FUNGAL LEAF PATHOGENS ON NATIVE AND ALIEN SPECIES IN THE BOTANICAL GARDEN

MASTER THESIS

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Investigation of fungal aboveground pathogens on native, naturalized and non-naturalized plant species gives support to the enemy release hypothesis and indication for adaptive events of native pathogens

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Abstract

1.   Plant invasions as driver or result of community compositional shifts under changing environmental conditions (such as climate and land fragmentation) is still a very complex ecological field of research and its driving forces not yet completely identified. Different explanatory approaches highlight distinct forces permitting plant invasion: community composition, plant traits and resulting species interactions all deliver their part to the emerging pattern. Enemy release is shown to be one major responsible factor for plant invasions, for which we also found evidence.

2.   Here we set up an investigation framework with conditions very similar to a common garden experiment, comparing aboveground fungal pathogens on native and alien (naturalized and non-naturalized) plant species growing in the botanical garden of Bern (Switzerland). A set of 488 plant species was investigated for fungal infestations three times from spring to autumn. Infestation incidence and severity, herbivory, sun exposure, neighboring plants, and plant (population) size were assessed. Plant nativeness status, range size, phylogenetic structure as well as Landolt temperature indicator values were taken into account. Pathogen fungi were identified down to the species level.

3.   Natives suffer significantly more heavily from fungal infestations, a finding that supports the enemy release hypothesis. Interestingly naturalized species show a similar sensitivity to infestation as natives, which indicates an accumulation of fungal pathogens. A possible bias for our findings is the higher proportion of powdery mildews on natives, who characteristically cover higher areas on their hosts.

4.   Herbivory and fungal infestation show signs of a connection thru contrasting patterns. In the summer census they are negatively correlated, whereas they are positively correlated in the autumn census. Possible interaction pathways are destroyed defense mechanisms by herbivory, preference of non-infested plants by herbivores on the other hand, and differing resource allocation towards herbivore and pathogen attacks between plant species. Interestingly there is no mean effect for plants with

a main range deviant in mean temperature (as it is the case for some naturalized species and alpine plants) in relationship of fungal pathogen sensitivity and severity.

5.   The investigations presented here reveal some insight into the interaction pathways concerning fungal pathogen infestations in relationship with various environmental conditions and plant traits encountered in the field. Plant status accounts apparently for a big part of variation in infestation sensitivity and severity, which gives support to the enemy release hypothesis in the invasion context.

Key words: plant invasions, enemy release hypothesis, fungal pathogens, infestation sensitivity, infestation severity, herbivory, range size, neighborhood effects, vegetative stage, Landolt temperature indicator value

Introduction

Invasion drivers

Uncontrolled spread of a species in a new ecosystem is the general definition of a biological invasion. Alien species can become more competitive than native ones and even dominate whole communities. The drivers of plant invasions are still investigated and their relative importance is not yet clear. In general, shifted biotic interactions and changing abiotic conditions are at the origin of biological invasions. One major explanation theory for invasion success is the *enemy release hypothesis (ERH)*. ERH explains invasion success with the following consideration: Species (partly) loosing their natural enemies when introduced into a new range, resulting in a gain of competitive advantage relative to native species (Flory & Clay 2013). Pathogens could potentially accumulate later on (by introduction from the home range or evolutionary adaptation of pathogens in the introduced range, Mitchell et al. 2010). Such a pathogen accumulation can possibly reduce the effect of enemy release and decrease invasiveness, or in contrast increase it by spilling back onto native species (Flory & Clay 2013).

Other relevant biotic interactions in the invasion context are such with competitors, pollinators and soil mutualists. Razanajatovo et al. (2015) found that entomophilous alien plants that have not established naturalized populations are less successful than native plants in attracting flower visitation and concluded that the ability to attract pollinators is a driver in the establishment process. Newly gained positive interactions with soil mutualists in the introduced range might interfere with the enemy release hypothesis (Vasquez & Meyer 2011). Possibly, also a loss of allelopathic competitors

might contribute to the understanding of invasion processes. Altogether, one has to consider the sum effect of biotic interaction patterns, and the fact that aliens are mostly released from some but not all enemy guilds what results in a net effect of losses versus gains (Vasquez & Meyer 2011).

The strongest support for ERH is coming from studies comparing enemy damage of a species in the native and introduced rather than from community level studies investigate natives versus exotics in the same place (Mitchell & Power 2013, Colautti et al. 2004; Liu & Stiling 2006). Mitchell & Power (2003) show high loss of fungal pathogens in the introduced range for species invasive in the United States. Van Kleunen & Fischer (2009) found 58% fewer fungal pathogen species in the introduced range (Europe) for North American plant species, with significant release from smut fungi, rusts, and downy mildews but a significant gain of powdery mildew species. They postulate that release of fungal pathogens might not be the major determinant of noxiousness and invasiveness of alien plants.

Interestingly, Parker & Gilbert (2015) found an equal effect of pathogens on introduced as on native plant species (origin not driver of susceptibility) by focusing on necrotrophs rather than on the specialized biotrophic fungi as Mitchell & Power (2003) did when they found support for the enemy release hypothesis.

Studies have showed that increased host abundance will increase disease transmission (i.a. Anderson & May 1979) and disease severity (i.a. Mitchell et al. 2002). Parker & Gilbert (2015) found evidence for a rare-host-advantage, meaning, that locally (low abundance) and phylogenetically rare hosts enjoy an advantage resulting in less pathogen load. Clay (1995) rather highlights a species' range size in the introduced range as a predictor for the number of fungal pathogens found on an exotic species. Mitchell et al. (2002) confirm the importance of the range size as they also found that disease proneness was significantly positively correlated with regional geographical extension, but interestingly not with local abundance.

Fungal leaf pathogens

Here, we focused on the enemy guild of fungal leaf pathogens. Fungal pathogens are known to be highly host specific and in most cases limited to one are a few species (Farr et al. 1989). As a consequence this group of pathogens is more diverse than the known viral and bacterial plant diseases (Agrios 1988). There is a higher probability of alien species to accumulate pathogens in the introduced range through adaptation of native pathogens when closely related species are abundant

(Agrawal & Kotanen 2003; Parker & Gilbert 2007). This is going hand in hand with the finding that species without close relatives in introduced range are more likely to become invasive (Hill & Kotanen 2009). However, another possible explanation could also be that phylogenetically distant species use resources with a higher probability in a different way and may therefor occupy empty niches more frequently.

Fungal pathogens exert multiple effects on their hosts: as one of the first reactions, the respiration rate and permeability of the cell membranes are increased leading to a loss of glucose and electrolytes, also in resistant individuals. In the affected leaf tissues, chlorophyll content is reduced, but the remaining chlorophyll seems unaffected (in contrast to viral and bacterial infections where a toxin inhibits enzymes involved in the photosynthesis). Further, fungi reduce the size of the water transporting xylem tubes, which will reduce water tension; transpiration is increased in infected leafs which leads to a loss of turgor and wilting of leafs. Viruses would additionally act negatively on the phloem. Last, transcription and translation (also of defense proteins) are reduced, as the fungus is using its hosts' RNA (Agrios 1997). A main concern when investigating ERH as a potential invasion driver is the effect of a fungal pathogen on its hosts' fitness, particularly on its reproductive success. It has been shown that the proportional plant area visually infested may be used as a measurement for harvest diminution due to the pathogen (Waggoner & Berger 1987, Campbell & Madden 1990). This gives us the link between the scale of fitness reduction and infested area by the pathogen. An estimation of the proportionally infested area of the host is therefore the best measure known and applicable for our investigation to estimate the extent of fitness relevant enemy escape.

Here we investigated pathogens that reduce the fitness of plants: this means no decomposing, but biotrophic and necrotrophic fungi were analyzed. The distinction of the two latter ones is somewhat arbitrary. Van Kan et al. (2014) highlight with the example of *Botrytis cinerea*, that a strict distinction of biotrophic and necrotrophic fungi is often not possible. Several cases of *Botrytis cinerea* infestations were found. The found infestations were included, as necrotrophs attack vital hosts and induce their hosts' death. Necrotrophs should therefor generally be included in a pathogen study. Further necrotrophs than *B. cinerea* were not found, or eventually mistaken as decomposing fungi. Decomposers were excluded because they are active during and after senescence and hence not acting on the fitness. To estimate the scale of pathogen attack we assessed the total amount of diseased leaf area according to Campbell & Madden (1990, see material and methods).

This study

This study is part of a study series on the effects of plant nativeness status (which are here: native, naturalized and non-naturalized) on different ecological properties carried out in the botanical garden in Bern (BoGa). Herbivory severity is being assessed since several years, and pollinator diversity and frequency of visits related to plant status was studied by Razanajatovo et al. (2015). Here, we would also like to detect a possible correlation between the two enemy guilds of herbivory and fungal pathogens.

Most studies investigating enemy release only include widespread invasive species. Non-successful invaders or simply naturalized but non-invasive exotic species are rarely investigated (Van Kleunen & Fischer 2009). To make a statement on the extent of enemy release of established and invasive species it is decisive to compare them with non-naturalized alien plants in the introduced range. As proposed by Van Kleunen & Fischer (2009) we will test for ERH by comparing the damage due to fungal leaf pathogens between native, naturalized and non-naturalized plants similar to the previous herbivory and pollination studies in the BoGa.

Mitchell et al. (2002) recommend using range size (at a regional, not local, scale) in continuous numbers instead of categories such as „rare" or „common". Further, when investigating the enemy damage of exotic plant species, habitat fertility, relatedness of aliens to natives and species diversity are the major community predictors (Dostál et al. 2013), and the probability to accumulate pathogen in habitats with closely related species increases (Agrawal & Kotanen 2003; Parker & Gilbert 2007). Therefor we included range size (in Switzerland), herbivory degree, plant size and site-related factors such as shading and neighbourhood of close relatives as explanatory factors. Additionally, plant family respectively a phylogenetic tree of all investigated plant species served as random factor/correlation matrix.

A strong point of our investigation method is, that we include naturalized species without regard to native relatives, and non-naturalized species. A paired analysis (native versus phylogenetically related exotic) might exclude phylogenetically less related species and so ignore the most informative species. Including non-naturalized species can add useful insight to the drivers of establishment of alien species (see also Vasquez & Meyer 2011). If a susceptible host and pathogen occur together, a disease develops only as permitted by the physical environment (Campbell & Madden 1990). To compare the susceptibility of different hosts, it is therefor crucial to have common environmental conditions. In our case data are as far comparable as it took place the same year at the same place (for further detail see material and methods).

Concrete questions and hypotheses of our investigation:

1.   Are native plants more frequently and strongly infested by foliar leaf pathogens than alien species? We expect natives more frequently and severely infested compared to naturalized and non-naturalized species, as predicted by the ERH.

2.   Are rare species (small(er) range size in Switzerland) profiting from less frequent and lighter pathogen infestation compared to wider distributed plant species in Switzerland? We expect it so and hypothesize a significant effect of range size on pathogen infestation.

3.   Are naturalized plants more infested than other aliens? Native pathogens had a bigger chance to adapt to naturalized plants, we therefor suggest signs of adaptation.

4.   Are taxonomically close relatives in the immediate neighborhood (radius 1m) increasing the severity of pathogen infection? We expect higher infestation sensitivity in case of members from the same plant family in the surrounding neighborhood, with even an increase if they belong to the same genus.

5.   Is there a relationship between herbivory incidence/degree and pathogenic infestation? And if yes: What might the underlying biological patterns be? Is herbivory facilitating fungal infestation? Or is a fungal disease rather reducing the attractivity for herbivores? Can we detect both patterns indicating distinct defense allocations between different plant species?

6.   Are plants more frequently/severely infested before or after seed production? This question relates to the question on the effect of a fungal pathogen on the fitness in terms of reproductive success.

7.   Do plants with larger deviation from the Landolt temperature indicator value (LTIV) from the local LTIV (estimated at 3.25) suffer more from fungal pathogens due to resource allocation towards establishment in the deviant climate? Or will we rather encounter a kind of enemy release due to a shift towards the edge of the ecological niche of the plants' pathogen?

Material and methods

A set of 502 native, naturalized and non-naturalized plant species growing in the botanical garden containing herbs, shrubs, trees and grasses have been investigated for foliar leaf pathogens. Infestation occurrence, percentage of visible infestation expansion have been recorded. In the case of an infestation, the fungus species has been identified.

Botanical garden and species

The set-up in the botanical garden is a nearly perfect common garden situation with very similar environmental conditions (temperature, rain fall, but not soil composition and hence microbes), with plants from all parts in the world, including successfully established in Switzerland and non-naturalized alien plants. With its high plant and linked fungal pathogen diversity our set-up creates a kind of regional pathogenic-reality-check (which fungi infest possibly which plant species – as all kind of fungi might be represented) for the investigated plant species with their respective plant status. To assort a list of the plants to be investigated, we took orientation from the former studies performed at the botanical garden: from the species list of Razanajatovo et al. (2015) we found 350 species (out of 466) still labeled in the botanical garden. We extended our list to 502 species by adding species from the ongoing herbivory studies and supplemented it with grasses (*Poaceae* and *Juncaceae*) and trees as those groups have been underrepresented in Razanajatovo et al.s' list. The species list was assorted in early spring (march) when some plants did not yet to appear. Later we realized that some of the selected species didn't grow anymore. Also we noticed that we accidentally doubled some species growing more than once in the garden when we added the species from the other lists. In the end, our list included 488 plant species with members of all three defined statuses (215 native, 34 naturalized, 239 non-naturalized). Not all plants have been present in every census (spring, summer and autumn) as some were early bloomers which disappeared by summer and others "late-appearers" who were still absent in spring. This resulted in a varying and individually reduced plant list for each census.

At each site, the local population (immediately grouped together around the label) was assessed. In some cases, the sample consisted of one individual plant (mainly trees and shrubs).

Assessed plant traits and environmental factors

<u>Species status and distribution</u> have been recorded. The Swiss „info flora" database served as reference for status (native, naturalized, non-naturalized), range size (in terms of number of grid cells of 50x50m with records in Switzerland) and Landolt Temperature indicator value (LTIV) for native and naturalized species. We estimated niche mismatch of the plant species by calculating the <u>deviation of the species' temperature indicator value from the local LTIV</u> at the study site. The local LTIV was estimated by observing common plant species in neighboring semi-natural habitats and taking the mean of their relative LTIVs. To account for microclimatic differences that might affect fungal growth (i.e. moisture and temperature), a categorical description of the <u>sun exposure</u> was made („sunny", „half-shady" resp. „shady") for each plant placement within BoGa.

The biotic environment is thought to exert an influence on pathogen infection probability (fugal spores are mainly transmitted thru water droplets of repelled rain, Agrios 1997). To account for potential pathogen sharing with related plant species we checked whether there was a <u>neighbor belonging to the same plant family</u> and if yes if it was of the <u>same genus</u>. Neighborhood was defined as a radius of one meter from the target plant; if the target plant (population) extended to one meter or more in diameter, all direct neighbours were checked.

The <u>diameter and height</u> were noted of all plants at each census to account for the spatial extension of the plant. Additionally, the <u>vegetative status</u> (host life stage) was assessed, following the consideration that a pathogen infestation has a different effect on a plant's fitness (especially the reproductive success) regarding to the life cycle stage at which the infestation happens (compare with Campbell & Madden 1990). Following categories were used: 1=vegetative growth before flowering, 2=plant flowering, 3=seed production, 4=vegetative state after seed production, 0=retired into soil for overwintering.

<u>Herbivory incidence and degree</u>: In all censuses herbivory incidence (binomial: Yes/No) was recorded. Four degrees of herbivory have been additionally distinguished in the second and third censuses: 1=no or very little herbivory (0 to 2%), 2=few traces of herbivory (3 to 14%), 3=major herbivory incidence (15 to 49%), 4=substantial herbivory incidence (50% and more).

Assessment of fungal leaf pathogens

<u>Disease incidence</u> (binomially assessed: yes/no) <u>and severity</u> (quantity) in terms of percentage of plant tissue visually infested relative to the total area were assessed three times in 2016. The <u>spring census</u> took place from 25th of April to 20th of May, the <u>summer census</u> from 20th of June to 5th of July, and the <u>autumn census</u> from 29th of august to 21st of September. Each census took approximately two and a half to three and a half weeks, depending on evolving experience, number of species present and infested, and weather conditions (heavy rain rendered writing in the field sometimes impossible).

Assessing infestation severity is more difficult and time-consuming than incidence, but it is a more important and useful measure of disease for many pathosystems as it relates to the influence of a pathogen on reproductive success of the host. Infection estimation is best done in terms of percentage of leaf area infected, which is often proportional to the effects of the disease on the host (Campbell & Madden 1990, Mitchell et al. 2002). There is also evidence from crop physiology and crop loss research that plant yield (which is a proxy to the reproductive success) may be determined by the total amount of diseased area (Campbell & Madden 1990). The disease severity was estimated

visually after some training with leaf-damage templates (see Vasquez & Meyer 2011) and coaching by members of the Plant Ecology research group (University of Bern).

Samples from infested plants were collected, herbarized and later on analysed in the lab. Without fungal structures (at least hyphae) it wasn't possible to identify whether a leaf spot was due a fungal, viral or bacterial infection. We anyway included unidentified leaf spots into our analysis, as recommended by Stefan Blaser. Given the fact, that leaf spot incidence decreased with advancing time, and fungal infestation increased, we can assume that fungal infestation account for the majority of all phenotypic leaf spot disease (especially in the early season). If fungal structures were found, the type of fungus was categorized. The main groups were rusts, smuts, powdery mildews and the polyphyletic group of hyphomycetes (mostly belonging to the ascomycota). For classification the reference book of Klenke & Scholler published in 2015 and containing all recently reported fungi in the German speaking areas of Europe was used, as well as the long-standing classic „Parasitische Pilze an Gefässpflanzen in Europa" (Brandenburger 1985) if the fungal pathogen was not of one of the groups contained in Klenke & Scholler (2015). To examine the collected plant samples a binocular was used to determine the group of fungi followed by a microscope analysis for further classification down to the species level.

Statistical Analysis

For the statistical analysis we used R version 3.3.2 (31.10.2016) and the packages lme4, ape, car and effects. Data were explored following the procedure described by Zuur et al. (2010): The data set was checked for outliers and homoscedasticity by *plot()* and *boxplot()*, correlations by *cor()*, *pairs()* and visually with *plot()* for non-numeric factors or response variables. The relationship of explanatory variables (plant status and others, see table 2 and 4) and exploratory variables (infestation sensitivity, resp. severity), was checked with multipanel scatterplots using *plot()* using many different factors and response variables. Further, potential interactions were researched using the function *coplot()* and *interaction.plot().* Also the normal distribution of residuals after modelling was tested with *plot()* and *hist()*, and as found for the analysis of infested area (percentage), a logit-transformation improved the normal distribution of the residuals and was therefor applied. Additionally we had a look at the quantity of zeros in our response variables to select adequate models.

For each model, interactions of plant status (resp. native status and success status for contrasts) have been tested and relieved from the full model (because no indication for an interaction was found) to allow complete calculation (no dropped columns). The models were then stepwise simplified by AIC based selections.

We added either plant family or a phylogenetic tree (for details see section on infestation severity) as a random factor respectively correlation matrix depending on the model requirements to account for the phylogenetic structure (see Razanajatovo et al. 2015).

For all analyses, if not mentioned otherwise, we included the following independent variables: plant height, plant diameter, sun exposure, neighbors of same plant family, neighbors of same plant genus, range size, vegetative status, herbivory incidence, herbivory level, fungus type, plant status.

Infestation sensitivity

Disease sensitivity (infestation yes/no) has been analyzed using generalized linear mixed-effects models (glmer) with the plant family (host) as random factor. At first, a single factor analysis with the species status as only independent variable was performed for the infestation sensitivity. Followed by a multivariate analysis including all recorded explanatory factors mentioned. Models were selected using AIC values, p-values were obtained using Likelihood Ratio Test. An *Anova()* (working for glmer/lmer and calculating p values by Wald chisquare tests) was performed. Each census was analyzed separately (C1 = "spring census" ≈ may / C2 = "summer census" ≈ July/ C3 = "autumn census" ≈ September), and additionally all censuses pooled together (with census number as additional random factor and plant species within plant family to account for differences between censuses and repetition of species).

The multivariate analyses of the infection incidence are dominated by the factor „fungi types" (infesting the respective plants), due to a majority not infested plant species holding the category „No Fungus" as fungus type. We therefore added another full model analysis excluding the factor „fungi types" for each census separately and all censuses pooled, after completing the statistical analyses.

Infestation severity

The percentage of leaf area infested, was analyzed with a generalized least square model (gls). A phylogenetic tree was constructed using PhyloMaker in the package phytools (Qian & Jin 2016) and integrated into the linear mixed effect model as a corPagel correlation matrix. Due to badly distributed residuals, the data were logit transformed, which improved residual normal distribution. At first, a single factor analysis with the species status as only independent variable was performed for the infestation severity. Next, a mutlivariate analysis was conducted including all recorded explanatory factors mentioned. Models were selected using AIC values, p-values were obtained using Likelihood Ratio Test. With gls, all censuses have been analyzed separately performing an *anova()*.

To analyze infestation severity pooled over all censuses, a linear mixed-effects model was used with plant species within family and census number as random factors. We used linear effect models instead of gls because including the phylogenetic tree was not possible with repeated measures.

Grouped analyses for nativeness and establishment in Switzerland

We further performed two grouped analyses. For the first grouping for nativeness, we grouped „native" versus „alien" together. In the second grouping, plants were pooled regarding their establishment success: successful (native and naturalized) versus non-successful (non-naturalized) species. Both groupings were analyzed regarding infestation sensitivity as well as severity. (A more precise measure of success gives the distribution of a plant: the range size was included in the general full models anyway.) Severity was analysed by an *anova()* with a generalized least square (gls) model, with the phylogenetic tree as correlation matrix. For sensitivity we performed an *Anova()* using generalized linear mixed-effects models (glmer) with plant family as random factor. All recorded explanatory factors (see above) have been included, and each census was analyzed separately.

Deviance from the local Landolt temperature indicator value (LTIV)

Finally, we tested the effect of a deviance from the local LTIV for native and naturalized plant species on infestation sensitivity in a single factor glmer model with plant family as random factor, and for severity in a gls model without correlation matrix, both for each census separately. With pooled data a glmer respectively a lmer was performed. Variation in microclimatic conditions was corrected by addition of the factor sun exposure, soil differences are not corrected for due to an exceeding effort it would have meant.

The guidelines for the statistical procedure were taken from Razanajatovo et al. 2015, further inspiration came from Vasquez & Meyer (2011) concerning grouping after nativeness/establishment and Mitchell et al. (2002) for using Swiss mean range size (found records from infoflora, see above).

Results

In general, main fungi types were rusts, powdery mildews, and unidentified leaf spots. More rare were smuts, hyphomycetes and some special cases (e.g. coelomycetes). Rusts have been found in all three status groups. In spring, no powdery mildew was observed at all. By summer, only infestations of native plants have been found. In autumn, powdery mildews infested again mainly natives (around 70% of the cases), and some non-naturalized plant species (30% of all powdery mildew cases).

First we analyzed infestation severity (% of infested area) and sensitivity (presence/absence of pathogen infestation) only with plant status as an explanatory variable (further called single-factor analysis). Table 1 gives a summary of infestation rates and scales for each census and plant status with significance indications. Figure 1 (for sensitivity) and 2 (for severity) illustrate these results with bar plots including error bars. We detected a significant effect of plant status from C2 respectively C3 onwards, and for pooled results over all censuses (see table 1 and figures 1 and 2). The three different censuses and two response variables each give a different picture. In C1, naturalized plants showed the least infestation sensitivity (24.14%) and severity (0.59%). The mean infestation sensitivities of natives and naturalized are at a comparable level (38.03% resp. 34.36%). Severity of natives is at 1.35%, and 1.36% for non-naturalized plant species. In C2, naturalized plants suddenly reached the highest level of infestation sensitivity (64,52%), compared to 44.88% in natives and 34.78% in non-naturalized species. Differences in infestation sensitivity thus lead to significant results in C2. Severity in C2 is only marginally significant. Natives show relevant higher infestation scales (2.18%) in comparison to naturalized (1.23%) and non-naturalized (0.97%) plant species. In C3, sensitivity is significantly lower for non-naturalized species (20.36%) in contrast to natives (34.33%) and naturalized ones (33.33%). Natives tough reach the highest infestation severity (2.18%), and naturalized (1.10%) and non-naturalized (1.08%) almost the same level of infestation. Over all censuses (pooled data), non-naturalized show a significant lower sensitivity (29.94%), compared to 39.10% (natives) and 41.11% (naturalized, see figure 1). Despite similar sensitivity, natives show a significant higher overall infestation severity (1.89%) compared to naturalized (0.98%) and non-naturalized (1.14%) with a similar level here (see figure 2).

Table 1: Infestation levels (severity) and rates (sensitivity) per plant status and census

	Severity (in % Cover)			Sensitivity (% infested species)		
	Native	Naturalized	Non-nat.	Native	Naturalized	Non-nat.
C1	1.35	0.59	1.36 ns	38.03	24.14	34.36 ns
C2	2.18	1.23	0.97 .	44.88	64.52	34.78 **
C3	2.18	1.10	1.08 *	34.33	33.33	20.36 **
all	1.89	0.98	1.14 **	39.10	41.11	29.94 ***

Significance codes yielded from single-factor anovas for plant status:

p ≤ 0.001 '***' p ≤ 0.01 '**'   p ≤ 0.05 '*'   p ≤ 0.1 '.'

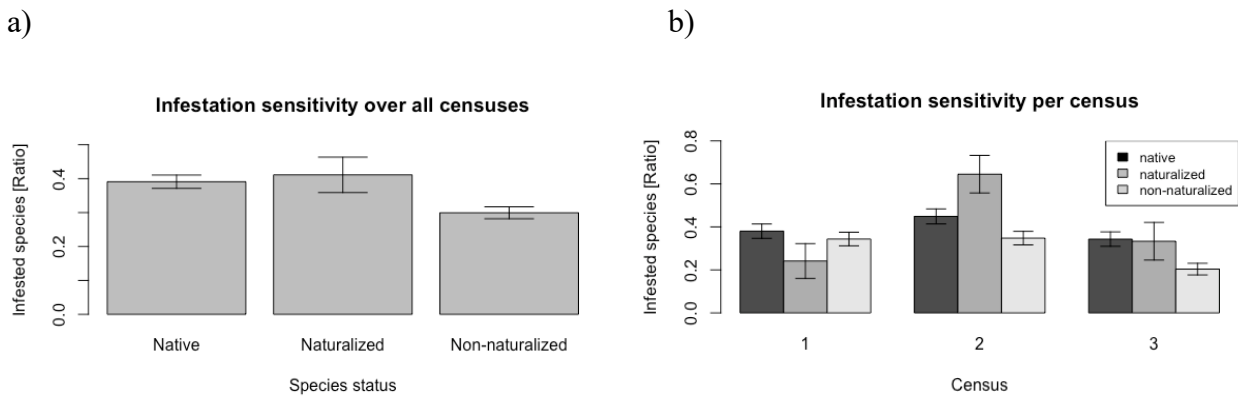a)   b)

Figure 1 Infestation sensitivity for pooled data (a) and for each census separately (b). See also table 1.

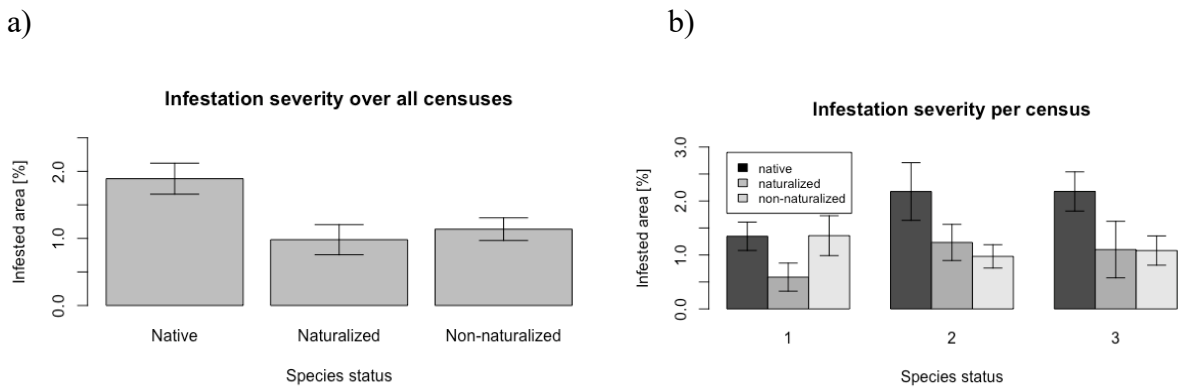a)   b)

Figure 2: Infestation severity for pooled data (a) and for each census separately (b). See also table 1.

Infestation sensitivity

In all censuses, only fungus type showed a significant effect on infestation sensitivity. This result is due to the high portion of non-infested plant species and therefor dominates over other eventual effects by absorbing a lot of statistical power. In C2 we find a significant effect (p=0.02) of herbivory degree and a marginally significant effect of herbivory incidence (p=0.06), with less infestation sensitivity with increasing herbivory (see table 2). In C3 no additional significant effect was found, but two marginally significant are noteworthy: Plant status showed the tendency, that non-naturalized plant species are less susceptible to fungal infestations (Table 2, p=0.09). And range size seems to correlate with infestation sensitivity, with higher infestation sensitivity for larger range size (Table 2, p=0.06).

The analyses excluding the factor „fungus type" (done to improve statistical power of all other factors) yielded following significant results (not presented in a table here): In C1 herbivory incidence was correlated with a higher ratio of pathogen infestation (p<0.01). In C2, plant status became

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Table 2: Infestation sensitivity (% of incidence), best models including Fungi types for C1-C3, simplified full model for pooled censuses

Response variables	Infestation C1: Yes /No				Infestation C2: Yes /No				Infestation C3: Yes /No				Infestation all censuses		
Fixed factor	*Df*	*Chisq*	*P-value*		*Df*	*Chisq*	*P-value*		*Df*	*Chisq*	*P-value*		*Df*	*Chisq*	*P-value*
Plant height													1	0.0506	0.822
Diameter					1	6.2686	0.01229	*	1	2.1299	0.1445		1	0.011	0.9165
Sun exposure									2	4.0157	0.1343		2	0.0213	0.9894
Neighbors of same family									1	16245	0.2025		1	0.0385	0.8445
Range size									1	3.2082	0.0733	. 5)	1	0.0029	0.9567
Neighbors of same genus									1	1.0198	0.3126				
Vegetative status													3	2.9739	0.5622
Herbivory yes/no					1	3.4156	0.0761	. 3)					1	0.8212	0.3648
Herbivory degree					1	5.2770	0.0216	* 3)	1	2.9362	0.08661	. 6)			
Fungi types	3	57.8364	1.704e-12	*** 1)	7	113.1342	< 2e-16	***2)	6	70.7972	2.81e-13	*** 2)	8	36.0216	1.74e-05 ***2)
Plant status	2	2.3021	0.3163		2	5.5542	0.06222	.	2	5.7392	0.0567	. 4)	2	0.8936	0.8936
Random factor:															
Plant family													plus census and species		

Table contains results of a Analysis of Deviance with Type II Wald chisquare tests

1) Due to NoFungus (***) and leaf spots (***)

2) Due to NoFungus

3) Less infestation if herbivory

4) Non-naturalized are less susceptible

5) Trend: The more found (wider distribution in Switzerland), the more sensitive to a fungal infestation

6) More infestation if herbivory

the only significant factor (p<0.01, see also figure 1), with naturalized being the most sensitive status. In C3 we found again significant results for the plant status (p=0.0072, see figure 1), with a significant lower mean sensitivity for non-naturalized compared to the other statuses. Marginally significant results for the plant diameter (p=0.0658) have been found in C3, what shows that populations/individuals with a larger diameter (mean diameters 150.5 cm compared to 127cm) have a higher ratio of infested species. Pooled data over all censuses yielded several highly significant results (presented in table 3): Sun exposure (p< 2e-16) shows the highest infestation sensitivity under half-shady conditions. Neighborhood (p< 2e-16) indicates more infestations in presence of neighbors of the same plant family. Herbivory incidence (p< 2e-16) shows more frequent fungal infestation if there is herbivory. And significant different infestation sensitivity depending on vegetation status (p< 2e-16), with most infestations occurring during flowering (39.63%), followed by seed production (38.78%) and vegetative stage before flowering (35.36%), and clearly reduced after seed production (infestation level at 26.35%). Plant status, as well highly significant with p< 2e-16, shows the least infestations on non-naturalized plant species (see also figure 1). There was no significant effect for the range size. Mean range sizes (in recorded Swiss-wide findings of 50x50m gridlines, not presented in a table) are: 479.46 for natives, 129.29 for naturalized and 4.88 for non-naturalized plants (mainly cultivated/ornamental species).

Table 3: Results for infestation sensitivity excluding fungi types for pooled data of all censuses

	Df	Chisq	P-value	Sign.	Direction
Height	1	3.0831e+00	0.07911	.	More infest. on high species
Diameter	1	1.3989e+00	0.23691		
Sun exposure	2	6.0499e+04	< 2e-16	***	most infest. in half-shade
Same.fam.neighb.	1	1.9798e+03	< 2e-16	***	more infest. if nb of same f.
Range size	1	8.4290e-01	0.35857		
Veg. status	4	1.2505e+09	< 2e-16	***	most infest. during flowering
Herbivory	1	4.8907e+04	< 2e-16	***	more infest. if herbivory
Plant status	2	6.5865e+05	< 2e-16	***	least infest. on non-nat.

Infestation severity

For infestation severity the only factor that was consistently significant over all censuses was the fungus type (see table 4), due to powdery mildew (generally covering higher areas) and the case of non-infection (categorized as „No Fungus") with zero cover. In C2 we additionally found a significant negative effect (table 4, p=0.01) in case of members of the same plant family in the neighbor-

Table 4: Infestation severity (area in % covered by fungus): best models including Fungi types for C1-C3, simplified full model for pooled censuses

Response variables 1)	Infested area (in %) C1				Infested area (in %) C2				Infested area (in %) C3				Infested area (in %) all censuses		
Fixed factor	*Df*	*F-value*	*P-value*		*Df*	*F-value*	*P-value*		*Df*	*F-value*	*P-value*		*Df*	*Chisq*	*P-value*
Plant height					1	1	0.4577						1		0.2954
Diameter					1	1	0.2701						1	1.0951	0.5852
Sun exposure					2	1	0.5847						2	0.2979	0.572
Neighbors of same family					1	7	0.0081	** 3)					1	0.0167	0.8973
Range size					1	2	0.1178						1	1.6245	0.2025
Neighbors of same genus					1	0	0.9765								
Vegetative status					3	1	0.4401						4	3.9541	0.4123
Herbivory yes/no													1	0.9186	0.3378
Herbivory degree					1	1	0.2285								
Fungi types	3	78.2209	<.0001	*** 2)	7	29	<.0001	***	6	115	<.0001	***	8	802.7164	<2e-16***5)
Plant status	2	0.0224	0.9778		2	1	0.2886		2	1	0.4474		2	0.1167	0.9433
Correlation matrix													*Random factors:*		
for C1-C3:													census,		
phylogenetic tree													species within family		

Table shows results for C1-C3 of a analysis of variance [anova()]; for pooled data over all censuses the results are of Type II Wald chisquare tests [*Anova()*]

1) data are logit transformed

2) Due to NoFungus

3) Species with neighbours of the same plant family show less infestation cover (in C2)

4) The less sun, the more areainfested

5) Mean infestation cover by the different fungi types:

powdery mildews : 16,1%	leaf spots : 3,3%
rusts : 7.9%	coelomycetes: 3%
hyphomycetes: 5.8%	diff ascomycetes: 2%
smuts : 5.7%	ustilaginales: 1%

hood. In C3 we detected a marginally significant relationship with sun exposure (table 4, p=0.06): the more sun, the less infested area.

In contradiction with the single factor analyses presented in table 1, we find no significant effect of plant status in the simplified full models (models with the best AIC values).

Contrast Native vs. Alien (Non-naturalized and Naturalized)

Native plants are significantly more frequently and highly infested by fungal leaf pathogens than alien plant species (see table 5). The latter result is due to more frequent infestation by powdery mildews on native plant species, which leads to higher infestation areas. These mean trends becomes more pronounced with the seasonal advancement.

Table 5: Mean results of grouping native vs. alien plant species

	Severity (in % Cover)			*Sensitivity (% of species)*		
	Alien	*Native*		*Alien*	*Native*	
C1	1.27	1.35	ns	33.20	38.03	ns
C2	1.00	2.18	*	38.31	44.88	.
C3	1.08	2.18	***	21.91	34.33	**

Significances resulting from single-factor analysis for grouped nativeness status (native/alien) as factor

In the full models, a significant effect of fungus type on the infestation severity and sensitivity is shown in all censuses (both p<0.0001, not presented here). Marginally significant effects (both p=0.07, not presented here) were found in C3 for the sun exposure and the neighborhood: Less sun exposure as well as members of the same family in the immediate surrounding (< 1m) tend to increase infestation severity.

Mean infestation severity for C3 (% of infested area) in relationship to:

- Sun exposure: shady (2.28%), half-shady (1.78%) and sunny (1.42%)
- Neighborhood: Without neighbor(s) of same plant family (1.59%), with n.b. (1.62%)

No effect could be shown for nativeness status with the full models.

There was a significant negative correlation (p=0.03, not presented here) of herbivory degree (and marginally significant with p=0.07 for herbivory incidence) and infestation sensitivity in the C2 full model:

- Herbivory degree (infest. plant sp.s): 1 (42.54%), 2 (41.38%), 3 (27.27%),
  no case of herbivory degree 4

Range size showed a marginal significant (p=0.08, not presented here) effect on infestation incidence (in C3, full model), with an elevated sensitivity for species with larger range size.

With the full models, there is no significant correlation found for the grouping analysis native vs. alien over all censuses but fungi type.

Grouping non-successful vs. successful (native and naturalized)

In a single factor analysis, successfully established plant species show significant more frequent and severe fungal infestations in census two and three compared to non-successfully (i.e. non-naturalized) established plant species. In the first census the trend is the same, but differences not significant (see table 6).

Table 6: Mean results of grouping successful vs. non-successful plant species

	Severity (in % Cover)			*Sensitivity (%infested species)*		
	NoSuccess	*Successful*	*Sign.*	*NoSuccess*	*Successful*	*Sign.*
C1	1.36	1.26	ns	34.36	36.36	ns
C2	0.97	2.05	**	34.78	47.46	***
C3	1.08	2.04	**	20.36	34.20	**

Significances resulting from single-factor analysis for grouped establishment success status as factor

In the full model analyses, infestation severity shows highly significant correlation with the fungi type in C2 and C3 (both p<0.001, not presented here), due to powdery mildew infestations only found on successful plant species and provoking higher areas covered than with other fungal infestations.

Additionally, in C2, a significant correlation (p=0.03, not presented here) with plant height was found. In C3, height turns out marginally significantly (p=0.09, not presented here) correlated to infestation severity and plant diameter significantly (p=0.02, not presented here). Smaller (in height or diameter) plants/populations show in some cases and much higher infestation severity. The infested area may rise to levels never found in tall individuals or species/populations with large diameters, see figure 3 below).
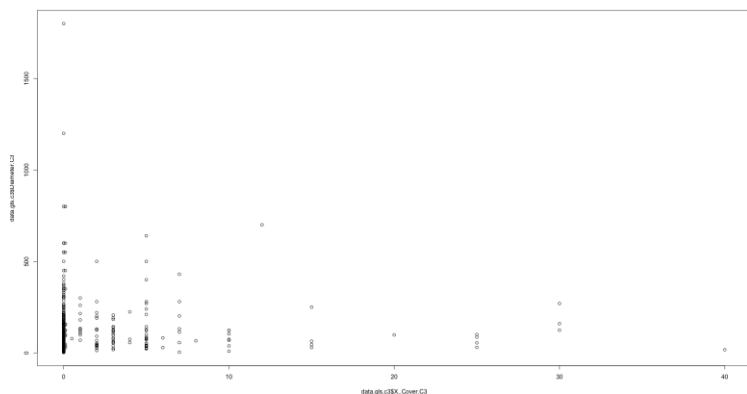
Figure 3

Relationship of infestation severity (x axis) and diameter (y axis)

Further, in C2 there was a highly significant (p<0.001, not presented here) negative correlation of herbivory incidence and infestation sensitivity (41.85% compared to 40.59% without resp. with herbivory incidence).

Deviance from local Landolt temperature indicator value (LTIV)

No significant or nearly significant results merged from the separate analysis of deviance (either positive or negative deviance) from the local LTIV (results not presented here).

Discussion

Different ways of data analysis, and possible bias by unidentified leaf spots and powdery mildews

We conducted two respectively three different types of analyses for the infestation severity and sensitivity, namely the conservative full models (including fungi types) who were stepwise simplified, the single-factor analyzing regarding solely plant status, and additionally (reduced) full model analyses for sensitivity excluding fungi types. Results of the first analysis mentioned are most conservative whereas the following ones highlight the role of plant status. The high level of zeroes due to non-infested plants led to the result that the factor "fungus type" explains a lot of variation, but undermines the effect of other factors. We regard the latter as to be taken with caution, but assume the effects of plant status being a significant pattern in the field, which could also be detected with the first type of analysis with a greater sample size.

Coming to the grouped analyses investigating the effect of nativeness and establishment success on infestation: An effect of pooling the data without weighting is that naturalized species are

underestimated because of a massively smaller sample size. At the other hand, this procedure compensates for the higher error probability due to a smaller sample and reflects approximately the relative abundance existing in the Swiss flora.

A possible bias exists for the mean infestations in C2. A lot of „unidentified leaf spots" registered in C2. In C3 the total number of leaf spots was suddenly lower, but many decomposers emerged, and as such not included in the fungal pathogen statistics. Eventually those leaf spots of C2 evolved into decomposers in C3.

Further, powdery mildews take a special role in our study: They cover characteristically high percentages of a plant/population compared to other fungal pathogens in the case of an infestation and thereby bias the analyses for infestation severity in relationship to the fungi types and plant status. The fact that none have been found on naturalized plants is possibly biased by their smaller sample size (34 vs. 215 natives, resp. 239 non-naturalized plant species).

Effects of plant status and range size on infestation:
Support for the enemy release hypothesis and signs of pathogen adaptation

The results of the first census do not allow us any statement about the effect of plant status. Following results give support to the ERH: By C2 and C3, non-naturalized showed the lowest infestation sensitivity and severity compared to natives and naturalized species. In C2, natives are significantly more severely infested than alien species. In C3, natives remain the most severely infested group. Naturalized and non-naturalized species keep up at a comparable level at this period. This pattern was confirmed with the single factor analyses. The simplified models of C2 and C3 (table 2) lead to the assumption (marginally significant results) that plant status also accounts for difference in sensitivity towards fungal infestations. The full model for pooled data excluding fungi types (table 3) confirms the significant effect of plant status. Therefore we suggest that the analyses for infestation sensitivity also give support to the ERH. Also the grouped analysis for nativeness gives support to the ERH: Natives show higher infestation severity and sensitivity than alien species. This pattern became more evident later in the season. Significant differences have been registered for sensitivity in C3, and for severity in C2 and C3.

Some indications counting against the ERH have also been found. First, naturalized species are the most frequently infested group in C2. With their smaller sample size (due to less representatives under natural conditions and therefor the BoGa as well), their rates seem to be more influenced by chance. This counter indication has therefor to be taken with care. But also in terms of infestation sensitivity, naturalized species suffer even frequently from fungal pathogens than natives. Only the

fungus type explains variation of sensitivity over all censuses consistently in the full models, but not plant status. (Some show marginally, but not significant effects of plant status.) Additionally, powdery mildews were abundant on natives and absent on naturalized species that influenced the found contrast. The support for the ERH has therefore to be relativized.

Naturalized species are shown to suffer even frequently from fungal infestations than natives. This ERH contradicting finding indicates their "intermediate stage" in terms of evolutionary adaptation of fungal pathogen to them. Similarly, successfully established species (natives and naturalized) show higher mean infestation sensitivity than non-naturalized species with advanced growth season. An underlying pathogen accumulation process by evolutionary adaptation of pathogens in the introduced range (as described by Mitchell et al. 2010) could be involved: First, the identified fungi do not include any neo-pathogens (as recorded in Klenke & Scholler 2015, and for some generalists identified with Brandenburger 1985). And second, non-naturalized plants suffer significantly less frequent and strongly from fungal infestations. Regarding the fact, that some naturalized plants are very common and a longstanding part of the Swiss flora, this does not surprise because pathogens had decades to adapt to them. Interestingly the local fungal pathogen community of the botanical garden seems not to be adapted to non-naturalized species. This finding for fungal leaf pathogens is in contrast to Razanajatovo et al. (2015) who found that insect pollinators had adapted to the local flora at BoGa.

The evidence that regional range size is tighter linked to infestation sensitivity than local abundance in BoGa, gives support to the accurateness of using regional (in our case Swiss-wide) distribution rather than the local scale when regarding fungal pathogens. In C3 we find a marginally significant result for the range size of naturalized species, with the trend that plant species with a larger range size show more frequent a fungal pathogen infestation. This is in accordance with Mitchell et al. (2002) who found that regionally common species suffered from higher pathogen attack. Van Kleunen & Fischer (2009) also report higher pathogen load on species with a larger range size for naturalized species in Europe, a fact that contradicts ERH.

Concretely, we can confirm our first hypothesis that natives are more strongly infested than alien species, only partly for severity. For infestation sensitivity, we have to distinguish naturalized and non-naturalized species. Our second hypothesis concerning range size depending infestation occurence shows signs of correctness, but isn't yet satisfactorily replied. The third hypothesis on pathogen adaptation can be confirmed with our results from the infestation sensitivity analysis. For a definitive statement we would propose to test for adaptation with an additional investigation.

It does not surprise that we found support for the ERH with our investigation, because it goes hand in hand with the known specificity of fungal pathogens (Farr et al. 1989). If most fungal patho-

gens are specific to an individual plant species (exceptionally for a genus) it is a logical consequence that plants growing away of that pathogens' geographical range will be (mainly) relieved from infestations by pathogens of the new range.

To conclude, we found partly support for the enemy release hypothesis, namely for infestation severity differences. Eventually, there was a significant enemy release at the establishment stage of nowadays' naturalized species that enhanced their establishment success chances. We also found evidence for fungal pathogenic accumulation on naturalized species. A process that followed the establishment success of the species. It seems important to us to highlight, that the increased infestation severity is excerting a proportional effect on reproductive success (Campbell & Madden 1990, but see Waggoner & Berger 1987) and thus acting on establishment (and invasion) success in the new range. Our findings contrast the findings of Van Kleunen & Fischer (2009), who report only a small release in number of fungal pathogens from the native to the introduced range. In our study, infestation sensitivity and severity are clearly higher for natives compared to alien species, a result that supports the ERH. When it comes to explain the invasion success of some alien species we agree with Vasquez & Meyer (2011) that invasion success cannot be explained by escape from one solely enemy guild.

Effects of neighborhood, herbivory and other factors on fungal infestation

Concerning the investigated effect of neighbor plants, we found indeed significant results with the multivariate analysis for infestation severity in C3 but confusingly with an even lower infestation ratio for plants with neighbors of the same plant family. This finding is difficult to explain biologically, and as the difference between the two ratios is small, a statistical artifact might be the case here. In C2 we additionally found a significant negative effect in case of members of the same plant family in the neighborhood. This finding is in contradiction to our hypothesis of same family neighbors facilitating and enhancing fungal infestations. Should this result remerge in further studies, we will have to revise this hypothesis and eventually reduce it to facilitated infestation incidence, but not enhanced infestations. Adversely for the pooled data analyzed without fungi types, we find a highly significant effect with higher infestation incidence in the case of same family neighbors. Concluding, we cannot make any definite statement on the effect of neighboring plants and cannot confirm or reject our fourth hypothesis.

We find two marginally significant and opposing patterns indicating possible links between herbivory and fungal pathogens. In the multivariate analysis we found lower degrees and less fre-

quent herbivory incidence in case of a fungal infestation in C2. That would suggest that herbivores avoid infested plants, or support the hypothesis of a distinct resource allocation either towards herbivory or pathogenic defense. In C3 we find the contradicting result of more frequent infestations with increasing herbivory degrees. This pattern is also found with the model excluding fungi types (pooled data over all censuses) for infestation sensitivity. This correlation would lead to a biological interpretation that fungal infestation follows herbivory attacks, by injured plant tissue breaking down the cell wall defense against pathogens. Do both patterns happen under natural conditions? It is difficult to judge on this question, and whether the first pattern (supported by the significant result of the multivariate analysis) or the second (supported mainly by the significant results of the analysis excluding fungi types) is more important. We also have to take into account that decomposer infestations are not considered (who dominate in autumn, resp. C3) who might help us detect to the dominant pattern. Our fifth question can therefor not be replied on a functional level. Nevertheless, both imagined patterns seem to exist in nature.

The only significant result concerning the vegetative status is found with the analysis of sensitivity excluding fungi types (pooled censuses). Infestation is lowest and the less frequent after seed production (vegetative stage four). At this stage, decomposers become predominant over other fungi, which have not been included in our analysis. What we see is, that pathogens are most common/abundant during flowering and seed production and are therefore likely to exert an influence on reproduction. Campbell & Madden (1990) report, that the effect on fitness and reproductive success (measured in terms of yield) is proportional to the visually infested area on the plant. In our opinion, life stage of the plant logically has to be taken into account. To exactly quantify the impact of fungal pathogens on plant fitness. The initial question on the existence of distinct infestation events depending on vegetative status can be answered positively, but not yet concluding.

Remarkably there is no detected effect for a deviance from the local Landolt temperature indicator value (LTIV). We can therefore not state anything on the faith of Alpine species or the resource allocation effects (benefits or costs) for species coming from a distinct climate. Our hypothesis of sensitivity/severity differences due to different LTIV has to be rejected with our present data. Further we can report significant effects of sun exposure, with the highest infestation severities occurring at half-shady placements. The combination of elevated humidity and warm temperatures seem to promote fungal growth at the best, and the lower infestation severity at dryer sunny and colder shady locations would be a logical consequence as our data make suggest.

We also found higher infestation sensitivity for populations/species with a larger diameter. A potential explanation is the larger surface that a fungal spore can drop on. This correlation opposes the diameter effect found in the success contrast in C2. The latter is possible due to opportunist spe-

cies, being eventually smaller in size, and investing fewer resources into defense. This hypothetical explanation is though very speculative.

Outlook

In contrast with the findings of Van Kleunen & Fischer (2009) who report a gain of novel powdery mildews in the introduced range (for naturalized species), we found quite the opposite in our case. While other major fungi types such as rusts are found in all plant status groups, powdery mildews mainly occured on natives, and none was found on naturalized plants. We suppose that the gain or loss of particular fungi types for alien species is not yet well enough studied.

Further there are signs for the diversity-disease hypothesis by Elton (1958, cited according to Mitchell et al. 2002), as our infestation rates found in the highly diverse botanical garden seem smaller than those detected in an ongoing open grassland study with naturally occurring species numbers conducted by Seraina Cappelli, a PhD student at our institute. A confirmation of distinct infestation rates in her study would lead to another field of research in regard to plant invasion mechanisms possibly examined. A loss of plant diversity could in this case also facilitate plant invasions thru an increase in pathogen infestations.

Leishman et al. (2014) found that different compositions of leafs (e.g. leaf nitrogen) lead to different vulnerabilities concerning fungi. An idea for further research would be to investigate the distinct leaf compositions (leaf nitrogen, cell wall construction and amount of secondary metabolites), and to add those as an explanatory factor for infestation sensitivity and severity besides the plant status. It is imaginable that these plant traits could add to the picture of fungal and general pathogen sensitivities. Eventually there is a correlation between climatic origin of a species and leaf/plant tissue traits (and as a conclusion of fungal pathogen sensitivity). Our analysis to detect the effect of the Landolt temperature indicator value only included native plants; alien plants were not analyzed in regard to their climatic origin. Future research should also investigate the relationship of life stage depending foliar infestation and reproductive success (in terms of number of produced and ratio healthily germinating seeds).

We propose a continuation of investigation of diverse enemy guilds through different study approaches – biogeographical, community level, transplant experiments, common garden combined with microbial soil inoculation etc.

Conclusion

Our study gives support to the enemy release hypothesis explaining invasion success for some plant species. Alien species suffer less strongly from fungal pathogens, and non-naturalized also less frequently from pathogenic fungal infestations. We also found evidence for adaptation of native pathogens towards alien species. Range size is positively correlated with infestation sensitivity, in general as well as for naturalized species in particular. Further we can report of the effect of the fungus types explaining a lot of variability in infestation sensitivity and severity. The effects of sun exposure, neighbors from the same plant family, herbivory and plant size are ambiguous.

Future research should further investigate the effect of different fungal pathogen types on reproductive success, climatic plant origin on defense (leaf composition), distinct resource allocation (defense/growth) and the situation for belowground infestations and interactions.

Contributions

Main directories for set-up and statistical analysis came from Markus Fischer. The detailed set-up, concrete questions, analyses and interpretation were conceived and conducted by Joëlle Michel. Conceptual as well as concrete support in data structuration and analysis is own to Sebastian Keller. He specially contributed the phylogenetic tree and valuable review comments on a former version of this thesis. Stefan Blaser provided a practical introduction into field and lab work comprising plant collection, infestation estimation and fungal categorization.

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