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# Spatial variation in soil biota mediates plant adaptation to a foliar pathogen

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## Summary

- Theory suggests that below-ground spatial heterogeneity may mediate host–parasite evolutionary dynamics and patterns of local adaptation, but this has rarely been tested in natural systems.
- Here, we test experimentally for the impact of spatial variation in the abiotic and biotic soil environment on the evolutionary outcome of the interaction between the host plant *Plantago lanceolata* and its specialist foliar pathogen *Podosphaera plantaginis*.
- Plants showed no adaptation to the local soil environment in the absence of natural enemies. However, quantitative, but not qualitative, plant resistance against local pathogens was higher when plants were grown in their local field soil than when they were grown in nonlocal field soil. This pattern was robust when extending the spatial scale beyond a single region, but disappeared with soil sterilization, indicating that soil biota mediated plant adaptation.
- We conclude that below-ground biotic heterogeneity mediates above-ground patterns of plant adaptation, resulting in increased plant resistance when plants are grown in their local soil environment. From an applied perspective, our findings emphasize the importance of using locally selected seeds in restoration ecology and low-input agriculture.

## Introduction

Community ecology has unambiguously demonstrated that below-ground–above-ground interactions play a key role in terrestrial communities (Bezemer & van Dam, 2005), and we now have many examples on how variation in the soil environment can have pronounced consequences for the dynamics of above-ground host–parasite interactions in both natural and agricultural systems (Weller *et al.*, 2002; Tack *et al.*, 2015). As a corollary, below-ground heterogeneity may also play a major role in host–parasite coevolution, patterns of local adaptation and the maintenance of variation in plant resistance and pathogen aggressiveness (Gavrilets & Michalakis, 2008; Tellier & Brown, 2011). Nonetheless, we lack a general understanding of how interactions between the below-ground abiotic and biotic environment and plant and parasite genotype affect the (co)evolutionary trajectories of hosts and parasites (Bezemer & van Dam, 2005; Bonte *et al.*, 2010; van Dam & Heil, 2011; Tack *et al.*, 2015). Notably, whether the host or parasite has a coevolutionary advantage in its home ground may inform us about the use of locally selected genetic resources in low-input agriculture (Ceccarelli, 1996) and restoration projects.

Despite the increasing awareness that spatial heterogeneity plays a fundamental role in host–parasite interactions (Laine & Tellier, 2008), the majority of studies on host–parasite coevolution are still conducted under uniform laboratory conditions. When the interaction between genotype and environment is important, such studies may misinform us about the actual coevolutionary outcome in the field (Ridenhour & Nuismer, 2007; Nuismer & Gandon, 2008). Using a more elaborate design, experimental manipulations of the environmental context may change our perception of the direction and strength of local adaptation and pinpoint the key environmental factors affecting the evolution of host and parasite. Several scenarios are possible. The parasite may adapt directly to the local environment or to environmentally induced changes in its host, thereby increasing performance in its local environment (Bonte *et al.*, 2010). As one alternative, the host plant may be adapted to the local environmental conditions and therefore demonstrate a higher resistance or tolerance when attacked in its local environment. Few studies have aimed to assess the evolutionary impact of spatial heterogeneity on host–parasite interactions in wild systems. Laine (2008) showed how spatial variation in temperature mediates patterns of local adaptation of a wild plant parasite. A study by Cory & Myers (2004) suggested that virus isolates of the nucleopolyhedrovirus were adapted to the western tent caterpillar *Malcosoma californicum pluviale* when present on the locally most abundant host plant. Alongside demonstrating that the environment plays a key role in our understanding of host–parasite coevolution, these studies also imply that temporal changes in environmental conditions may have direct consequences for the ecological and

evolutionary dynamics of host–parasite interactions (Mostowy & Engelstädter, 2011; Poisot *et al.*, 2012).

Studies to date have highlighted that a wide range of environmental factors may interact with host and pathogen genotype to shape host–parasite dynamics (as reviewed in Wolinska & King, 2009; Chamberlain *et al.*, 2014; Tao *et al.*, 2015), but few studies have explored how the interaction between host/pathogen genotype and spatial heterogeneity in the below-ground abiotic and biotic components may shape geographic mosaics of natural selection (Piculell *et al.*, 2008; Tack *et al.*, 2015). The abiotic component may consist of soil chemistry, soil type and soil structure, whereas the biotic component will contain biota ranging from pathogenic to mutualistic. Overall, it seems surprising that while community ecology has now accepted the role of above-ground–below-ground interactions in shaping the population dynamics of above-ground species interactions (Bezemer *et al.*, 2005; Ueda *et al.*, 2013; Tao *et al.*, 2015), we have few insights into the evolutionary consequences. In a recent study, Tack *et al.* (2015) showed that variation in the abiotic and biotic soil environment between two habitat types may underlie the spatial differentiation in coevolutionary trajectories of the wild flax and its rust pathogen.

Soil heterogeneity and genetic differentiation in hosts and pathogens are both expected to increase with spatial scale (Ettema & Wardle, 2002). Hence, the interaction between the soil environment and genotype may be contingent on the geographical distances between sampling locations. Experimental studies that sample variation in soil, pathogens and hosts across multiple spatial scales may then inform us about the most relevant spatial scale for assessing genotype × environment interactions and subsequent evolutionary host–parasite trajectories.

Here, we assess how the abiotic and biotic soil environment mediates patterns of local adaptation of the host plant *Plantago lanceolata* and its obligate foliar pathogen *Podosphaera plantaginis*. More specifically, we study the impact of the abiotic and biotic soil environment on plant local adaptation; assess the impact of the abiotic and biotic soil environment in mediating patterns of local adaptation between sympatric host and pathogen genotypes; and investigate whether patterns of adaptation increase (or decrease) with geographical distance between the sampling locations of hosts, parasites and soil. Plant local adaptation was detected as higher quantitative resistance against their local pathogens when grown in their local soil, as evidenced by reduced pathogen aggressiveness and increased time to sporulation. However, no consistent pattern of local adaptation was detected for qualitative resistance. The pattern of local adaptation was robust when extending the spatial scale beyond a single region. Local adaptation disappeared after soil sterilization, suggesting that the soil biota mediate host–parasite evolutionary dynamics.

## Materials and Methods

### Study system

The plant pathogen *Podosphaera plantaginis* (Castagne; U. Braun & Takamatsu) is a powdery mildew specialized on the perennial herb *Plantago lanceolata* L. Like all powdery mildew species (Erysiphaceae), it requires living host tissue throughout its life cycle. The pathogen produces wind-dispersed asexual spores that are growing in vertical chains on the leaf surface (Bushnell, 2002). During the winter, *P. plantaginis* can survive with the help of specialized resting structures (i.e. chasmothecia; Tack & Laine, 2014). Unlike in most powdery mildews, these resting structures can be produced by selfing (Tollenaere & Laine, 2013).

The perennial herb *P. lanceolata* (ribwort plantain) is an obligate outcrosser as a result of protogyny and a gametophytic self-incompatibility system (Ross, 1973). Pollen are dispersed by wind, seeds are frequently dropped close to the mother plant, and clonal reproduction takes place via the production of side-rosettes from the axillary meristems (Bos, 1992). The powdery mildew lowers plant fitness by extracting resources from the host plant and reducing photosynthesis by covering the leaf with mycelium (Jarvis *et al.*, 2002). Moreover, infection can induce host mortality when coinciding with other stressful events (Laine, 2004). Within the powdery mildew–ribwort plantain study system, pathogen infection has been shown to underlie rapid evolution of plant resistance at both small and large spatial scales (Laine, 2006; Ovaskainen & Laine, 2006; Jousimo *et al.*, 2014).

Reciprocal replant–transplant studies of *P. lanceolata* have shown higher seedling emergence and vegetative growth in the local environment (Antonovics & Primack, 1982; van Groenendael, 1985; van Tienderen & van der Toorn, 1991; van Tienderen, 1992; Bischoff *et al.*, 2006; Crémieux *et al.*, 2008), indicating that these plant traits respond to natural selection. Moreover, vegetative growth of *P. lanceolata* is positively correlated with the production of offspring (van Groenendael, 1985; Lacey *et al.*, 2003).

### The collection of plant seeds, pathogen strains and soil

To investigate the impact of abiotic and biotic soil composition on plant and parasite adaptation, we collected soil, plant seeds and pathogen strains from three populations in each of two regions in 2011 (Fig. 1). Plant seeds were collected in July, and pathogen strains and soil were sampled in September–October. Sampling across two distinct spatial scales (i.e. within regions and among regions) may allow for additional insight into the spatial scale of soil-mediated host and parasite adaptation.

We used a shovel to randomly collect multiple soil samples of the top soil layer (i.e. in the rooted zone, *c.* 5–30 cm) in each population (cf. Felker-Quinn *et al.*, 2011). Samples were collected within several meters of mildew-infected plants. Individual soil samples were mixed using a thoroughly rinsed and disinfected concrete mixer, resulting in a total of *c.* 25 l of soil per population. Soil samples were stored at *c.* 4°C upon collection. A single sample of the soil from each population was send to Viljavuuspalvelu (Mikkeli, Finland) for chemical analysis. To disentangle the effect of the soil physical and chemical properties and the soil biotic community, half of the soil from each population was sterilized (cf. Felker-Quinn *et al.*, 2011). Soil was gamma-irradiated by Steri (Scandinavian Clinics Estonia OÜ; Alliku küla, Harjumaa, Estonia) using 32.8 kGy (range estimate:

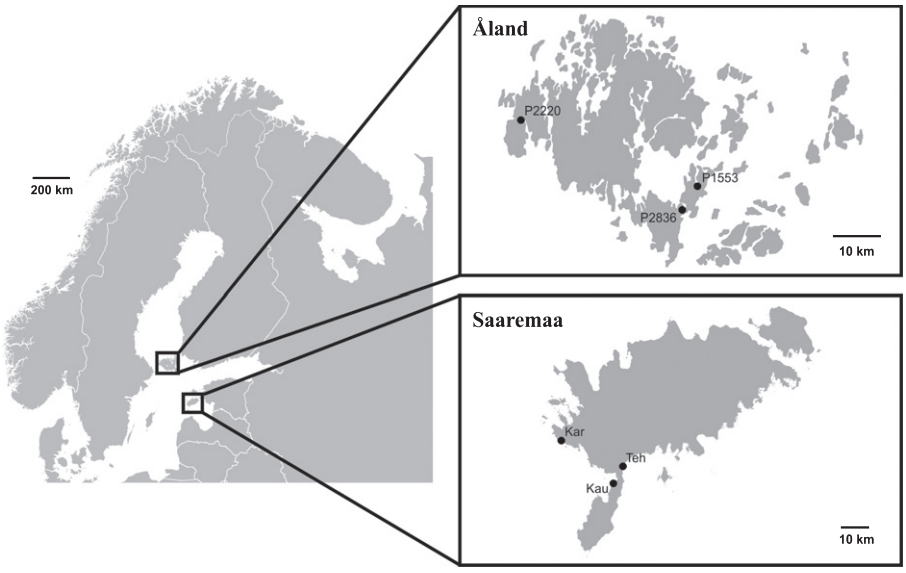


**Fig. 1** Map of the sampling locations. On the left is a map of northern Europe with the location of the two regions (Åland and Saaremaa) given by squares. The regional maps on the right show the three sampling locations (black dots) in Åland (upper) and Saaremaa (lower).

30.9–34.9). While all methods of soil sterilization may cause unwanted changes in soil chemical and physical characteristics, gamma-irradiation may be among the best methods available to date (McNamara *et al.*, 2003). While the nonsterilized soil may potentially contain sexual resting structures (chasmothecia) from the powdery mildew, we did not expect this to result in incidental infections in the glasshouse, as chasmothecia of *P. plantaginis* remain tightly attached to the surface of the senescing leaf, in a similar manner to chasmothecia of *Podosphaera aphanis* on strawberry (Gadoury *et al.*, 2010), and are hence unlikely to disperse into the soil; and chasmothecia are not known to mature and reinfect plants under indoor conditions (see Notes S1 in Tack & Laine, 2014). Following our expectation, we did not detect any incidental powdery mildew infections on the experimental plants in the glasshouse experiment.

From each population, we collected seeds from 10 plants and five pathogen strains. Pathogen strains were purified and maintained in the laboratory using methods described in Laine (2007a).

### Plant adaptation to the abiotic and biotic soil environment

We used a reciprocal planting experiment to test for local adaptation of the plant to its abiotic and biotic soil environment. A similar design was used for the field and sterilized soil. For each population, seeds were sown in 10 (0.5 l) pots with local soil, five pots each of two foreign (i.e. nonlocal) soils originating from the same region, and five pots each of two foreign soils originating from the other region (see Supporting Information Table S1 for the planting matrix). We sowed three (and, in some instances, four to five) seeds to improve the survival estimate, and increase the likelihood of a single seedling emerging for use in the inoculation experiment (see 'The impact of soil heterogeneity on host–parasite (co)evolution' subsection). A single seedling was retained after emergence to prevent competition among siblings (cf. van Tienderen & van der Toorn, 1991; Bischoff *et al.*, 2006). We used seeds from 10 and five mother plants for sympatric and allopatric plant–soil combinations, respectively (Table S1). Replication in the sympatric plant–soil combinations was higher in order to improve statistical power for detecting local adaptation (Adiba *et al.*, 2010; Blanquart *et al.*, 2013). The experiment was conducted in a glasshouse. On day 75, we recorded the length and width of the largest leaf and the total number of leaves. Total leaf area was calculated as the log-transformed number of leaves × leaf length × leaf width (van Tienderen, 1992; Lacey *et al.*, 2003). Notably, seedling survival (a direct measure of plant fitness) and plant growth (an indirect measure of plant fitness) are the most commonly used measures of plant adaptation to the soil abiotic and biotic environment (Pickles *et al.*, 2015; Rúa *et al.*, 2016).

### The impact of soil heterogeneity on host–parasite (co) evolution

To investigate the impact of the abiotic and biotic soil composition on parasite adaptation to sympatric plants, we conducted an inoculation experiment. The main aim was to test whether the evolutionary outcome between sympatric host and pathogen genotypes was mediated by the abiotic and biotic soil environment, which was tested for each of six sympatric host and pathogen combinations (note that we did not include nonsympatric host and pathogen combinations). By testing patterns across six sympatric host and pathogen combinations, we were able to assess the consistency of the local evolutionary outcome as mediated by the soil. Importantly, validating ecological and evolutionary patterns across a range of background conditions is an important approach to assess the generality or predictability of species interactions (Adiba *et al.*, 2010; Woodward, 2010; Linquist, 2015). More specifically, for each of six populations, we inoculated five parasite strains on leaves from local plants grown in three or five different field soils (Table S2). Sympatric inoculations were performed on offspring from each of 10 mother

plants, whereas allopatric crosses were conducted on offspring from each of five mother plants. The total number of inoculations for the field soil was 766. A similar but more limited design was implemented for the sterilized soils, where only pathogens and plants were used from the populations in Åland ($n = 367$ inoculations; Table S2). Replication varied slightly among population/soil combinations (Table S2), mainly as a result of differential survival of plants, ranging from 45 to 50 for sympatric population–soil combinations and from 15 to 25 for allopatric population–soil combinations.

For inoculations, detached leaves were placed on moist filter paper in 9 cm Petri dishes, and spores from an infected leaf were gently brushed with a fine paintbrush over the leaf surface (Laine, 2005, 2008; Tack *et al.*, 2014). Colonies of similar age and size (*c.* 1.0 cm diameter) were used for the inoculations to obtain spore densities as close to each other as possible. Petri dishes were placed in a growth chamber (20 ± 2°C with a 16 : 8 h, light: dark photoperiod). Leaves were checked for the first appearance of (asexual) conidial spores on days 6, 7, 8, 9 and 12 (days 6–9 have been observed as the four most common days for the initiation of sporulation; Laine, 2007a). When infections were first detected on day 12, we conservatively noted the day of first sporulation as day 10. At day 12, when new infections are exceedingly rare, we scored infection intensity on the modified Bevan scale, defined as follows: 1, sparse mycelium but no conidia; 1.5, mycelium producing very few conidia and colonies visible under a dissecting microscope; 2.5, colonies visible with the naked eye but exhibiting sparse sporulation; 3, profuse sporulation on colonies of moderate size (< 5 mm diameter); 4, profuse sporulation on large colonies (Tack *et al.*, 2014). Leaves were checked for the presence/absence of sexual resting structures (chasmothecia) on day 20, although some leaves had to be discarded because of contamination by other microbes.

The use of detached leaves or leaf segments has a long-standing tradition to assess qualitative and quantitative host resistance as measured on whole plants, and there is a large agricultural literature that confirms the general applicability of this method (reviewed in Nicot *et al.*, 2002). Moreover, previous experimental work in our system has shown that patterns of parasite local adaptation –in terms of both infectivity and fitness – can be assessed using detached leaf assays (Laine, 2007b, 2008; Tack *et al.*, 2014).

## Analyses

To analyse the data, we used the framework of generalized linear mixed-effects models (Littell *et al.*, 2006). All models were fitted with procedure GLIMMIX in SAS 9.3 (Cary, NC, USA). Below we provide a brief description of the models used. For a detailed summary of all statistical models, response variables and link functions, we refer to Tables S3 and S4.

**Plant adaptation to the abiotic and biotic soil environment** We first tested whether plant growth was affected by soil origin, plant provenance and soil treatment, as well as their interactions. For this, we modeled ('model 1') seedling emergence and vegetative growth as a function of 'soil origin (S)', 'plant provenance (P)', 'soil treatment (T)' and their interactions. To account for variation among mother plants from each population, we included the random factor 'mother plant' (nested within 'plant provenance'). Similar models ('models 2 and 3') were run separately for each soil treatment to further explore differences among soil treatments in the role of soil origin, plant provenance and their interaction on seedling emergence and vegetative growth. We focused the analysis on the full set of measured plant traits (Table S4) to allow for comparison with previous local adaptation studies on *P. lanceolata* and for the identification of plant traits that are most important for the adaptive response of the plant.

To investigate local adaptation of plants to their local soil, we assessed differences in seedling emergence and vegetative growth in local (sympatric) and nonlocal (allopatric) soils. For this, we conducted separate models ('models 4 and 5') for each soil treatment. In these models, we included the factors 'soil origin', 'plant provenance' and the variable 'sympatry' (Blanquart *et al.*, 2013). The main effects 'soil origin' and 'plant provenance' were included to account for consistent variation in plant growth in particular soils or among plant provenances, which, if not accounted for, can obscure patterns of local adaptation (Blanquart *et al.*, 2013). The dummy variable 'sympatry' was coded with two values, where 'sympatric' referred to plants that were grown in their local (sympatric) soil and 'allopatric' referred to plants that were grown in nonlocal (allopatric) soil (Blanquart *et al.*, 2013). The variable 'sympatry' was nested within 'plant provenance' (Laine, 2005). Hence, the model estimated, for each plant population, the difference between sympatric and allopatric population–soil combinations. A significant value for the dummy variable 'sympatry' then indicates either local adaptation (where performance on sympatric soils is consistently higher or lower) or a mosaic pattern of local adaptation (i.e. spatial inconsistency in the difference between sympatric and allopatric combinations; e.g. Laine, 2005). To test for consistency in local adaptation, we used the population-specific least-squares means estimates of 'sympatry' to define a linear contrast (representing the difference in parasite performance on local and nonlocal soils across populations). We included the random variable 'mother plant' as nested within 'plant provenance' to account for variation among mother plants within populations.

**The impact of soil heterogeneity on host–parasite (co)evolution** To investigate the performance of pathogens when inoculated on their local host plant genotypes grown in either their local (sympatric) or nonlocal (allopatric) soil, we modeled each pathogen life-history trait ('model 6') as a function of 'soil origin', 'population' (as pathogens were only tested on local hosts, the term 'population' here refers to the location where both pathogens and plants were collected; see Table S2) and the dummy variable 'sympatry' nested within 'population' (Laine, 2005). Significance of the variable 'sympatry' then indicates whether pathogen performance varies among sympatric plants grown in local and nonlocal soils, suggesting either a consistently higher or lower performance on local or nonlocal soil (i.e. local adaptation) or a mosaic pattern

of adaptation (i.e. spatial inconsistency in the difference between sympatric and allopatric combinations; e.g. Laine, 2005). As described earlier, we used the population-specific least-squares means estimates to test for local adaptation. To account for variation among mother plants and strains within each population, we included the random variables 'mother plant' and 'pathogen strain' (nested within 'population'), respectively. We note that the inverses of the response traits infectivity and aggressiveness are measures of qualitative and quantitative resistance, respectively (Susi & Laine, 2015); hence, parasite adaptation can be interpreted as plant maladaptation and, inversely, parasite maladaptation can be interpreted as plant adaptation.

**The impact of spatial scale on patterns of local adaptation** Finally, we probed whether spatially consistent patterns of local adaptation were dependent on the geographical distance between the location of soil origin and pathogen/plant collection. Such a pattern of adaptation was detected for plant adaptation to natural enemies when the plant was grown in its local soil (see the Results section). For this, we modeled ('model 8') the response variable as a function of 'soil population', 'pathogen population' and 'symp2', where 'symp2' was coded using three categorical values: 'sympatric', plants grown in the local (sympatric) soil; 'allopatric 1', plants grown in allopatric soil from the same region; and 'allopatric 2', plants grown in allopatric soil from the other region (Adiba *et al.*, 2010; Blanquart *et al.*, 2013). To account for variation among mother plants and strains within each population, we included the random variables 'mother plant' and 'pathogen strain' (nested within 'population'). We then used the least-squares means contrast between symp2 values 'allopatric 1' and 'allopatric 2' to test for any differences in parasite performance on local plants grown in soil from the same region or from the other region.

## Results

### Plant adaptation to the abiotic and biotic soil environment

Seedling emergence and plant growth were strongly affected by the origin of the soil, whereas plant provenance played a minor role (Table 1). Moreover, there was a strong effect of soil treatment and the interaction between soil treatment and soil origin (Fig. 2a,b). The interaction between soil treatment and soil origin suggests that soil biota may play a different role in soils from different origins: for example, the total leaf area was positively affected by sterilization of soils from four locations, whereas it was negatively affected by the removal of soil biota from soils originating from two other locations (Fig. 2b). When data were analyzed separately for the two soil treatments, we detected interactions between soil origin and plant provenance for the response variables leaf width and total leaf area when plants were grown in the field soil, whereas no interactions were detected when plants were grown in the sterilized soil (Table S5; Fig. 2c). This suggests that interactions among soil environment and plant provenance may be dependent on the soil biota.

Plants did not show local adaptation to either the field soil or the sterilized soil (final two columns in Table 1; Fig. 2c).

### The impact of soil heterogeneity on host–parasite (co) evolution

For the field soil, there were clear signs of adaptation; however, the exact pattern varied depending on the trait examined (Table 2; Fig. 3a–c). For infectivity, we detected a strong mosaic pattern of adaptation: pathogens infected a significantly larger proportion of plants grown in their local soil environment in population 'Kau', whereas they infected a lower proportion of plants grown in their local soil environment in population 'Kar' (Fig. 3a), a pattern that was inconsistent with that in the sterilized soil (where infectivity was lower in the local soil in P2220; Fig. 3d). In contrast to the highly variable direction of adaptation for the trait infectivity, pathogens consistently developed slower and exhibited lower aggressiveness on plants grown in their local field soil (Fig. 3b,c; Table 2), a pattern that became less consistent after soil sterilization (Fig. 3e,f; Table 2). There was no impact of the soil environment, plant provenance or sympatry on the presence of sexual resting structures in either the field or sterilized soil (Table 2). Overall, the patterns of infectivity, time to sporulation and aggressiveness in the field soil and sterilized soil did not match well (cf. Fig. 3a–c vs 3d–f), suggesting that soil biota play a key role in mediating pathogen responses to the local and nonlocal soil environment.

**Table 1** The impact of soil origin, plant provenance, soil treatment and their interactions on seedling emergence and growth of *Plantago lanceolata*

| | Soil origin (S) | Plant provenance (P) | Soil treatment (T) | S × P | S × T | P × T | S × P × T | Local adaptation field soil | Local adaptation sterilized soil |
|---|---|---|---|---|---|---|---|---|---|
| Seedling emergence | **< 0.0001** | 0.799 | **< 0.0001** | 0.764 | **0.003** | 0.635 | 0.633 | 0.576 | 0.244 |
| Leaf length | **< 0.0001** | **0.005** | **< 0.0001** | **0.005** | **< 0.0001** | 0.089 | 0.994 | 0.948 | 0.593 |
| Leaf width | **< 0.0001** | 0.122 | **< 0.0001** | 0.215 | **< 0.0001** | 0.683 | 0.916 | 0.285 | 0.740 |
| Leaf allometry | **< 0.0001** | 0.122 | **< 0.0001** | 0.215 | **< 0.0001** | 0.683 | 0.916 | 0.390 | 0.717 |
| Number of leaves | **< 0.0001** | **0.015** | **0.001** | 0.544 | **0.000** | 0.198 | 0.883 | 0.873 | 0.336 |
| Total leaf area | **< 0.0001** | 0.666 | **< 0.0001** | 0.070 | **< 0.0001** | 0.776 | 0.977 | 0.434 | 0.342 |

Shown are *P*-values of the fixed effects as estimated with (generalized) linear mixed models, where significant *P*-values are in bold. Patterns of local adaptation were calculated separately for each soil treatment. A significant *P*-value for local adaptation indicates consistently higher or lower response values when plants are growing in local as compared with nonlocal soil. A significant mosaic pattern of local adaptation would be indicated by an asterisk in the same column. For more details, see models 1, 4 and 5 in Supporting information Table S3.

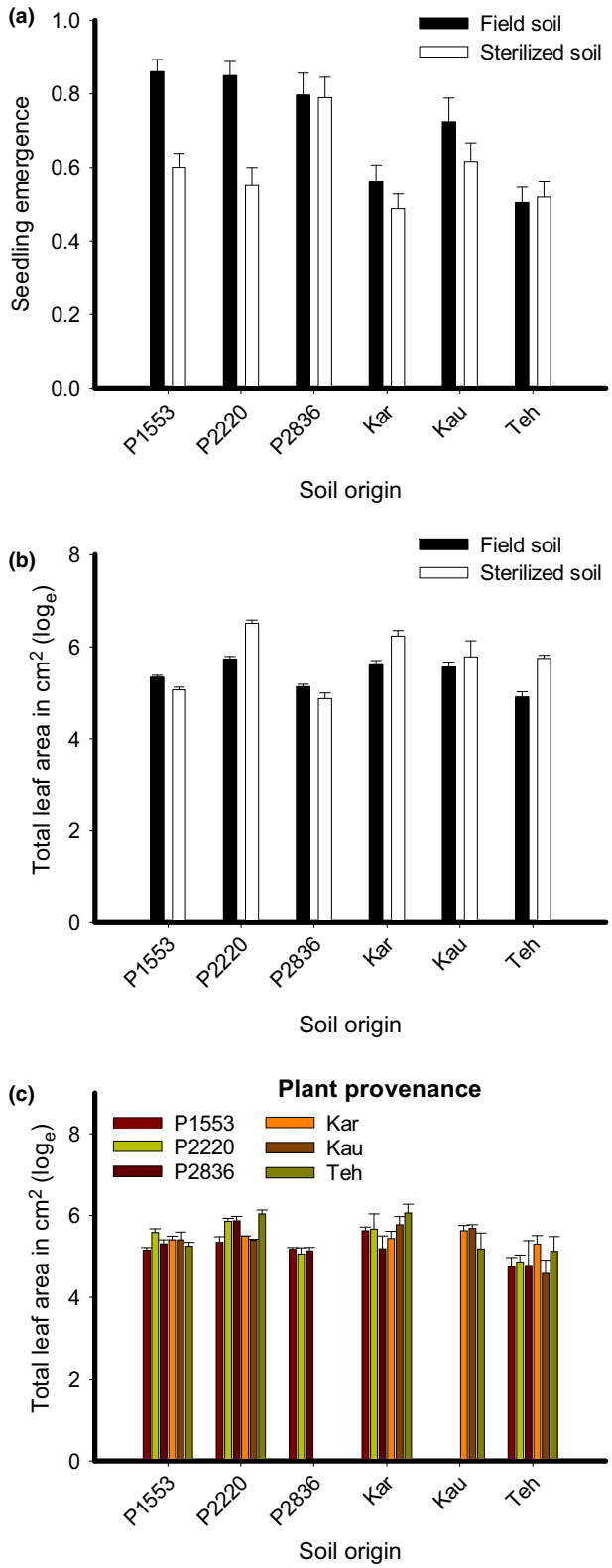


**Fig. 2** Factors affecting seedling emergence and total leaf area of *Plantago lanceolata*. Panels (a) and (b) show the impact of soil origin and soil treatment on seedling emergence and total leaf area, respectively. (c) The total leaf area for plants from different provenances growing in a range of field soil environments. Data are empirical means ± SE.

Notably, the pattern of slower development and lower aggressiveness on local plants grown in local field soil was not dependent on the distance between the mildew–plant population and the location of soil origin: pathogens performed equally well on allopatric soils from within the same region and allopatric soils from the other region (aggressiveness, $t_{479} = -0.17$, $P = 0.86$; time to sporulation, $t_{479} = -0.68$, $P = 0.50$; Fig. S1), despite pronounced differences among populations in the abiotic soil environment (Table S6).

## Discussion

Our study highlights two novel findings. First, plants showed no adaptation to the local soil in the absence of their natural enemies; however, in the presence of natural enemies, plants showed higher quantitative, but not qualitative, resistance when grown in their local soil environment. Second, the reduction of pathogen aggressiveness and increased time to sporulation in plants that were grown in their local soil environment was mediated by the local soil biota, as the pattern of local adaptation was inconsistent after soil sterilization. Overall, these results emphasize that the often-ignored below-ground spatial heterogeneity may have a major impact on the evolution of plant resistance against above-ground natural enemies and patterns of local adaptation.

### Plant adaptation to the abiotic and biotic soil environment

Based on the large body of experimental work on plant adaptation, Linhart & Grant (1996) concluded that natural selection is the principal force shaping the genetic architecture of plants in natural populations. A substantial number of replant–transplant studies has also shown the adaptive nature of genetic variation in natural *P. lanceolata* populations for the fitness traits (seedling emergence and vegetative growth) that we examined in our study (Antonovics & Primack, 1982; van Groenendael, 1985; van Tienderen & van der Toorn, 1991; Joshi *et al.*, 2001; Bischoff *et al.*, 2006). Unfortunately, these reciprocal replant–transplant experiments cannot unambiguously pinpoint the environmental factors that drive local adaptation. In one attempt, climatic differences could not explain strong patterns of local adaptation of *P. lanceolata*, even at the large European scale (Joshi *et al.*, 2001). As an alternative, they suggested that the plant may face spatial variation in the community of natural enemies like herbivores and plant pathogens. While the impact of natural enemies on plant local adaptation is rarely studied, previous studies have shown that specialist beetle feeding (Crémieux *et al.*, 2008) and mammalian grazing (van Tienderen, 1992) were lower on sympatric than on allopatric *P. lanceolata*. Our inoculation experiment provides strong support that plant local adaptation to environmental conditions may only be apparent in the presence of natural enemies: while no local adaptation was detected in the absence of natural enemies, the powdery mildew *P. plantaginis* had a coevolutionary disadvantage when grown on local plants growing in the local soil environment.

**Table 2** The impact of soil origin on life-history traits of the plant pathogen *Podosphaera plantaginis* when inoculated on local genotypes of the plant *Plantago lanceolata* that were grown either in their local soil (sympatric) or nonlocal (allopatric) soil environment

| | Field soil | | | Sterilized soil | | |
|---|---|---|---|---|---|---|
| | Soil origin | Population (plant and pathogen) | Local adaptation | Soil origin | Population (plant and pathogen) | Local adaptation |
| Infectivity | **0.001** | 0.399 | 0.055*** | 0.150 | **0.045** | 0.985** |
| Time to sporulation | 0.213 | 0.223 | **0.004*** | 0.672 | 0.082 | 0.592 |
| Aggressiveness | **0.027** | 0.133 | **< 0.0001*** | 0.749 | 0.468 | 0.781 |
| Sexual spore production | 0.518 | 0.127 | 0.060 | 0.949 | 0.185 | 0.991 |

Shown are *P*-values of the fixed effects as estimated with (generalized) linear mixed models, where significant *P*-values are in bold. A significant *P*-value for local adaptation indicates consistently higher or lower response values when plants are growing in local as compared with nonlocal soil. We indicated a mosaic pattern of local adaptation by an asterisk in the same column: *, $0.01 < P < 0.05$; **, $0.001 < P < 0.01$; ***, $P < 0.001$. See models 6 and 7 in Supporting information Table S3 for more details.

The two key fitness traits (seedling emergence and vegetative growth) were affected in opposite ways by soil sterilization: seedling emergence was generally higher in the field soil, whereas plant growth was generally higher in the sterilized soil. The lower seedling emergence in the sterilized soil suggests that mutualistic soil biota increase seed germination or decrease mortality in the short period between germination and emergence of the seedling above ground. The decreased growth rate of plants in the field soil compared with the sterilized soil may be a result of interactions with bacterial or fungal root pathogens or mutualistic soil biota, possibly involving the costs associated with the induction of systemic acquired resistance or potentiation of defense-related pathways (i.e. Conrath *et al.*, 2002; Jung *et al.*, 2009; see Susi & Laine, 2015 for empirical estimates of the costs of resistance in this study system), even though sterilization-induced changes in soil characteristics (McNamara *et al.*, 2003) may also affect this pattern. While the exact mechanism is hard to pinpoint, our findings suggest that the defense response against the pathogen, and not plant growth *per se*, was more efficient in local soils: while pathogens showed reduced growth rates when inoculated on local plants growing in the local soil as compared with nonlocal soils, plants did not show an increased growth rate in response to their local soil or local soil biota.

## The impact of soil heterogeneity on host–parasite (co)evolution

Spatial heterogeneity in the soil environment strongly affected pathogen performance and mediated patterns of host and parasite adaptation. However, the patterns were highly variable among parasite life-history traits.

Parasite infectivity was higher in some populations when inoculated on plants grown in their local soil as compared with the same plants grown in the nonlocal soil, but the reverse pattern was detected in other populations. Such a mosaic pattern of local adaptation indicates that evolutionary trajectories in terms of infectivity are hard to predict as a result of variable evolutionary outcomes across the landscape. In striking contrast, parasite aggressiveness was consistently lower, and development slower, in the local plants that were grown in sympatric soil, suggesting that plant adaptation to natural enemies is mediated by its local soil environment. This suggests that the parasite has a coevolutionary disadvantage when plants are grown in their local soil. Alternatively, reduced pathogen aggressiveness in sympatry may also be adaptive for the pathogen, as (too) high aggressiveness may lead to earlier host death and reduced pathogen transmission (May & Anderson, 1983; Dybdahl & Storfer, 2003). While previous work has shown that genotype × environment interactions may differ among pathogen life-history stages, our findings illustrate that the resulting evolutionary trajectories are also trait-specific.

The soil biota played a key role in mediating the slower development and lower aggressiveness of pathogens inoculated on plants grown in their local soil environment, as the pattern of local adaptation was not apparent after soil sterilization. Such a pattern may emerge from changes in nutritional quality, increased defense structures and compounds or plant priming in response to the local soil biota (Conrath *et al.*, 2002; van Dam & Heil, 2011). An interesting and largely unexplored future avenue would be to study soil-mediated plant resistance and soil-mediated priming in a spatial and evolutionary framework. Furthermore, our results support the emerging paradigm that soil biota mediate the expression of population-level genetic variation and, as a corollary, the potential for selection and plant–soil feedbacks (Pregitzer *et al.*, 2010; Felker-Quinn *et al.*, 2011; Lankau *et al.*, 2011; van der Putten *et al.*, 2013; Wagg *et al.*, 2015). While plant adaptation or plant–soil feedbacks resulted in predictably slower development and reduced aggressiveness of local pathogens, the spatial variation in the home advantage of plants for the trait infectivity suggests that plant populations may experience a range of feedbacks across the landscape (cf. Felker-Quinn *et al.*, 2011).

While we were able to detect the imprint of soil-mediated natural selection on quantitative resistance, the epidemiological consequences of these adaptive changes will be hard to predict. However, we may note that even small changes in pathogen aggressiveness and generation time may result in large changes in the seasonal epidemiology (e.g. through increased transmission and the potential for additional pathogen generations). Indeed, a study on the wild flax (*Linum marginale*) and its rust fungus

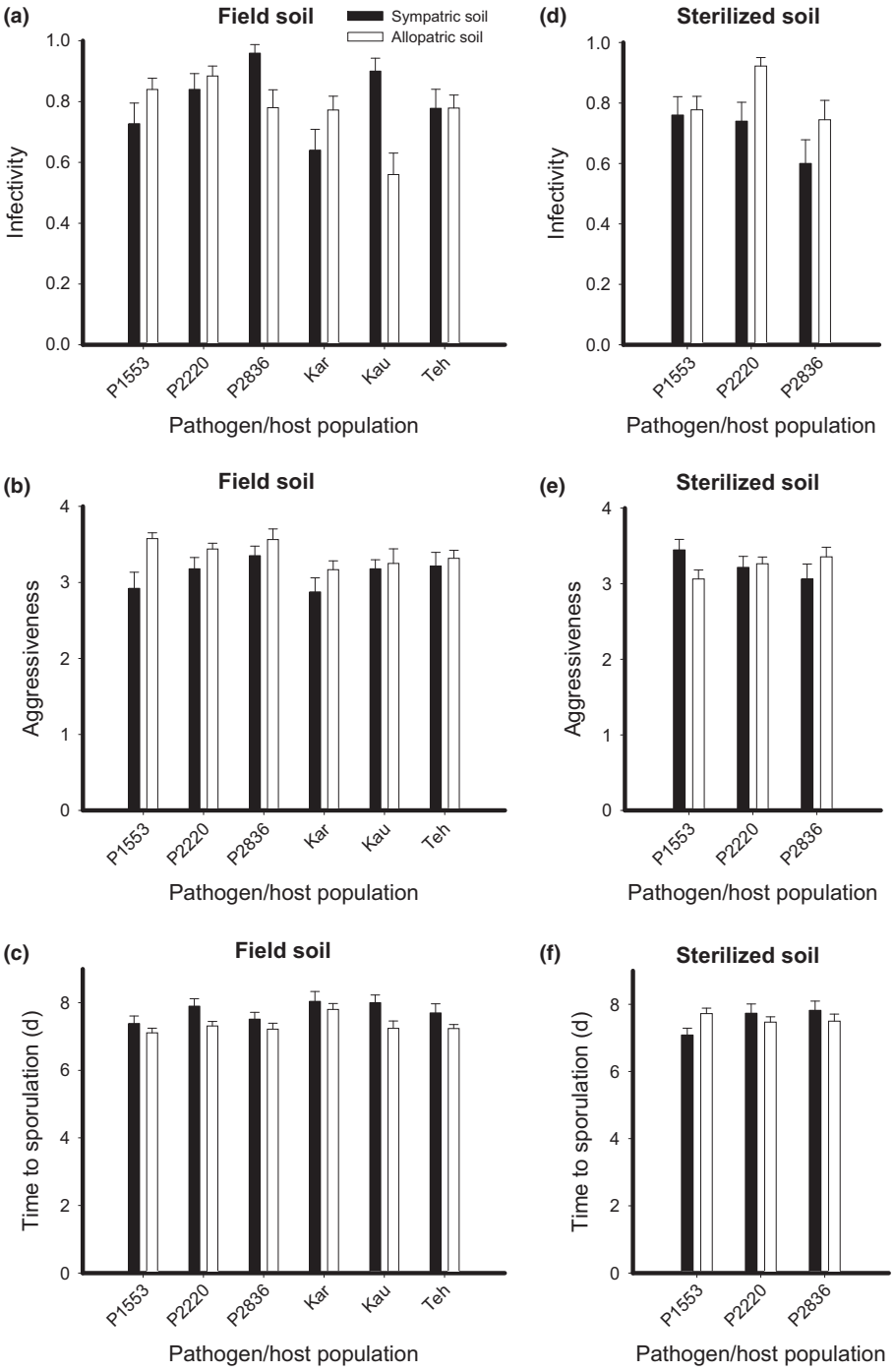


**Fig. 3** Performance of the pathogen *Podosphaera plantaginis* on local genotypes of the plant *Plantago lanceolata* grown in local (sympatric) or nonlocal (allopatric) soil, as shown for each of six populations. (a–c) Data for plants grown in sympatric and allopatric field soils; (d–f) data for plants grown in sympatric and allopatric sterilized soils. Data are empirical means ± SE.

(*Melampsora lini*) illustrates that the evolutionary differentiation of the host plant between two habitat types may have a large impact on the progression of the epidemiology during the growing season (Laine *et al.*, 2014; Tack *et al.*, 2015). Importantly, our findings illustrate that, despite the potential confounding and counteracting effects of gene flow, genetic drift and temporal variation in spatial heterogeneity, selection imposed by spatial variation in the soil environment can have an imprint on the evolutionary outcome of a host–parasite interaction in a natural system. This testifies to some degree to the strength of natural selection imposed by the soil environment (Kawecki & Ebert, 2004). We hope that future studies will focus on the consequences of soil-mediated local adaptation for the natural epidemiology under field conditions, disentangle the relative importance of soil-mediated natural selection as compared with other selective forces, and validate the generality of these findings across a range of natural and agricultural systems. Finally, an insightful but logistically challenging extension of the current experimental approach would involve manipulation of all three factors (plant origin, pathogen origin, and soil origin) in a three-way factorial experiment, in the ideal case even replicated through time, and thereby give additional insights into the

impact of below-ground heterogeneity on the coevolutionary dynamics in a natural system.

### The spatial scale of soil-mediated effects on host–parasite coevolution

Our findings shed some light on the spatial scale at which soil heterogeneity affects host–parasite coevolution and patterns of local adaptation. While the abiotic and biotic soil environment varies at a highly localized spatial scale (Ettema & Wardle, 2002), the patterns uncovered illustrate that variation in the soil environment at a larger spatial scale (i.e. the scale of the local population, represented by an area of several to tens of square metres) was a key driver of plant and pathogen performance. Mixed soil from populations that were separated by 6–40 km were highly dissimilar, and strongly mediated patterns of adaptation. Overall, these findings indicate that small-scale soil heterogeneity does not obscure the evolutionary impact of among-population differences in the soil environment. This conclusion is supported by Macel *et al.* (2007), who demonstrated that among-population soil heterogeneity had a stronger impact on plant performance than within-population soil heterogeneity. Notably, our findings also illustrate that relevant (i.e. for host–parasite interactions) soil heterogeneity did not increase beyond tens of kilometers: the response of plant and parasite to soil heterogeneity was not affected by expanding the spatial scale of soil origin beyond a single region (i.e. across islands separated by *c.* 200 km).

### Conclusion

Our study indicates that spatial patterning of soil biota can have important above-ground consequences for plants and their pathogens. Unlike previous studies, our findings suggest that plants do not directly adapt to local soil conditions as measured by seedling emergence and plant growth rate. Instead, the soil environment modified the coevolutionary interaction between plants and pathogens, where local pathogens were maladapted to local plants growing in their local soil as compared with local plants growing in their nonlocal soil. Our study corroborates theoretical and empirical findings that genotype × environment interactions are not only highly relevant for ecological interactions, but also that these ecological interactions can result in predictable (co)evolutionary trajectories and the maintenance of genetic variation. Furthermore, our study pinpoints the fact that the absence of local adaptation in studies in laboratory settings may be a result of the lack of ecological context, as we would not have detected any patterns of plant adaptation in the absence of its natural enemies. From an applied perspective, our finding that locally selected seeds may have higher performance than nonlocal seeds as a result of their higher soil-mediated resistance to local natural enemies emphasizes the importance of using locally selected plant genotypes or varieties in low-input agricultural environments and ecological restoration projects.

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## Author contributions

A.J.M.T. and S.M. designed the study. S.M. conducted the experiments. A.J.M.T. wrote the first draft of the manuscript, and S.M. contributed to the revisions.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Pathogen performance on local plant genotypes grown in field soil originating from three geographical distances.

**Table S1** Planting matrix to test for plant local adaptation

**Table S2** Inoculation matrix to test for parasite local adaptation

**Table S3** A summary of the generalized linear mixed models fitted for analyses

**Table S4** The response variables examined in the models described in Table S3

**Table S5** The impact of soil origin, plant provenance and their interaction on seedling emergence and vegetative growth separately for the two soil treatments

**Table S6** Characteristics of the soils used in the experiment

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