult to formulate, a consensus is that mountains are characterized by an inclination and ruggedness of land (Kapos *et al.*, 2000; Karagulle *et al.,* 2017; Körner, 2004; Körner *et al.,* 2021). The chosen study sites here are considered mountains in all of the definitions. Ten summits and their surrounded mountainous territories were selected based on four criteria:

- *Elevation:* I selected summits within a small elevation range to have data as comparable as possible and to minimize the random effect of elevation. The selected summits’ elevations were between 2,672 and 3,103 meters above sea level (m.a.s.l.; Figure 1).

- *Vegetation records:* I choose summits where vegetation of the uppermost ten meters has been surveyed in 2010 and 2020 for assessing the number of species which have newly arrived.
- *Summit books:* I used summit books present on mountaintops in which hikers can record their passage to assess visitor frequentation. Therefore, I selected summits for which the total number of entries in the book had been counted in summer 2020.
- *Accessibility:* summits had to be reachable by public transport and not be dangerous because I had no personal car and worked by myself.

The selected summits (hereafter called summits of interest) are Aroser Älpihorn (2,839 m.a.s.l.), Haldensteiner Calanda (2,805 m.a.s.l.), Monte Vago (3,059 m.a.s.l.), Piz Beverin (2,997 m.a.s.l.), Piz Daint (2,967 m.a.s.l.), Piz La Stretta (3,103 m.a.s.l.), Piz Tomül (2,945 m.a.s.l.), Rossbodenstock (2,837 m.a.s.l.), Strel Arosa (2,672 m.a.s.l.), and Valbellahorn (2,763 m.a.s.l.; Figure 1).

Samples were collected from hikers encountered on the summits of interest and on trails leading to these summits. Sampling elevations ranged between 1,700 m.a.s.l. and 2,970 m.a.s.l. (Figure 1, Appendix A). A project-presentation sheet translated into German, Rumantsch, English, French, and Italian was shown to the hikers (Figure 2, Appendix B). To take part in the study, participants agreed on material collection from their footwear and on answering an anonymous survey. Field work was conducted during two weeks in late July and early August 2021 (July 19th - 25th and August 2nd - 8th).

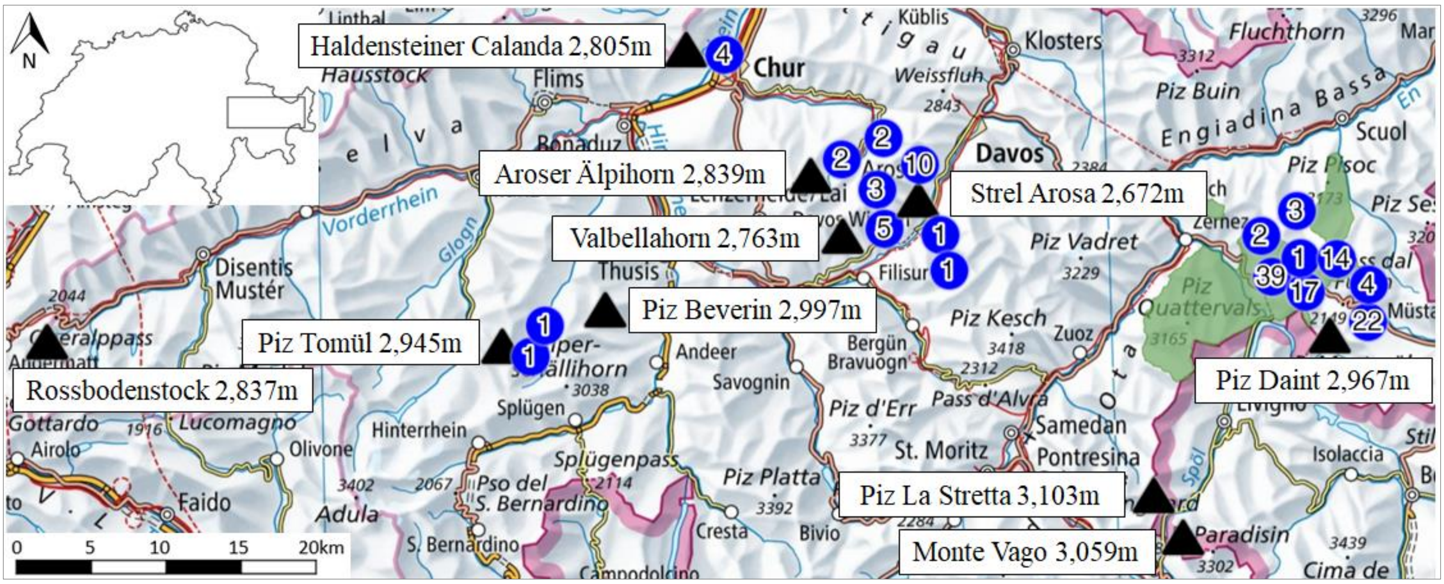


Figure 1. Map of the study area showing the summits of interest and the sampling locations. Black triangles are the ten summits of interest with their respective elevation in m.a.s.l.. Blue circles show the 18 sampling locations with the number of participants (i.e. sampling units). The green area delimits the Swiss National Park. Map made using SwissTopo (Office fédéral de topographie, 2021)

Footwear sampling

I collected the material transported on hikers' footwear to assess human impact on mountain ecosystems. For simplicity, I focused on footwear only and did not sampled pants or socks. Sampling equipment is shown on Figure 2. Soil was collected on site, directly from hikers' shoes. A sampling unit was considered as a pair of shoes. Participants placed their foot in a tray big enough to fit a hiking shoe in. Using a brush and a fork, the top and the sole of the shoe were cleaned until all visible material was removed (Figure 2). The soil collected was transferred into a freezer bag and each bag was tagged with a unique identifier (date and number) linked to the participants' survey (see below "Survey"). In between samples, sampling equipment was cleaned to avoid sample contamination (I removed visible material from the tray and from the brush). Lastly, samples were dried in the sun for three days until perfectly dry and stored in freezer bags for ten weeks at room temperature until the start of laboratory work.

Figure 2. Sampling equipment and example of sampling procedure. **Left**: sampling equipment used in the field to collect material on participant's footwear and for participants to answer the survey. A: jacket from the Swiss National Park. B: project presentation sheet (Appendix B). C: tablet to answer the survey (Appendix C). D: white tray with a flat base. E: brush. F: fork. G: 1-liter freezer bag. H: permanent pen. **Right**: footwear sampling while the participant answers the survey on the tablet on Valbellahorn. Pictures from Isabelle Bole-Feysot.

Sorting

To determine and quantify what humans transport on their shoes in mountains, collected material was sorted in the greenhouse of the University of Lausanne in September and October 2021.

Organic and inorganic matter was separated by putting soil into a glass and adding tap water. The mixture was stirred and left until inorganic matter sank and organic matter floated (approximately five minutes). The organic matter was separated using a 200µm sieve. Inorganic matter, accumulated at the bottom of the glass, was extracted using a spoon. Organic and inorganic matter were deposited separately on paper towels and placed into a dryer at 45°C for six hours until completely dry. Dry samples were manually sorted under the microscope (magnification 64× and 160×) using tweezers. Inorganic matter included gravel and sand while organic matter corresponded to living-being material which could be **(1)** dead organic matter such as plant fragments (leaves, branches, stems, bark, roots) or insects; **(2)** bryophytes fragments which may have the potential to re-grow; or **(3)** seeds which may germinate. Lastly, I found plastic fragments such as filaments from clothing or pieces of rubber. Overall, the material was separated into five categories (Figure 3) and stored in paper envelopes.

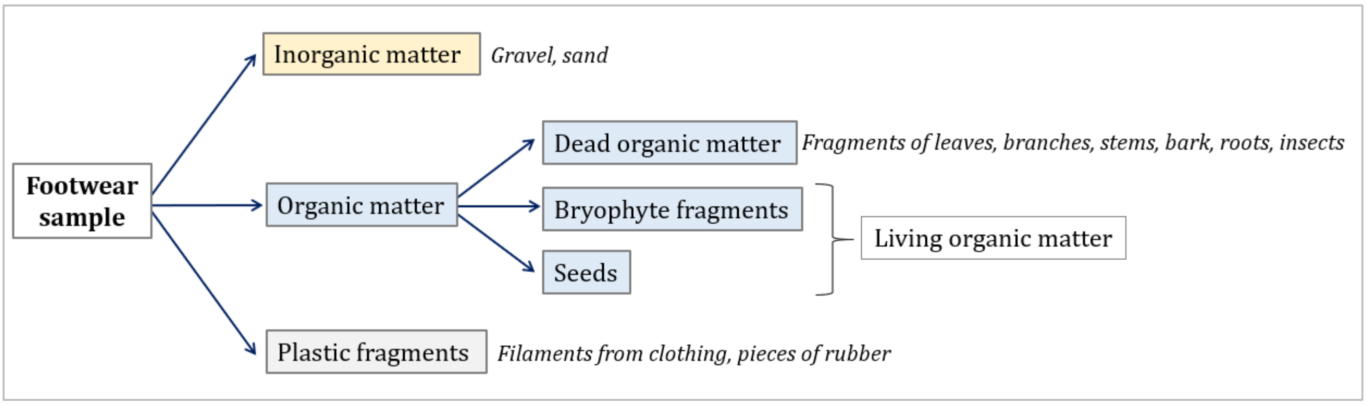


Figure 3. Samples were manually sorted into five categories: inorganic matter, dead organic matter, bryophyte fragments, seeds, and plastic fragments.

All material collected was weighted on a scale with a precision of 0.1mg. I used the weight to quantify material collected because it is the most relevant metric for the categories containing several small fragments (inorganic matter, organic matter…). In addition, measuring weight permits comparisons with other studies. For each sample, I measured the total weight (in grams), the presence of seeds (presence/absence), the number of seeds (count), the weight of seeds (in grams), the presence of bryophyte fragments (presence/absence), the weight of bryophyte fragments (in grams), the presence of plastic fragments (presence/absence), the weight of plastic fragments (in grams), the weight of dead organic matter (in grams), the weight of living organic matter (in grams, calculated as *weight of bryophyte fragments + weight of seeds*), and the weight of inorganic matter (in grams, calculated as *total weight – weight of plastic fragments – weight of living organic matter – weight of dead organic matter*).

Seed morphology

To assess whether some seed shapes favor attachment on footwear, the morphology of seeds was determined following Römermann *et al.* (2005) using a microscope (magnification 64× and 160×). Seed were classified into five categories: no appendage, elongated appendage, hook, balloon shape and flat appendage (Figure 4).

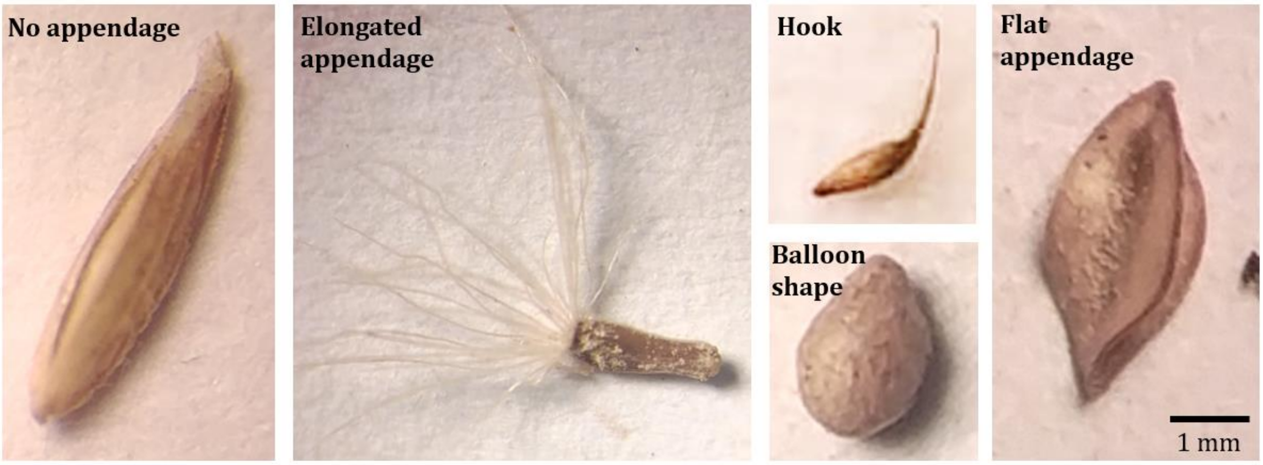


Figure 4. The five seed morphology categories according to Römermann *et al.* (2005), observed under a microscope (magnification 160×)

Control seeds

To ensure results concerning seed germination were reliable, 49 control seeds were collected on October 10th, 2021 in the massif des Bauges in France at 1,400 m.a.s.l.. For practical reasons, control seeds were collected in France and not Switzerland, but since the collection site is still in the Alps, results remain reliable. Because my hypothesis is that seeds from footwear have been transported up in elevation, control seeds have been collected at a lower elevation than my sampling locations. I collected seeds with an elongated appendage (one species, 16 seeds), seeds with a hook (one species, 10 seeds) and seeds with no appendage (one species, 23 seeds). I collected these seeds late in the season in fall to increase the chances to have mature seeds. In addition, control seeds had not been transported on people' shoes and did not suffer from any mechanical abrasion. They served to test whether the growing medium and the growing conditions were adequate for germination.

Germination

Germination rate was measured to estimate the capacity of plant species to establish via human-transported seeds. All following steps were performed the same way for control and footwear seeds. When dispersed in mountains, seeds usually spend a winter under the snow before germinating in spring. To mimic winter mountain conditions, seeds were exposed to cold and humidity. This process, called cold stratification, aims at triggering seed germination (Fernández-Pascual *et al.*, 2021; Yamauchi *et al.*, 2004). Seeds were placed on a wet paper

towel that was kept humid in a fridge at 1°C for 21 days (October 15th - November 5th 2021). To avoid contamination with bacteria and fungi, which may prevent germination, all seeds were sterilized with 70% ethanol for ten minutes, rinsed with 90% ethanol, and dried afterward. Under a laminar flow hood, seeds were deposited in petri dishes on a plant-specific growing medium composed of ½ Murashige & Skoog medium (Murashige & Skoog, 1962) with 1% plant agar. Gibberellic acid was added to the growing media to break seed dormancy and trigger germination (Yamauchi *et al*., 2004). Each single seed was carefully checked before being placed in a petri dish to ensure none was rotten or empty, and I did find some empty seeds. Finally, petri dishes were closed using micropore tape (allows gas exchanges but prevents contamination) and placed in a phytotron.
To assess germination rate in natural conditions, weather conditions of the sampling locations were simulated in the phytotron (Percival Scientific Inc, 2020). Mean climatic surface conditions from summits in the Grisons at similar elevation as the summits of interest were selected for the period June-September 2021 (Appendix D). I determined the duration of light and dark cycles, temperature and relative humidity for each cycle, as shown on Figure 5. Seeds were visually checked every 4 days to detect germination. The criterion for germination was a visible protrusion (≥2mm; Peng *et al.*, 2017). Seeds stayed in the phytotron for 63 consecutive days between November 5th, 2021 and January 7th, 2022.

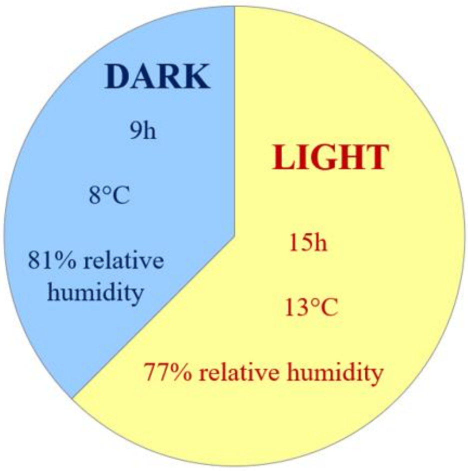


Figure 5. Growing conditions over a 24-hours cycle set in the phytotron to simulate natural conditions of the sampling locations for the period June-September 2021 at soil surface

Reference dataset

To compare the subset found on hiker's shoes to the natural pool of Alpine plant species, I used a reference dataset which was a list of the most common vascular Alpine species (Rumpf *et al.* 2018a). Seed morphology was given for 414 species, and germination rate was given for 156 species. I considered that the proportions observed in this dataset were the proportions expected by chance.

Summit frequentation

To estimate humans summit frequentation, I used the number of entries in summit books in 2020 for the summits of interest (Figure 1). One entry corresponds to one person who wrote something in a book. Since books have different starting dates, I calculated the mean daily number of entries since the beginning of the book. This metric is relative since not all hikers write in the summit book. In addition, I used the number of entries, and one entry may correspond to a different number of hikers. However, since this bias applies to all summits, counts may in general be an over- or underestimation but remain comparable between summits and it does not affect my analyses.

Yet, two summits were more frequented than the eight others. Piz Beverin and Haldensteiner Calanda had respectively 16.84 and 4.67 mean daily entries in their summit books, while the others had less than one (Table 1). I calculated the leverage effect of these summits which refers to the extent to which the coefficients in the regression model (detailed in the "Statistical analyses" section) would change if a particular observation was removed from the dataset. For both summits, leverage effects were approximately nine times greater than those of the other summits, meaning that the model significantly changed when Piz Beverin and Haldensteiner Calanda were not considered.

Personal observations lead me to realize that these two summits are very popular in the Grisons and are indeed highly frequented. They are both only a few kilometers from Chur, which is the main city of the canton and is a gateway for mountain activities. Haldensteiner Calanda and Piz Beverin are emblematic summits, and many hikers may want to record their passage in the summit books. I heard the testimony of a hiker who told me that in general she rarely notes her passage in summit books, but that for Haldensteiner Calanda she wrote in the book because this hike was special to her.

Thus, data in summit books for these two mountains could have been biased because they were probably more representative of reality than the other summits of interest due to their popularity. The frequentation of the other eight summits was probably underestimated, explaining the high leverage effect of Piz Beverin and Haldensteiner Calanda. For these reasons, I excluded Piz Beverin and Haldensteiner Calanda from vegetation analyses, summit book counts and generalized linear model. The eight remaining summits are: Aroser Älpihorn (2,839 m.a.s.l.), Monte Vago (3,059 m.a.s.l.), Piz Daint (2,967 m.a.s.l.), Piz La Stretta (3,103 m.a.s.l.), Piz Tomül (2,945 m.a.s.l.), Rossbodenstock (2,837 m.a.s.l.), Strel Arosa (2,672 m.a.s.l.), and Valbellahorn (2,763 m.a.s.l.; Figure 1).

Summit vegetation

I used lists of vascular plant species consisting of 11–68 species observed on each summits of interest (Figure 1). Because some records indicated subspecies while others only the species, I considered for all records species level when comparing data. In addition, I checked for synonyms using The Plant List (*The Plant List*, 2013) to ensure I did not double count some species.

Surveys

All 132 participants were asked to answer an anonymous eight multiple-choice questions survey those aim was to determine participants profile and habits in mountains, and to assess awareness of human mediated seed dispersal (Appendix C). For each question, people had to select among the answers proposed. General questions concerned home country, age, job, and whether people work outdoors. Mountains-related questions were how often participants are in the mountains, and where they hiked since they last cleaned their shoes. Finally, questions regarding shoe maintenance were why and how often participants clean their shoes.

The survey was created using the software KoboToolBox (Vinck *et al.*, 2021) and was presented to the participants using a tablet (Figure 2). KoboToolBox offers the possibility to collect data while being offline, which was convenient in the mountains. Participants could choose the language of the survey among German, English, French and Italian (Appendix C). Once completed, surveys were tagged with the same unique identifier as their footwear sample.

Statistical analyses

All analyses were conducted using the statistical programming software R version 4.0.3 (RStudio Team, 2020). Graphics were created with the package "ggplot2" (Wickham, 2016).

First, I assessed the number of species that were present in 2020 but absent in 2010 in the uppermost ten meters of each summit. These species, which have colonized summits between 2010 and 2020, are considered "new species" and will be called as such in the following. The percentage of new species on each summit was calculated as follows:

$$Percentage\ of\ new\ species\ in\ 2020 = \frac{number\ of\ new\ species\ in\ 2020}{total\ number\ of\ species\ in\ 2020} \times 100$$

To quantify the relative change in species richness between 2010 and 2020, I calculated the percentage of change in species richness for each summit as follows:

$$Percentage\ of\ change\ in\ species\ richness = \frac{nb\ species\ in\ 2020 - nb\ species\ in\ 2010}{nb\ species\ in\ 2010} \times 100$$

Second, I assessed whether human frequentation affects the colonization of vascular plant species on the summits of interest using a generalized linear model with a Poisson distribution and a logarithmic link function (function "glm"). More precisely, I used the mean daily number of entries in summit books as predictor variable and the number of new species per summit as response variable. The package "effect" was used (Fox, 2019).

Third, in order to detect whether some seed morphologies favored attachment, I looked for any dominant morphologies among the seeds transported on footwear. I took the reference dataset as a theoretical proportion and compared it with the collected seeds (empirical proportion). For each of the five morphologies, I performed an exact two-sided binomial test (function "binom.test"). Each test required (1) the number of successes (number of seeds collected with the morphology of interest), (2) the number of trials (total number of seeds collected, N=116), and (3) the probability of the null hypothesis (proportion of seeds with the morphology of interest in the reference dataset). The hypothesis that a morphology was significantly more present on footwear than expected by chance (that is, in the reference dataset) was accepted when the *p-value* was inferior to 0.05.

Fourth, I analyzed the answers to the surveys given to the hikers. I calculated the percentage of people who selected each answer.

Results

Unless stated differently, standard errors are given after the mean values (± SE).

Richness change and new species on summits

The number of species increased on five out of the eight summits of interest and decreased for Aroser Älpihorn, Monte Vago and Strel Arosa. On average, vascular plant species richness increased by 10% between 2010 and 2020 (Table 1).

Nonetheless, new species have appeared on all eight summits of interest between 2010 and 2020, with a mean of 12 (±2.7) new species per summit (median 13), corresponding to a rate of 1.2 new species per year. The minimum number of new species was recorded in Monte Vago (three new species), and the maximum was 22 new species in Rossbodenstock (Table 1). On average, 31% (±5.3) of the species observed in 2020 were new (i.e. were not present in 2010; median 33%). The highest percentage of new species was 53% on Valbellahorn and the smallest was 9% on Aroser Älpihorn and Monte Vago.

Summit frequentation and new species on summits

The mean daily number of entries in summit books for the eight summits of interest was 0.41 (±0.12) entries, with a median of 0.36. The minimum was 0.01 entries per day for Strel Arosa and the maximum was 0.97 for Valbellahorn (Table 1). There were on average 0.39 (± 0.33) new species per daily number of entries in summit books but this relation was not significant ($df = 7$, $Z = 1.181$, $p = 0.237$; Figure 6). Including all ten summits yielded qualitatively identical results (Appendix E).

Table 1. Number of species in 2010 and 2020 and mean daily number of entries in summit books for the eight summits of interest

Summit	2010	2020			Percentage change of species richness	Mean daily number of entries in summit book
	Number of species	Number of species	Number of new species	Percentage of new species		
Aroser Älpihorn	68	47	4	9 %	-31 %	0.07
Monte Vago	39	32	3	9 %	-18 %	0.34
Piz Daint	25	27	9	33 %	8 %	0.78
Piz La Stretta	11	13	5	38 %	18 %	0.37
Piz Tomül	40	50	20	40 %	25 %	0.35
Rossbodenstock	51	67	22	33 %	31 %	0.39
Strel Arosa	55	52	16	31 %	-5 %	0.01
Valbellahorn	22	34	18	53 %	55 %	0.97
MEAN	*39*	*40*	*12*	*31 %*	*10 %*	*0.41*

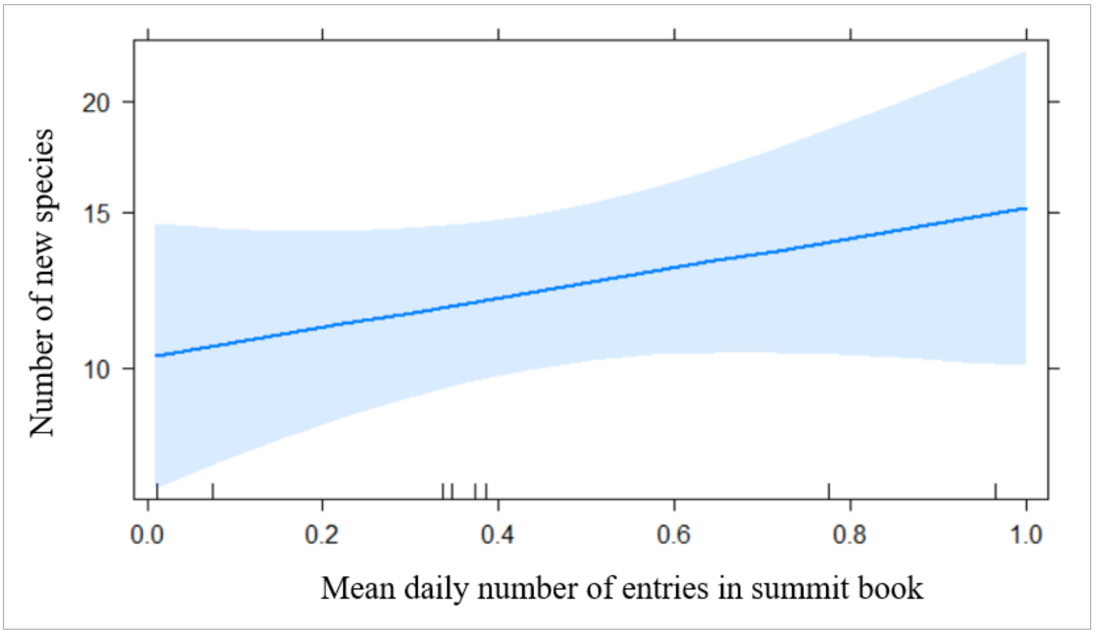


Figure 6. Relationship between mean daily number of entries in summit books and number of new species in 2020. Regression based on a generalized linear model with a Poisson distribution and a logarithmic link function. The relationship is not significant (*df* = 7, *Z* = 1.181, *p-value* = 0.237). Mean daily number of entries in summit book is calculated based on the total number of entries in the book at the time of record. New species are species present in 2020 but absent in 2010 in the uppermost ten meters of the summit. Shaded area is the 95% confidence interval.

Footwear samples

In total, I sampled the footwear of 132 persons and collected 296.005g of material. Participants transported a mean of 2,24g (± 0.64) of material per person, with a minimum, median, and maximum of $4.1 \cdot 10^{-3}$g, 0.43g, 76.27g respectively. Samples were composed of 94% (278g) inorganic matter, 5.94% (17.8g) dead organic matter, 0.03% ($9.7 \cdot 10^{-2}$mg) bryophytes fragments, 0.02% ($6.2 \cdot 10^{-2}$g) seeds and 0.01% ($4.6 \cdot 10^{-2}$g) plastic fragments (Figure 7).

I collected a total of 116 seeds, corresponding to a mean of 0.88 (± 0.17) seeds per sample. Seeds occurred in 44 (33%) of the samples, and participants who had seeds attached on their footwear transported on average 2.64 (± 0.4) seeds, with a minimum, median, and maximum of 1 seed, 2 seeds and 17 seeds, respectively (Figure 8).

All 116 seeds weighted in total 62.4 mg. On average, each participant was transporting 0.47 (±0.11) mg of seeds. Participants with seeds attached on their footwear were transporting a mean of 1.42 (±0.27) mg of seeds with a median and a maximum of 0.95 mg and 9.1 mg respectively.

Eighty-five participants (64%) were transporting plastic fragments, and 45 (34%) were transporting bryophytes fragments on their footwear.

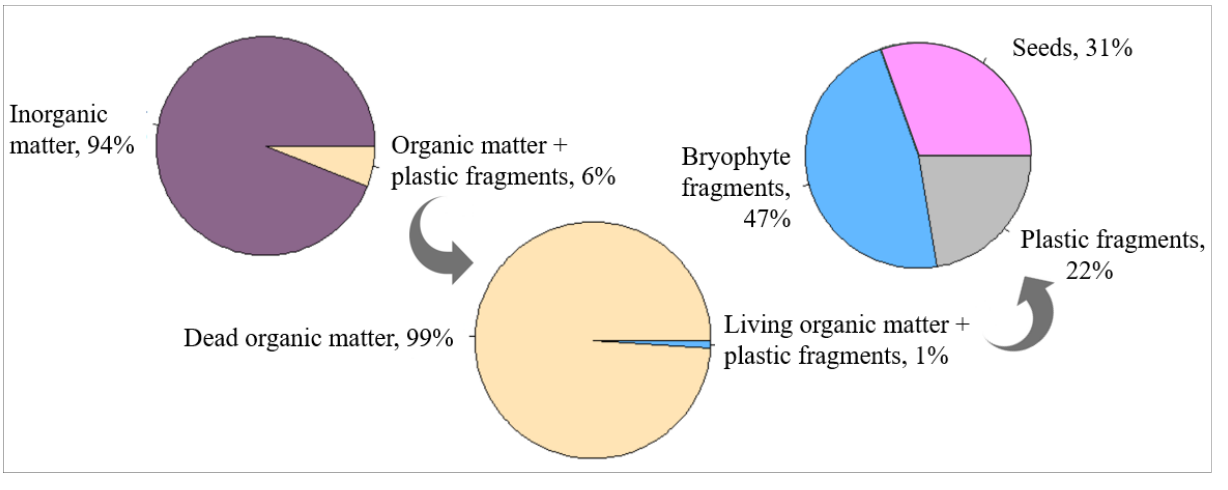


Figure 7. Composition of the material collected on the footwear of 132 hikers

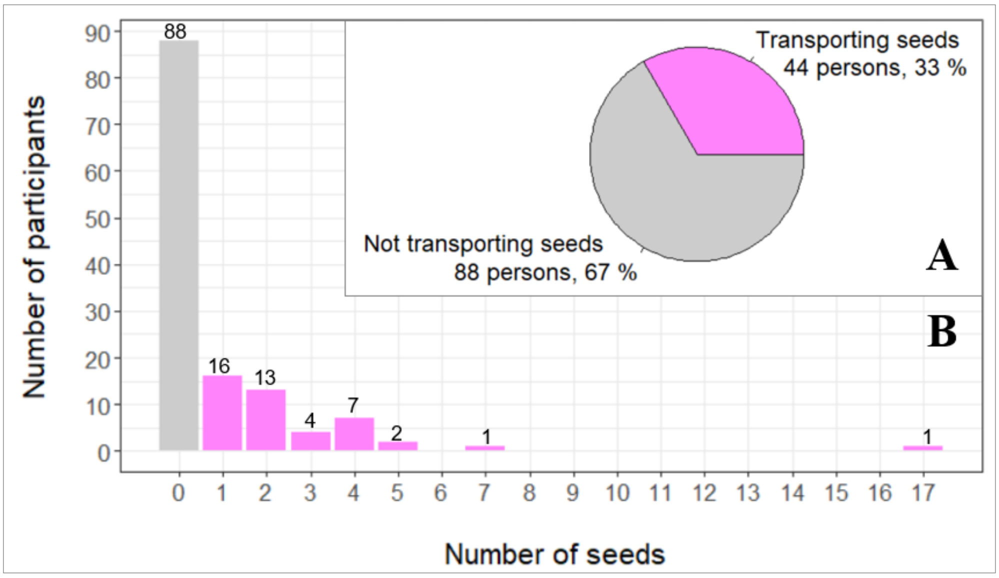


Figure 8. Seed transport of the footwear of the 132 participants. **(A)** Proportion of participants transporting seeds. **(B)** Number of seeds transported

Seed morphology on footwear and reference dataset

Significantly more seeds with a balloon shape (*p-value* $< 2.2 \cdot 10^{-16}$) or with a hook (*p-value* $= 1.8 \cdot 10^{-4}$), and significantly less seeds with an elongated appendage ($p = 3.4 \cdot 10^{-16}$) were collected on footwear than expected by chance. There was no significant difference in the number of seeds with a flat appendage (*p-value* = 0.1472), nor with no appendage (*p-value* = 0.6411) collected on footwear compared to the expectation by chance (Table 2, Figure 9).

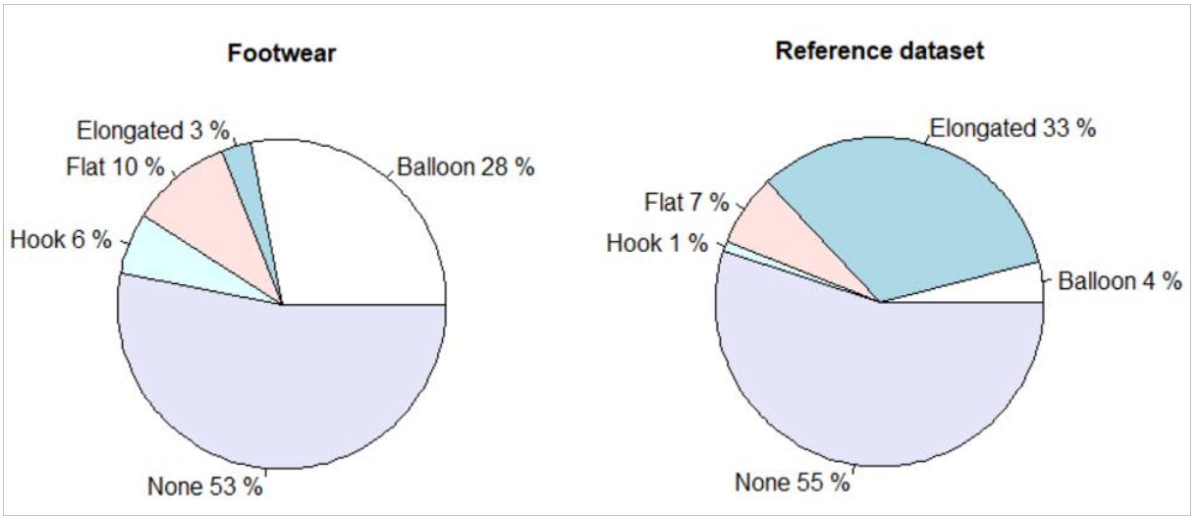


Figure 9. Proportion of the five seed shapes collected on hikers' footwear (left, N=116 seeds), and among the reference dataset (expectation by chance; right, N=414)

Table 2. Results of the exact two-sided binomial test to assess whether seed shapes differ between the footwear samples and the reference dataset.

Seed shape	Reference dataset		Footwear		Exact two-sided binomial test	
	Number	Percentage	Number	Percentage	*p-value* *(* significant)*	95% confidence interval
Balloon	15	4 %	33	28 %	$< 2.2 \cdot 10^{-16}$ *	0.21, 0.38
Elongated	138	33 %	3	3 %	$3.4 \cdot 10^{-16}$ *	0.01, 0.07
Flat	29	7 %	12	10 %	0.1472	0.05, 0.17
Hook	3	1 %	7	6 %	$1.8 \cdot 10^{-4}$ *	0.03, 0.12
None	229	55 %	61	53 %	0.64	0.43, 0.62
TOTAL	*414*	*100 %*	*116*	*100 %*	-	-

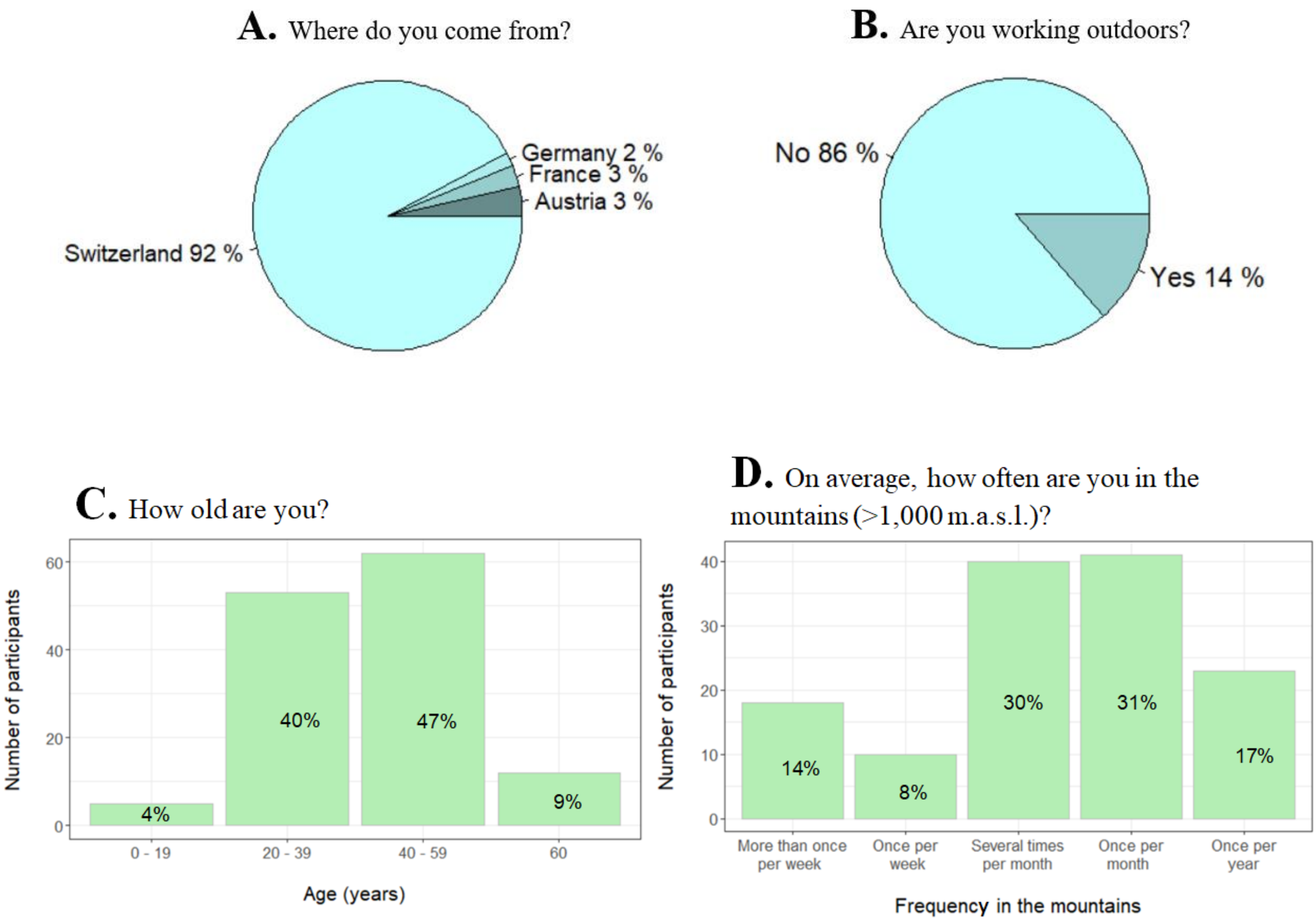
Germination

Among the 116 seeds collected on footwear, one seed germinated under the simulated mountain conditions (Figure 10), representing a germination rate of 0.86%. The seed which germinated was collected on footwear at 2333 m.a.sl. and germinated after ten days in the phytotron. In comparison, the mean germination rate of Alpine species is 72% (± 2.34; based on 156 species of the reference dataset). The 115 remaining seeds I collected did not germinate and neither did the control seeds. Petri dishes have been contaminated with fungi and bacteria (Figure 10).

Figure 10. Examples of seeds set for germination under mountain summer conditions after 63 days in the phytotron. **Left:** none of the 49 control seeds germinated. **Right:** one seed collected on footwear germinated among the 116 seeds collected. Mold has developed in the petri dish (dashed circle)

Hiker data

Most participants came from Switzerland and only a small fraction came from neighbouring countries. More than three quarters said that they were not working outdoors. The most represented age class was 40 – 59 years, followed by 20-39 years. Many participants were on average once or several times per month int the mountains (>1,000 m.a.s.l.). Only a small fraction of participants cleaned their shoes after each hike, and most cleaned them a few times per year or never. Since they last cleaned their shoes, half of the participants hiked in the Grisons, and the other half hiked in other regions of Switzerland. Hikers mainly cleaned their shoes because they were dirty, some did it to keep them in good condition, and no one cleaned shoes to prevent seed dispersal. Many participants would consider cleaning their shoes if they knew they may transport seeds of invasive species. A small fraction would not because they did not want to be bothered by it, they did not have time or were sure that they did not transport seeds of invasive species (Figure 11).



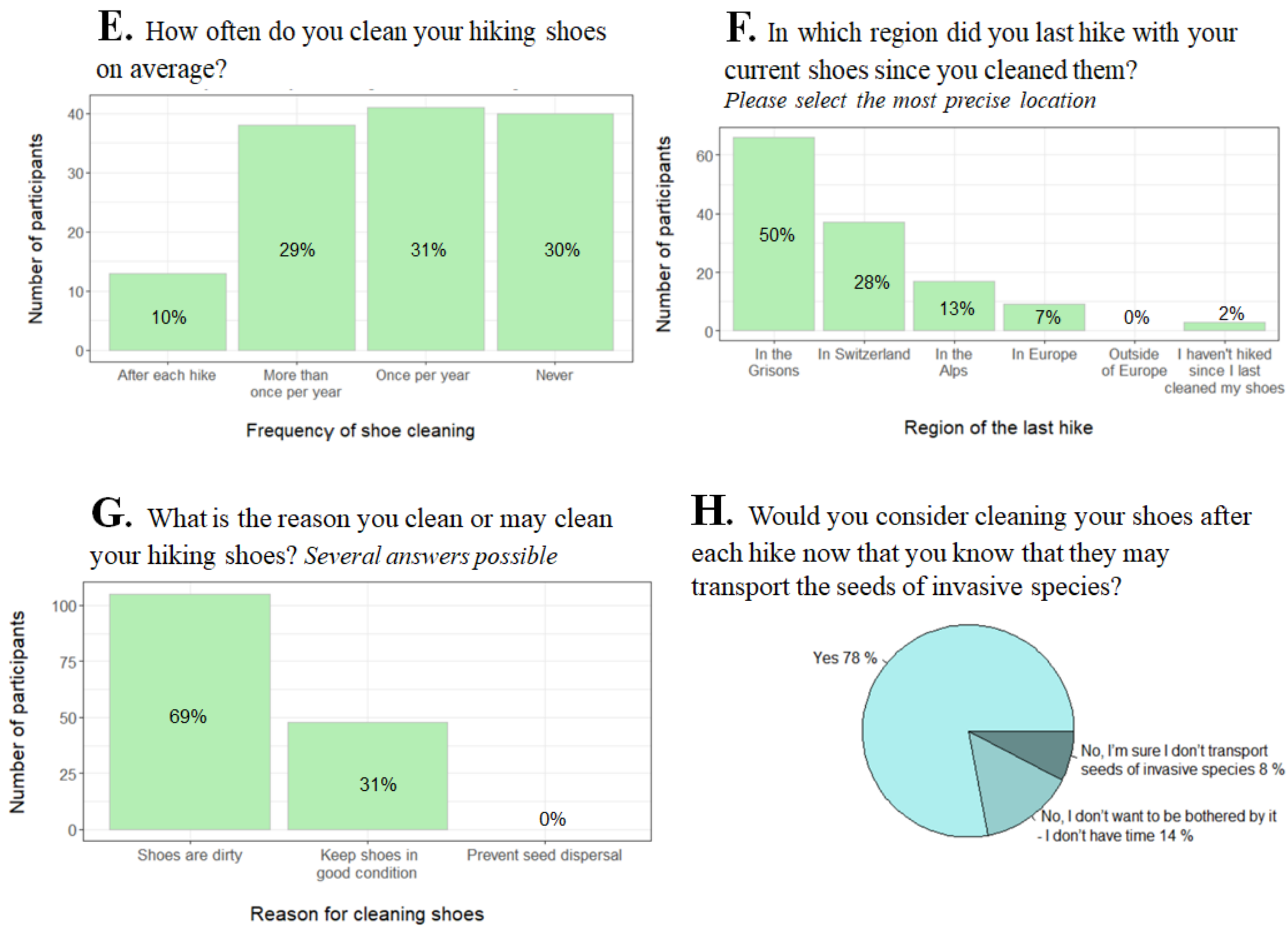


Figure 11. Results from the eight-questions survey given in the mountains to the 132 participants concerning their habits as hikers.

Discussion

This study shows an overall increase of vascular plant species richness in the summits of interest, and new species have established on all of these summits during only one decade. A third of the hikers were transporting seeds on their footwear, confirming the hypothesis that humans are vectors of seed dispersal in the Swiss Alps. However, I found no relationship between human summit frequentation and the number of new species. Furthermore, I was not able to assess whether the transported seeds can germinate under simulated mountain conditions, and the viability of the seeds collected on footwear thus remains unknown. Seeds with hooks and seeds with a balloon shape were more frequent than expected by chance on footwear, while seeds with elongated appendages were underrepresented. This finding reveals that seed dispersal by humans is selective, with some seed morphologies favoring or disfavoring attachment on shoes. Lastly, hikers were not aware of being seed dispersal vectors, and most of them were ready to change their behavior to prevent seed dispersal.

Richness change and new species on summits

Results show a 10% increase of vascular plant species richness on summits of interest between 2010 and 2020, in line with previous studies. Holzinger *et al.* (2008) calculated in 2004, based on records from the 120 previous years, an increase in vascular plant species richness of 11% per decade on 12 summits in the Grisons. In addition, my findings give support to the work of Steinbauer *et al.* (2018) who showed a continent-wide increase in richness change based on 302 European mountain summits spanning 145 years. New species have established on all summits of interest and one third of the species found in 2020 were absent in 2010. The presence of new species on summits means they found suitable conditions there even though several filters could have prevented dispersal, germination, and establishment in a new environment (D'Amen *et al.*, 2018; Scherrer *et al.*, 2019). First, a source population must produce viable seeds that are transported to a mountaintop via a dispersal vector (dispersal filter). Second, abiotic conditions like temperature or soil composition as well as biotic conditions such as competition or facilitation must be favourable for germination (germination filter). Lastly, abiotic and biotic conditions have to remain favorable for the individual's persistence in the long term. An example of species interaction can be competition for light. A species with large leaves can overshadow another species, slowing down its development. The increase of species richness on summits means that ecological filters have changed and now make the establishment of new species possible. Species originally present on summits will then have to cope with the arrival of low-elevation more competitive species. Ultimately, this might lead to a restructuration of alpine ecosystems with new competitors and new challenges for alpine species.

Some summits show a decrease of species richness but still have new species establishing, meaning species have been replaced by others. This process is called species turnover and describes changes in species composition resulting from the extinction of some species and the immigration of others and involves species competition as well as climatic conditions (Ndiribe *et al.*, 2014). Put it differently, species richness can remain constant while species composition is changing markedly, highlighting the importance to also look at which species are present in addition to the species number. Descombes *et al*. (2017) showed that turnover rates in the Western Swiss Alps vary with elevation, with highest rates around 1,800 – 2,200 m.a.s.l..

Summit frequentation and new species on summits

I encountered 132 hikers during the two weeks of fieldwork, confirming that summits in the Grisons are frequented by humans in summer. I found a high variation in summit frequentation. Some summits with no trails and no signs were very little visited (Strel Arosa, Aroser Älpihorn), while others were more popular and attracted more hikers (Valbellahorn, Piz Daint). Two summits were removed from the analysis (Haldensteiner Calanda and Piz Beverin) because they were not comparable to the eight others due to their high popularity. The use of summit books to assess the number of people on summits is not an exact metric and results on summit frequentation should hence be considered with care.

I found no significant relationship between human summit frequentation and the number of new species. A possible explanation might be that, as previous studies showed, human presence impacts ecosystems negatively by trampling. For example, Barros & Pickering (2015) and Cole & Monz (2002) measured a reduction of vegetation height and cover after human trampling. More humans do hence not necessarily mean more species since hikers are associated with disturbance and trampling, which can hinder species establishment, robustness and/or persistence. In addition, hikers may play a role in species turnover because they bring species to the summits while contributing in the meantime to the reduction of other species through trampling.

Although non-significant, the regression I obtained for the relationship between summit frequentation and new species shows a positive trend worth exploring. It would be interesting to conduct a complementary study with more summits of different frequentations and popularities to assess whether the observed tendency is confirmed.

Footwear samples

One third of the hikers were transporting seeds on their footwear, validating the hypothesis that humans are vectors of seed dispersal in mountain ecosystems. Contrary to animals, hikers start to walk at low altitudes with the mountaintops as goal and remain on trails. Due to this targeted movement, humans may speed up the colonisation of high elevation habitats by low elevation species by providing them with a mean to shift their range upward faster than they would have done naturally. Human-mediated dispersal could be a mean for species to overcome their natural dispersal limitations and may allow them to keep pace with climate change. Overall, such species might be the winners of the ongoing climatic changes.

A side-result of this project was that not only seeds, but also plastic fragments are transported on footwear, meaning plastic fragments can be found in remote locations such as mountains. This alarming finding is in line with Negrete Velasco *et al.* (2020) who found plastic fragments in a Swiss alpine lake. Such pollution negatively affects ecosystems (Li *et al.*, 2018) and reminds that humans have an impact on the entire planet.

The quantity of material (all components, not only seeds) I collected per participant is of the same order of magnitude as found by McNeill *et al.*, (2011) and Ware *et al*. (2012) who respectively sampled passenger's footwear at airports in New Zealand and on Svalbard. However, I found much less seeds than these two studies (0.88 seeds per sample compared to 3.9 seeds per sample for both McNeill *et al.* (2011) and Ware *et al*. (2012)). One explanation could be that alpine ecosystems contain less seeds than the ecosystems frequented by the passengers sampled at the airports. Namely, Ware *et al.* (2012) found that walks in forests result in a higher seed load compared to other environments. Ware *et al.* (2012) also showed that scientists carry more seeds on footwear than the average, and many scientists travel to Svalbard for research, probably more than in the Grisons. The presence of bryophyte fragments and plastic fragments on footwear is consistent with McNeill *et al*. (2011) and Ware *et al.* (2012).

Seed morphology on footwear and reference dataset, and attachment rate

Significantly more seeds with hooks and seeds with a balloon shape are transported by humans on their footwear in mountains than expected by chance, suggesting these morphologies promote attachment on shoes. Hooky seeds favoring attachment on shoes is in agreement with Auffret & Cousins (2013) and Johnson *et al.* (2020). By contrast, seeds with an elongated appendage were less present than expected by chance. These results indicate that human-mediated seed dispersal is selective since not all seeds have the same probability to attach on footwear. Species with seeds attaching easily on shoes may arrive first on summits and benefit from the priority effect. Priority effect occurs when one or more species arrive earlier or grow faster than others and leads to a different community structure than would form if all species arrived or began to grow simultaneously (Dickson *et al.*, 2012). Hence, because early arriving species can drive community assembly, the ecosystem that will develop on summits may be co-determined by the species initially transported on footwear (Bullock & Pufal, 2020). If selective seed dispersal by humans occurs on summits at large scale, a homogenization of vascular plant species on summits could be expected (Jurasinski & Kreyling, 2007).

Results show a high variability in seed pick-up rates, with one third of participants transporting between 1 and 17 seeds. Seeds can be transported both on the top and on the sole of the shoe. On the top, seeds are mainly attached or deposited, while on the sole, seeds either stick in the profile or are transported in the mud accumulated on the sole (personal observations). Factors determining pick-up rates can be classified in three categories: seed characteristics, human characteristics, and trail characteristics (Jurasinski & Kreyling, 2007).

Seed characteristics. Not only seed morphologies but also seed exposition height and distance to the trail plays a role in attachment rate. Indeed, low-growing vegetation close to the trail is more likely to deposit seeds on shoes compared to higher and more distant vegetation because seeds can be directly in contact with the shoe (Liedtke *et al.*, 2020).

Human characteristics. Heavier walkers carry more soil because they exert more pressure on the ground, and, counterintuitively, low profile shoes carry more soil than high profile shoes (Werner *et al.*, 2019). The effect of shoe size is controversial since Werner *et al.* (2019) found that larger shoes carry more soil, while Wichmann *et al.* (2009) did not find any effect of shoe size on seed pick-up rates. Human behavior is also expected to play a role, with hikers going off trail probably bearing more seeds.

Trail characteristics. Humid soils and soils with a high clay content favor soil transport on footwear (Werner *et al.* 2019). Not surprisingly, bare soils and landscapes with scarce vegetation have lower pick-up rates than vegetated areas. Some of my samples came from rocky areas with no vegetation, while others were collected on grassy areas. I observed that grassy samples seem to have more seeds than rocky ones, a finding that may deserve to be studied further.

Pickering & Mount (2010) highlighted that weather and time of the year play a considerable role in pick up rates, with obviously more viable seeds transported after the growing period, when seeds are mature. Under wet conditions (rain, dew, rivers, snowmelt…), soil sticks more easily on footwear, and if seeds are contained in the mud, they are transported on hikers' shoes.

Indeed, the sample containing 17 seeds was collected in a meadow at 2,074 m.a.s.l. during a rainy day, and the hiker had big quantities of mud on her or his footwear (76g of material, 33 times more than the mean). This person had the most material on her or his footwear as was the one transporting the most seeds among all participants.

Germination

The germination rate of 0.86% is extremely low compared to the results of Ware *et al.* (2012) (26% germination) and to the mean germination rate the reference dataset (72% germination). Seeds may have been viable at the time of collection and render non-viable after transport on footwear due to the shoe mechanical abrasion. If validated, this finding would mean that plant dispersal on footwear can not result in establishment because seeds are broken. However, this hypothesis is very unlikely since none of the control seeds germinated, suggesting a technical problem rather than a biological phenomenon.

I suggest four hypotheses why seeds did not germinate: (**1**) The cold stratification period was not long enough or inadequate to mimic winter conditions, and despite the hormonal treatment with gibberellic acid (which aims at breaking dormancy) seeds may still have been dormant when placed in the phytotron. I selected 1°C because, at the elevations of the summits of interest, seeds mainly spend winter under the snow which forms a protective layer that prevent temperature from falling below 1°C approximately (Körner, 2003). In comparison, Yamauchi *et al.* (2004) put them at 4°C and Ware *et al.* (2012) at -20°C. (**2**) Seeds did not stay long enough in the phytotron and did not have time to germinate. Previous studies observed seeds from footwear germination in less than 56 days (Alsos *et al.*, 2011; Hughes *et al.*, 2010; Ware *et al.*, 2012) but they applied favorable temperatures and 24h-light while my seeds grew under harsher mountain conditions. (**3**) Conditions in the phytotron were too harsh for the seeds to germinate. Although the aim was to mimic summer mountain conditions, the variation seeds may experience in the natural environment were not reproduced precisely in the phytotron. For example, it is possible that particularly hot summer days play a role in triggering germination, and seeds in the phytotron did not experience such changes in temperature. (**4**) Seeds were colonized by fungi and bacteria. Despite the precautions taken during sowing (sterilisation and manipulations under laminar flow hood), fungi and bacteria developed in petri dishes and might have profoundly decreased germination rates.

Hiker data

Mountains in the Grisons are mainly visited by people from Switzerland, suggesting that most of the seeds came from local environments. However, these results are possibly impacted by the Covid19 pandemic and people may have traveled more within their country due to travel restrictions. Hence, I can expect more hikers coming from foreign countries under a non-pandemic situation, and these visitors may bring on their footwear seeds from more distant ecosystems. As a consequence, exotic species could be introduced to the local species pool.

The majority of the participants were between 20 and 49 years old. Although I tried to sample everyone passing by, asking kids to fill in the survey was not always possible, and their footwear sample was then discarded. The number of participants aged between 0-19 years old is thus likely underrepresented. Under the assumption that children hop around and go off-trails more than older people, kids might have a higher seed load on their shoes compared to adults, even though they weigh less and are thus less likely to collect mud on their soles. The number of collected seeds may hence be underestimated.

Low shoe cleaning frequency combined with participants regularly making consecutive hikes in similar environments results in a high establishment potential because seeds are dispersed in an environment comparable to their origin. Ultimately, this can increase species range because species can settle on habitats where they were not present before. In addition, people remaining in the same region for hiking decreases the potential of introducing species from other regions and continents, which may threaten alpine ecosystems if introduced species are more competitive or even invasive. Yet, the threat does not only come from invasive species, and generalist species from the valleys can be competitive to alpine specialized species on summits (Alexander *et al.*, 2015).

Although no participant spontaneously answered she or he cleans her or his shoes to prevent seed dispersal, a majority would consider doing so if they knew they transported seeds of invasive species. This study confirms the previously untested assumption that seed dispersal on footwear is unintentional.

Future implications

Multiple dispersal vectors

As proposed by Wichmann *et al.* (2009), seeds can be dispersed by wind on trails. The round structure and the hardness of the balloon-shaped seeds favors blending with mud on trails which may attach on hiker' shoes and be transported further away. This hypothesis suggests seeds might already have been dispersed via another mean before dispersing on footwear. Seed dispersal via multiple dispersal vectors is a common phenomenon in plant communities, with an average of 2.15 vectors per species (Ozinga *et al*., 2004). Therefore, dispersal distances can be additive and seeds may travel even greater distances than previously tought.

Negative aspects of human-mediated seed dispersal

Under climate change, conditions in alpine ecosystems become suitable for low elevation species which then competite with alpine species for ressources. Some scientists suggest that the current increase in species richness in alpine ecosystems hides a forthcoming decrease of species richness (Dullinger *et al.*, 2012; Losapio *et al.*, 2021; Rumpf *et al.*, 2019). Alpine species may already co-occur with the new arriving species, but in the long-term alpine species might be outcompeted and progressively disappear under the pressure of lower elevation species. This phenomenon, known as extinction debt, poses a threat to biodiversity conservation and may lead to a decrease in species richness and an extinction of endemic alpine species (Kuussaari *et al.,* 2009; Spalding & Hull, 2021).

On a wider scale, unintentional human-mediated seed dispersal can be responsible for the introduction of invasive species worldwide that poses a serious threat to native species. Several studies rise awareness of this phenomenon which also concern mountains and is expected to be amplified by climate change (Alexander *et al.,* 2016; Petitpierre *et al.,* 2016). As shown by Liedtke *et al. (*2020), hiking trails are corridors for the spread of non-native species in mountains, and several studies highlighted that a majority of species found on footwear were non-native from the continent where they were collected (Pickering & Mount, 2010; Ware *et al.,* 2012; Wichmann *et al*., 2009).

Positive aspects of human-mediated seed dispersal

Although often perceived as negative, human-mediated seed dispersal can also have positive consequences on alpine ecosystems. Because they can disperse seeds over long distances, hikers may help species reaching new habitats and expand their range, increasing species resilience and maintaining genetic connectivity (Trakhtenbrot *et al.,* 2005). Ultimately, species dispersing on footwear may be able to better cope with a changing climate (Corlett & Westcott, 2013; Matteodo *et al.*, 2013).

Conclusion

Hikers in alpine ecosystems are selective seed dispersal vectors. By carrying on average 0.88 seeds on their footwear, people disperse seeds along trails and towards summits. Because humans are long distance dispersal vectors, each transported seed can be an opportunity for species to colonize new habitats and expand their ranges. The differences observed in species range shifts could be partly explained by different seed attachment rates, with species attaching on shoes being more likely to shift upward. Species richness on summits of interest has increased by 10% between 2010 and 2020, and new species established on all of them. While global warming makes living conditions on summits becoming favourable for low elevation species, hikers provide species with a means to quickly disperse towards summits. Taken together, these two phenomena probably play a substantial role in the colonisation of summits by low elevation species and quantifying the dispersal via shoes is crucial to understand vegetation dynamics on alpine summits. Overall, dispersal of seeds by humans is a complex topic since it can have both positive and negative consequences on ecosystems. Dispersal on footwear can help species expand their range and better cope with climate change, but it also represents the risk to introduce highly competitive species. With growing interest in mountain activities and tourism, managing human-mediated seed dispersal is crucial to preserve alpine ecosystems. I showed that hikers are not aware they may transport seeds but are ready to make efforts to prevent seed dispersal. Hence, informing people and rising awareness should be done systematically.

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Appendices

Appendix A. Description of the 18 sampling locations, with the name of the nearest summit of interest, the number of samples collected, the elevation (meters above sea level), the element-s of interest (if any), the GPS coordinates and the date of collection

Nearest summit of interest	Number of samples	Elevation (m.a.s.l.)	Elements of interest	GPS coordinates	Collection date *(dd.mm.yyyy)*
Piz Daint	22	2967	Mountain peak, cross	46.61875° N, 10.29092° E	20.07.2021
Piz Daint	4	2328	-	46.65093° N, 10.28236° E	21.07.2021
Piz Daint	1	2309	-	46.68179° N, 10.23916° E	22.07.2021
Strel Arosa	2	2491	Mountain pass, signs	46.74817° N, 9.71493° E	23.07.2021
Valbellahorn	5	2763	Mountain peak, cross	46.73967° N, 9.70166° E	23.07.2021
Valbellahorn	3	2268	Lake, mountain hut	46.75202° N, 9.70121° E	23.07.2021
Aroser Älpihorn	2	1860	Waterfall, bench	46.76067° N, 9.68957° E	23.07.2021
Strel Arosa	10	2443	Mountain pass, signs, mountain hut	46.77048° N, 9.73353° E	24.07.2021
Valbellahorn	1	2527	-	46.69198° N, 9.80517° E	25.07.2021
Valbellahorn	1	2667	-	46.70263° N, 9.79473° E	25.07.2021
Haldensteiner Calanda	4	2074	Mountain hut	46.88304° N, 9.48219° E	03.08.2021
Piz Tomül	1	1702	Mountain hut	46.62476° N, 9.27602° E	04.08.2021
Piz Tomül	1	2320	-	46.61005° N, 9.24950° E	04.08.2021
Piz Daint	2	2480	-	46.68431° N, 10.23835° E	06.08.2021
Piz Daint	3	2646	Mountain pass, bench, signs	46.68854° N, 10.24482° E	06.08.2021
Piz Daint	39	2261	Bench, explanatory signs on wildlife	46.67848° N, 10.23889° E	06.08.2021
Piz Daint	14	2333	Mountain peak, signs	46.67658° N, 10.24253° E	07.08.2021
Piz Daint	17	1958	Mountain hut, benches, signs	46.66322° N, 10.24125° E	08.08.2021

Appendix B. Presentation sheet (German, Rumantsch, English, French, and Italian)

Guten Tag, ich bin eine Studentin der Universität Lausanne und schreibe meine Masterarbeit über die Beziehung zwischen Klimawandel, Mensch und Bergvegetation. Durch den Klimawandel verschieben sich die Verbreitungsgebiete von Gebirgspflanzenarten, aber nur wenige Arten können der Geschwindigkeit des Klimawandels folgen. Ich interessiere mich für den direkten Einfluss des Menschen bei diesen Verbreitungsveränderungen. Um das Potenzial der Samenverbreitung durch Wanderer abzuschätzen, wäre ich Ihnen sehr dankbar, wenn Sie mir erlauben würden, die Erde und die Samen zu sammeln, die Sie an Ihren Schuhen und Ihrer Kleidung tragen. Während ich Ihre Ausrüstung reinige, können Sie die kurze anonyme Umfrage unten ausfüllen. Diese Umfrage wird mir bei der Bestimmung der Samen helfen, damit ich genauer weiss, woher sie kommen könnten. Herzlichen Dank für Ihre Teilnahme !

Allegra, eu sun üna studenta da l'università da Lausanne e scriv mia lavur da master sur da la relaziun dal müdamaint dal clima, l'uman e la vegetaziun illas muntognas. Tras il müdamaint dal clima as spostan ils territoris da derasaziun da las spezchas da plantas da muntognas. Ma be pacas spezchas sun bunas da seguir la sveltezza dal müdamaint dal clima. Eu m'interess per l'influenza directa dal uman pro quists müdamaints da derasaziun. Per stimar il potenzial da la derasaziun dals sems tras viandants füss eu fich cuntainta sch'eu pudess ramassar la terra ed ils sems chi tachan vi da Lur s-charpas e vestits. Dürant ch'eu pulisch Lur roba pudessan Els per plaschair implir oura il questiunari anonim qua suotvart. Quist questiunari am güda pro la determinaziun dal sems per savair d'ingionder chi derivan. Grazia fich per Lur partecipaziun !

Hello, I am a student at the University of Lausanne, and I am doing my master's thesis on the relationship between climate change, humans and mountain vegetation. Climate change is causing mountain plant species to shift their distribution, and I am interested in the direct impact of humans on their redistribution. To estimate the potential of hikers to disperse seeds, I would be very grateful if you allowed me to collect the soil and seeds you carry on your shoes and clothing. While I am cleaning your equipment, you can fill in the short anonymous survey below. This survey will help me to determine the species of the seeds you carry, as I will know where they might be coming from. Thank you very much for your participation !

Bonjour, je suis étudiante à l'Université de Lausanne et j'effectue mon travail de master sur la relation entre le changement climatique, les hommes et la végétation en montagne. Le changement climatique impacte les plantes de montagne en modifiant leurs aires de distribution, et je m'intéresse au rôle que joue l'homme dans ces nouvelles distributions. Afin d'estimer le potentiel des randonneurs à disperser des graines, je vous serai très reconnaissante si vous acceptiez que je récupère la terre et les graines que vous transportez sur vos chaussures et vêtements. Pendant que je procède au nettoyage de vos équipements, vous pouvez remplir le petit questionnaire anonyme ci-dessous. Ce dernier me sera d'une grande aide pour déterminer la plante à partir de la graine. Merci beaucoup de votre participation !

Buongiorno, sono una studentessa dell'Università di Losanna e sto facendo la mia tesi di master sulla relazione tra il cambiamento climatico, l'uomo e la vegetazione di montagna. Il cambiamento climatico influisce sulle piante di montagna modificando le loro aree di distribuzione e di sviluppo, solo poche specie possono adattarsi a queste nuove condizioni, in questa ricerca mi interesso all'influenza dell'como sulle nuove distribuzioni. In questo scopo, il ruolo dell'uomo e la sua influenza su queste nuove distribuzioni mi interessa. Per poter valutare il potenziale di dispersione degli escursionisti le savei grata se mi permettesse di campionare terra e semi dalle sue scarpe e vestiti. Mentre raccolgo i campioni, potete riempire il breve questionario anonimo qui sotto. Questo mi sarà di grande aiuto per determinare la specie della pianta che avete trasportato. Grazie mille per la vostra partecipazione !

Appendix C. Survey (German, English, French and Italian)

06/07/2021 Seed dispersal by humans in mountains

Seed dispersal by humans in mountains

Guten Tag, ich bin eine Studentin der Universität Lausanne und schreibe meine Masterarbeit über die Beziehung zwischen Klimawandel, Mensch und Bergvegetation. Durch den Klimawandel verschieben sich die Verbreitungsgebiete von Gebirgspflanzenarten, aber nur wenige Arten können der Geschwindigkeit des Klimawandels folgen. Ich interessiere mich für den direkten Einfluss des Menschen bei diesen Verbreitungsveränderungen. Um das Potenzial der Samenverbreitung durch Wanderer abzuschätzen, wäre ich Ihnen sehr dankbar, wenn Sie mir erlauben würden, die Erde und die Samen zu sammeln, die Sie an Ihren Schuhen und Ihrer Kleidung tragen. Während ich Ihre Ausrüstung reinige, können Sie die kurze anonyme Umfrage unten ausfüllen. Diese Umfrage wird mir bei der Bestimmung der Samen helfen, damit ich genauer weiss, woher sie kommen könnten. Herzlichen Dank für Ihre Teilnahme !

Diese Umfrage ist anonym und freiwillig.

Wo leben Sie (Stadt + Land) ?

Was ist Ihr Beruf?

Arbeiten Sie im Freiland ?

- Ja
- Nein

Wie alt sind Sie ?

- 0 - 19
- 20 - 39
- 40 - 59
- + 60

Wie oft sind Sie durchschnittlich in den Bergen (>1000m Höhe) ?

- Einmal im Jahr
- Einmal im Monat
- Mehrmals pro Monat
- Einmal pro Woche
- Mehr als einmal pro Woche

https://kf.kobotoolbox.org/#/forms/aoxHsXJRhsWyDPUXmLWBQ/landing 1/2

06/07/2021 Seed dispersal by humans in mountains

Wie oft reinigen Sie Ihre Wanderschuhe durchschnittlich ?

- Nie
- Einmal im Jahr
- Mehr als einmal pro Jahr
- Nach jeder Wanderung

In welcher Region sind Sie zuletzt mit Ihren aktuellen Schuhen gewandert (>1000m Höhe), seit Sie sie zuletzt gereinigt haben? Bitte wählen Sie den genauesten Ort aus.

- In Graubünden
- In der Schweiz
- In den Alpen
- In Europa
- Ausserhalb von Europa
- Ich bin seit ihrer letzten Reinigung nicht mehr gewandert

Warum reinigen oder putzen Sie Ihre Wanderschuhe ?

- Weil sie schmutzig sind
- Ich möchte die Schuhe in gutem Zustand erhalten
- Um die Verbreitung von Samen zu verhindern

Würden Sie in Erwägung ziehen, Ihre Schuhe nach jeder Wanderung zu reinigen, jetzt wo Sie wissen, dass sie Samen von invasiven Arten in neue Umgebungen tragen können?

- Nein, das ist mir egal, dafür habe ich keine Zeit
- Nein, ich bin mir sicher, dass ich keine Samen von invasiven Arten transportiere
- Ja

Vielen Dank für Ihre Teilnahme !

https://kf.kobotoolbox.org/#/forms/aoxHsXJRhsWyDPUXmLWBQ/landing 2/2

Seed dispersal by humans in mountains

Hello, I am a student at the University of Lausanne, and I am doing my master's thesis on the relationship between climate change, humans and mountain vegetation. Climate change is causing mountain plant species to shift their distribution, and I am interested in the direct impact of humans on their redistribution. To estimate the potential of hikers to disperse seeds, I would be very grateful if you allowed me to collect the soil and seeds you carry on your shoes and clothing. While I am cleaning your equipment, you can fill in the short anonymous survey below. This survey will help me to identify the species of the seeds you carry, as I will know where they might be coming from. Thank you very much for your participation !

This survey is anonymous and on a voluntary basis.

Where do you live (town + country) ?

What is your job ?

Are you working outdoors ?

- ◯ Yes
- ◯ No

How old are you ?

- ◯ 0 - 19
- ◯ 20 - 39
- ◯ 40 - 59
- ◯ + 60

On average, how often are you in the mountains (>1000m of altitude) ?

- ◯ Once per year
- ◯ Once per month
- ◯ Several times per month
- ◯ Once per week
- ◯ More than once per week

How often do you clean your hiking shoes on average ?

- ◯ Never
- ◯ Once per year
- ◯ More than once per year
- ◯ After each hike

In which region did you last hike (>1000m altitude) with your current shoes since you last cleaned them? Please select the most accurate location.

- ◯ In the Grisons
- ◯ In Switzerland
- ◯ In the Alps
- ◯ In Europe
- ◯ Outside of Europe
- ◯ I haven't hiked since I last cleaned my shoes

What is the reason you clean or may clean your hiking shoes ?

- ☐ They are dirty
- ☐ I want to maintain my shoes in good conditions
- ☐ I don't want to disperse seeds

Would you consider cleaning your hiking shoes after each hike now that you know they may transport the seeds of invasive species ?

- ☐ No, I don't want to be bothered by it - I don't have time
- ☐ No, I'm sure I don't transport seeds of invasive species
- ☐ Yes

Thank you very much for your participation !

Seed dispersal by humans in mountains

Bonjour, je suis étudiante à l'Université de Lausanne et j'effectue mon travail de master sur la relation entre le changement climatique, les hommes et la végétation en montagne. Le changement climatique impacte les plantes de montagne en modifiant leurs aires de distribution, et je m'intéresse au rôle que joue l'homme dans ces nouvelles distributions. Afin d'estimer le potentiel des randonneurs à disperser des graines, je vous serai très reconnaissante si vous acceptiez que je récupère la terre et les graines que vous transportez sur vos chaussures et vêtements. Pendant que je procède au nettoyage de vos équipements, vous pouvez remplir le petit questionnaire anonyme ci-dessous. Ce dernier me sera d'une grande aide pour déterminer la plante à partir de la graine. Merci beaucoup de votre participation !

Ce questionnaire est anonyme et sur la base du volontariat.

Où vivez-vous (ville + pays) ?

Quelle est votre profession ?

Travaillez-vous à l'extérieur ?

- ◯ Oui
- ◯ Non

Quel âge avez-vous ?

- ◯ 0 - 19
- ◯ 20 - 39
- ◯ 40 - 59
- ◯ + 60

En moyenne, à quelle fréquence allez-vous en montagne (>1000m d'altitude) ?

- ◯ Une fois par an
- ◯ Une fois par mois
- ◯ Plusieurs fois par mois
- ◯ Une fois par semaine
- ◯ Plusieurs fois par semaine

En moyenne, à quelle fréquence nettoyez-vous vos chaussures de marche ?

- ◯ Jamais
- ◯ Une fois par an
- ◯ Plusieurs fois par an
- ◯ Après chaque randonnée

Dans quelle région avez-vous fait votre dernière randonnée (>1000m d'altitude) avec vos chaussures actuelles depuis leur dernier nettoyage? Merci de sélectionner l'endroit le plus précis.

- ◯ Dans les Grisons
- ◯ En Suisse
- ◯ Dans les Alpes
- ◯ En Europe
- ◯ Hors de l'Europe
- ◯ Je n'ai pas randonné depuis leur dernier nettoyage

Pour quelle raison nettoyez-vous ou nettoyeriez-vous vos chaussures de marche ?

- ☐ Elles sont sales
- ☐ Je veux garder mes chaussures en bon état
- ☐ Je ne veux pas disperser de graines

Envisageriez-vous de nettoyer vos chaussures après chaque randonnée maintenant que vous savez qu'elles peuvent transporter des graines d'espèces invasives ?

- ☐ Non, je ne veux pas m'embêter avec ça - Je n'ai pas le temps
- ☐ Non, je suis certain·e de ne pas transporter de graines d'espèces invasives
- ☐ Oui

Merci beaucoup pour votre participation !

06/07/2021 Seed dispersal by humans in mountains

Seed dispersal by humans in mountains

Buongiorno, sono una studentessa dell'Università di Losanna e sto facendo la mia tesi di master sulla relazione tra il cambiamento climatico, l'uomo e la vegetazione di montagna. Il cambiamento climatico influisce sulle piante di montagna modificando le loro aree di distribuzione e di sviluppo, solo poche specie possono adattarsi a queste nuove condizioni, in questa ricerca mi interesso all'influenza dell'como sulle nuove distribuzioni. In questo scopo, il ruolo dell'uomo e la sua influenza su queste nuove distribuzioni mi interessa. Per poter valutare il potenziale di dispersione degli escursionisti le savei grata se mi permettesse di campionare terra e semi dalle sue scarpe e vestiti. Mentre raccolgo i campioni, potete riempire il breve questionario anonimo qui sotto. Questo mi sarà di grande aiuto per determinare la specie della pianta che avete trasportato. Grazie mille per la vostra partecipazione !

Questo questionario è anonimo e su base volontaria.

Dove vive (città + paese) ?

Qual è la sua professione ?

Realizza lavori all'aperto ?

- ◯ Sì
- ◯ No

Quanti anni avete ?

- ◯ 0 - 19
- ◯ 20 - 39
- ◯ 40 - 59
- ◯ + 60

In media, quanto spesso siete in montagna (>1000m di altitudine) ?

- ◯ Una volta all'anno
- ◯ Una volta al mese
- ◯ Più volte al mese
- ◯ Una volta alla settimana
- ◯ Più di una volta alla settimana

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06/07/2021 Seed dispersal by humans in mountains

Quanto spesso pulisce i suoi scarponi da trekking in media ?

- ◯ Mai
- ◯ Una volta all'anno
- ◯ Più di una volta all'anno
- ◯ Dopo ogni escursione

In quale zona ha fatto l'ultima escursione (>1000m di altitudine) con le sue scarpe attuali dopo l'ultima pulizia? Si prega di selezionare la posizione più precisa.

- ◯ Nei Grigioni
- ◯ In Svizzera
- ◯ Nelle Alpi
- ◯ In Europa
- ◯ Fuori dall'Europa
- ◯ Non ho più fatto escursioni dalla loro ultima pulizia

Perché pulisce o vorrebbe pulire i suoi scarponi da trekking ?

- ☐ Perché sono sporchi
- ☐ Voglio mantenere le scarpe in buone condizioni
- ☐ Per prevenire la diffusione dei semi

Prenderesti in considerazione la possibilità di pulire le tue scarpe dopo ogni escursione ora che sai che possono portare semi di specie invasive in nuovi ambienti?

- ☐ No, non mi interessa, non ho tempo per questo
- ☐ No, sono sicuro di non trasportare semi di specie invasive
- ☐ Sì

Grazie per la vostra partecipazione !

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Appendix D. Determination of the conditions set in the phytotron to mimic summer mountain surface conditions

I used data coming from summits whose elevation falls between the elevational range of the sampling locations (approximately between 1700 and 2000 m.a.s.l.). At such elevation, growing period is in July and August.

Day and night durations were determined based on the summit Piz Beverin (2998 m.a.s.l.) using the mobile app PeakFinder (PeakFinder App, 2021). On July 31st, the sun rises at 06h00 and sets at 20h59. Hence, I considered the light period (day) lasts for 15 hours (from 06h00 until 20h59) and the dark period (night) lasts for 9 hours (from 21h00 until 05h59).

Day and night temperatures were fixed based on surface records over 3 years (2013, 2014, 2015) in four summits in the Grisons (Witihuereli, 2635 m.a.s.l.; Choerbschhorn, 2651 m.a.s.l..; Schwarzhorn, 2759 m.a.s.l.; Aroser Älpihorn, 2839 m.a.s.l.) (unpublished raw data from Kulonen, A. *et al.;* unpublished raw data from Lang, G.). Between 36 and 44 waterproof loggers were placed on each summit at different microsites below the soil surface, covered by a thin (3cm) layer of soil to avoid the effects of sun radiation. Temperature was recorded every 3 hours. I calculated the mean temperatures during the day (13°C) and the night (8°C) for July and August.

Day and night relative humidities were determined based on data from MétéoSwiss for the summits Weissfluhjoch (2691 m.a.s.l.) and Piz Martegnas (2668 m.a.s.l.) (MétéoSuisse, 2021). Relative humidity of the air at 2 meters above ground was recorded every hour. I calculated the mean relative humidity during the day (77%) and the night (81%) in July and August.

Appendix E. Regression plot for all ten summits of interest, including Haldensteiner Calanda and Piz Beverin that were removed in the study due to their biased number of entries in summit books. Haldensteiner Calanda and Piz Beverin had respectively 26 and nine new species in 2020 and on average 4.67 and 16.84 entries in summit book per day. With all ten summits, the relationship was negative with on average -0.0035 species per visitor on summits (*df* = 9, *Z* = -0.193, *p* = 0.847) and the number of new species in 2020 was not significantly associated with mean daily number of entries in summit books.