ORIGINAL PAPER

Fine-scale fern ecological responses inform on riparian forest habitat conservation status

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Abstract
The recognition of the ecological quality of ecosystems and habitats therein is increasingly important in the Anthropocene. However, there are still scarcely explored ways of how and what to assess to obtain a sound ecological status of habitats. Ferns are an understudied plant group, especially given their usefulness as ecological indicators. Disentangling biotic and abiotic factors that drive fine-scale fern distribution could provide insight into the quality of their habitats. We investigated the environmental factors affecting the distribution of different largely distributed fern species in Europe. We studied their presence and abundance at different life stages in a forest habitat of European priority conservation concern. Our aim was to understand whether fern species can be used as an ecological indicator group in riparian alderwood habitat. We sampled 120 plots of 50 m^2 in randomly selected transects along streams of a riparian forest habitat characterized by the presence of many fern species in the understory, controlling for the effects of geology and elevation. Within each plot, fern species were recorded, including vegetative and generative stages of each ramet (rosette of fronds). We modelled fern occurrence and abundance for the different fern life stages, and diversity indices of the fern community in relation to environmental predictors. We found that population- and community-level responses of ferns mainly depended on soil granulometry and, to a lesser extent, moss cover and stream orientation. We also found that the generative life stage compared to the vegetative adult stage benefits from different ecological characteristics for certain fern species. Alterations of the natural hydrology might lead to a general deterioration in habitat quality for ferns. We suggest that some fern species acting as early-warning species, and potentially their life stages, can be used as an ecological quality indicator for riparian forest habitats. This study deepened the understanding of the fine-scale ecology of an array of European ferns in riparian forests and provides valuable information to assist in the conservation of fern species and their populations.

Keywords Conservation · Early-warning species · Fern communities · Habitats Directive · Population · Riparian alderwoods

Communicated by Daniel Sanchez Mata.

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Introduction

Ferns contribute widely to biodiversity, with some 12,000 species making them the second-largest group of vascular plants after angiosperms (PPG I 2016). Ferns are widely distributed around the globe with some species being ubiquitous, aside from poles and deserts (Moran 2008).

Generally, abiotic factors drive fern species distribution patterns at all scales (Karst et al. 2005). Their distribution responds more directly to edaphic and other environmental factors than to geographic distance between sample sites, partly due to the wind-borne dispersal of spores, which makes ferns less dispersal-limited than other plants (Higgins et al. 2011; Jones et al. 2006; Tuomisto et al. 2003). The role of edaphic factors, including the underlying geology which impacts soil composition, is significant for ferns (Jones et al. 2006; Tuomisto et al. 2003). Although soil granulometry does not seem to be physiologically important for ferns, it correlates with other soil properties such as water, and nutrient retention and release (Zuquim et al. 2014). However, literature about fine-scale distribution of ferns in relation to soil granulometry is scanty.

Fern species distribution is influenced by orientation, which in turn affects light and heat (Sharpe and Shiels 2014). Previous studies have shown how populations of *Osmunda regalis* are favoured by north-east orientation as a combined effect of lower insolation and protection from dry summer winds (Landi and Angiolini 2008). Elevation gradients also have a profound effect on fern species distribution (Kessler 2000; Nervo et al. 2016; Rahbek 1995, 2005). Further, water largely contributes to the distribution of ferns because it is a necessary element for reproduction and growth (Kessler 2000). However, although earlier studies identified environmental factors driving fern distribution at a large scale, few studies have been conducted to investigate ecological responses that drive their distribution at the fine-scale (Barrington 1993; Kessler et al. 2011; Hernández-Rojas et al. 2020).

The influence of abiotic factors greatly contributes to shape the structure of fern populations. Plant population structure can be used as a means of addressing the demographics and thus the status of the population, often in the context of species conservation (Eckstein et al. 2004; Moora et al. 2007). Also, population structure is a more efficient and time-effective approach to analyse the demographics of the plant community than a full demographic study. Nevertheless, a few European studies have investigated fern population structure, and specifically fern life stages (Bucharová et al. 2010; Landi and Angiolini 2011; Rünk et al. 2006). Habitat characteristics associated with the life stage of a fern species are even less investigated (Cinquemani Kuehn and Leopold 1993; Landi and Angiolini 2011). The remaining studies investigated fern population structure as a means of describing the conditions of the populations by characterizing regional fern population dynamics (Aguraiuja et al. 2004, 2008; Bucharová et al. 2010; Rünk et al. 2006). Importantly, different life stages of fern species have distinct fine-scale habitat preferences (Cinquemani Kuehn and Leopold 1993; Landi and Angiolini 2011). Thus, if the success of species conservation depends on the knowledge about their ecology, an approach for the conservation of ferns must take into consideration a combination of life stages classes, meaning the abundance of sporophytes in each developmental stage of a fern's life history, and habitat features.

The close relationship between fern occurrence and environmental factors makes ferns good bioindicators (Della and Falkenberg 2019; Higgins et al. 2011; Zuquim et al. 2014). Ferns have been used as environmental indicators for vegetation, soils, environmental integrity, climate change, association with other organisms or contamination of air, soil

or water (Della and Falkenberg 2019). However, most studies focus on the tropics, where the most diverse array of ferns can be found (Jones et al. 2006; Ruokolainen et al. 1997; Tuomisto et al. 2002, 2003). Accordingly, the ecological knowledge of fern drivers in non-tropical ecosystems is relatively incomplete.

Studies assessing biotic and abiotic predictors of fern occurrence and abundance at fine scale can improve predictive models of fern distribution at wider, e.g. continental or global, scales. Our work concerns ten fern species widely distributed in Europe. We expect the presence of ferns with vegetative and generative sporophytes to reflect moisture and the different water dynamics, which characterize riparian alderwood habitats. By looking at factors influencing fern distribution measured on a fine scale, we might infer their predictive power as early-warning species and suggest particular species as ecological indicators of the investigated habitat. We aim to pinpoint environmental factors affecting fern communities and fern distribution in a riparian forest habitat of conservation interest. Specifically, we asked: (1) Which environmental factors in riparian *Alnus glutinosa* forest habitat drive fern species presence and abundance and their various life stages? (2) Do fine-scale fern responses help assess habitat conservation status?

Material and methods

Study area

The study area is located in the provinces of Siena and Grosseto (central Italy), at an elevation that ranges from 250 to 600 m a.s.l. The geology is composed of acidic sedimentary rocks affected by low-grade metamorphism (Carmignani et al. 2013). The macroclimate is classified as temperate, with a strong submediterranean influence (Pesaresi et al. 2017). Mean temperature ranges from 22.5 °C in July to 5.7 °C in January. Precipitation varies with seasonality, with winter months being wetter (60–90 mm/month) than the summer months (20–40 mm/month) (Climate-Data 2021). The area is characterized by a low human density, by the absence of industrial activities and by a well-conserved fluvial ecosystem. The study area is included in two Special Areas of Conservation (SACs) interest of the Natura 2000 network of protected areas (Alta Val di Merse—IT5190006 and Val di Farma—IT51A0003). Furthermore, sections of these Natura 2000 sites are categorized as Nature Reserves (Fig. S1 of the Supplementary material).

The area is almost entirely covered by mixed forests dominated by *Castanea sativa, Quercus cerris* and *Q. petraea*, while the upper and drier areas are dominated by pine forests of *Pinus pinaster*. The dominant broadleaf species occurring in the stream habitat is *Alnus glutinosa*, followed in decreasing order of frequency by *Fraxinus ornus*, *C. sativa*, *Q. ilex*, *Carpinus betulus*, *Corylus avellana*, *Q. cerris* and *Q. petraea*. The most frequent shrub species are *Ilex aquifolium*, *Rubus hirtus* and *Frangula alnus*. The habitat object of this study named "Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*)", is considered of priority importance in the list of European habitats of conservation interest (Natura 2000 code: 91E0; Habitats Directive 92/43/EEC) and it is included to the EUNIS habitat "*Alnus glutinosa–Alnus incana* forest on riparian and mineral soils" (code T12; Chytrý et al. 2020). At least in the Mediterranean, this habitat is characterized by periodical inundations but is otherwise well-drained. It requires oligotrophic waters and occurs in the upper and middle part of the streams, where erosion prevails on sedimentation, thus contrasting with the riparian woods with

Salix spp. and *Populus* spp. occurring in lower parts of rivers and streams where, on the contrary, sedimentation prevails on erosion. From the syntaxonomic point of view, this forest type is classified to the alliance *Osmundo-Alnion glutinosae* in the order *Populetalia albae* of the class *Alno glutinosae-Populetea albae* (Landi and Angiolini 2010; Mucina et al. 2016; Preislerová et al. 2022). This alliance occurs on acidic soils, and it is characterized by the presence of numerous fern species in the understory. Three fern species, *Dryopteris carthusiana, Equisetum telmateia* and *Osmunda regalis* occurring in our study area, are listed among the diagnostic species of the habitat for Italy according to the "Italian Interpretation Manual of the 92/43/EEC Habitats Directive" (Biondi et al. 2009).

Study species

We detected 14 native fern species largely distributed in Europe (Table 1). For species-specific responses, ecological investigation was possible for 10 fern species found in more than 10 plots. Fern species detected in this study are reported in Fig. 1. The overall number of ramets recorded in sampling plots and the number of plots with ramets for each fern are reported in Table 2. Distribution of the fern species is in accordance with Plants of the World Online (PoWO, 2019). Biological forms follow Pignatti et al. (2017). Nomenclature follows the Portal to the Flora of Italy (Portal to the Flora of Italy, 2021).

Sampling design and data collection

To investigate the effect of physical variables affecting the distribution of ferns, meaning to consider streams with similar ecological conditions, the perennial character of each of the streams investigated in our study was preliminary ascertained. To nullify the effect of particular environmental variables acting on ferns such as geology and elevation (Kessler 2000; Nervo et al. 2015; Tuomisto et al. 2003), sampling was conducted from mid-June to mid-August on plots within transects of similar elevation ranges and in a geologically homogeneous area. We thus selected twenty-two stream sections with similar slope (8–10%) and elevation (350–390 m a.s.l., from the lower to the upper part of the transect). We randomly selected four transects for each main orientation of the streams (i.e., North, East and South). Thus, twelve transects ($n = 12$) were selected out of the twenty-two possible. No westerly-oriented streams were present in the study area. A 250 m-transect was overlaid in the longitudinal direction along each stream section. In each transect, 10 sampling plots of 50 m^2 (5×10 m, perpendicular to water flow/running) were equally spaced at intervals of 20 m; thus, a total of 120 plots were made. The 10 m-wide plots encompassed both sides of each stream, thus including the whole fine-scale habitat variability: streambed, mid-slope, upper-slope. No epiphytic ferns were present in our study area.

For each plot we recorded tree, shrub, herbaceous and moss cover (%) as visual groundcover projected vertical estimation, including rocks, stumps and logs, and (sub-)horizontal surfaces for mosses. However, the cover of the shrub and herbaceous layers was not included in the statistical analysis. Shrub and herbaceous cover were deemed of low importance due to their low median coverage (6% for shrub cover; 5% for herbaceous cover), as opposed to the median tree cover of 85%. Moreover, only the tree cover could be used as a proxy for light availability. Moss cover was recorded because it is a proxy of humidity (Given 1993). In our sampling plots, we also recorded soil granulometry, i.e. soil sediment size (%) of sand (< 2 mm in diameter), gravel (2 mm to 7.6 cm in diameter), cobbles (7.6–25 cm in diameter), stones (25–60 cm in diameter),

Table 1 Fern species detected in this study, their distribution (PoWO, 2019) and biological forms (Pignatti et al. 2017)

Species	Distribution	Biological form
Asplenium onopteris	Western Europe to Mediterranean	Rosulate hemicryptophyte
Asplenium scolopendrium	Europe to Iran, North-Western Africa	Rosulate hemicryptophyte
Asplenium trichomanes	Cosmopolitan-temperate	Rosulate hemicryptophyte
Athyrium filix-femina	North-Western Africa, Europe to Mongolia	Rosulate hemicryptophyte
Dryopteris affinis	Europe to Caucasus	Rhizomatous geophyte
Dryopteris borreri	Europe to Caucasus	Rhizomatous geophyte
Dryopteris dilatata	Azores, Europe to Caucasus, South-Western Siberia to Mongolia, Japan	Rhizomatous geophyte
Equisetum telmateia	Europe to Iran, North-Western Africa	Rhizomatous geophyte
Osmunda regalis	Europe to Mediterranean and Iran	Rhizomatous geophyte
Polypodium cambricum	North-Western Europe to Mediterranean and Caucasus	Rosulate hemicryptophyte
Polypodium interjectum	Europe to Iran	Rosulate hemicryptophyte
Polystichum setiferum	Mediterranean to Iran	Rhizomatous geophyte
Pteridium aquilinum	Tropical Africa, Arabian Peninsula, Europe to Siberia and Iran	Rhizomatous geophyte
Struthiopteris spicant	North-Western Africa, Europe to Iran, Japan, South Alaska to West U.S.A	Rosulate hemicryptophyte

Nomenclature follows the Portal to the Flora of Italy (Portal to the Flora of Italy, 2021). Species are sorted alphabetically

Fig. 1 Fern species considered in this study. The species are sorted alphabetically. **a** *Asplenium onopteris*; **b** *Asplenium trichomanes*; **c** *Athyrium filix-femina*; **d** *Dryopteris affinis*; **e** *Dryopteris borreri*; **f** *Osmunda regalis*; **g** *Polypodium interjectum*; **h** *Polystichum setiferum*; **i** *Pteridium aquilinum*; **j** *Struthiopteris spicant*. Photo credits: G. Bonari (**a, b, c, d, f, i**), Portal to the Flora of Italy (**j, e, g, h**)

and boulders (> 60 cm in diameter), following the USDA system (Ditzler et al. 2017). Preliminary observations of soil sediment size distribution in sampling plots suggested the occurrence of three distinct categories of soils. We used a k-mean cluster analysis based on the soil granulometric variables to identify sampling plots belonging to soils with a prevalence of large-grained sediments (mainly boulders and stones; $n = 39$ plots), soils with a prevalence of fine-grained sediments (mainly sand and gravel; $n = 28$ plots) and soils with a prevalence of mixed-grained sediments, i.e. with an even distribution of all soil granulometric classes of sediments ($n = 53$ plots).

Within each plot, we recorded the life stages of each ramet (rosette of fronds) of the fern species: vegetative, generative and senile. However, this latter life stage was never found. In our sampling, we recorded the sporophytes only when an unequivocal determination

Table 2 The overall number of ramets recorded in sampling plots and the number of plots with ramets for each fern species

Species	No. of VR	No. of GR	No. of TR	No. of plots with ramets ($n = 120$)
Asplenium onopteris	22	92	114	33
Asplenium scolopendrium (*)	32	33	65	9
Asplenium trichomanes	8	39	47	18
Athyrium filix-femina	155	122	277	52
Dryopteris affinis	103	34	137	28
Dryopteris borreri	21	11	32	13
Dryopteris dilatata (*)	2	2	4	3
Equisetum telmateia (*)	1	2	3	2
Osmunda regalis	74	30	104	22
Polypodium interjectum	76	116	192	34
Polystichum setiferum	233	94	327	52
Pteridium aquilinum	109	2	111	39
Polypodium cambricum (*)	4	9	13	6
Struthiopteris spicant	184	55	239	37

VR Vegetative ramets, GR generative ramets, TR total ramets, (*) species excluded from GLMMs

to the species level was possible directly in the field, meaning that we did not consider young sporophytes with unclear or difficult attribution to a fern species due to the lack of identification characters. To quantify fern responses at the community-level, we calculated for each plot several indices of ecological diversity (Chao 1984; Legendre and Legendre 2012): richness (raw number of species), Chao-1 richness, Shannon diversity (H) and Simpson's dominance (D).

Statistical analyses

We investigated factors affecting population- and community-level responses of ferns in sampling plots using generalized linear mixed models (GLMMs; Zuur et al. 2009). We analysed two response variables for population-level responses: probability of presence and abundance of ramets, in each sampling plot. We modelled occurrence of ramet using binomial errors (link: logit) and ramet abundance using negative binomial errors (link: log), as customarily done when modelling presence/absence and count data, respectively. Models were fitted separately for the two vegetative stages of each species and for total fern ramets of each species. Population-level models could not be run for four species (*Asplenium scolopendrium*, *Dryopteris dilatata*, *Equisetum telmateia*, and *Polypodium cambricum*), and for abundance of generative ramets of *Pteridium aquilinum*, because inherent data included almost only 0 counts and models did not converge. Therefore, the ecological investigation was carried out for the remaining 10 fern species. For community-level responses, we used as response variables ecological indices calculated in each sampling plot. Richness, i.e. the number of species, was modelled through negative binomial errors (link: log), Shannon diversity and Chao-1 richness through gaussian errors (link: identity), and Simpson's

dominance using beta errors (link: log), following rule of thumb to model count data, real numbers and continuous variables bounded in the 0–1 range.

In all cases, for both population- and community-level and responses, we tested whether our response variables varied according to potentially influencing predictors while accounting for repeated measures conducted in each transect as a random intercept. Thus, random intercepts allowed the estimation of an average effect of each predictor in all transects. In each global model, we included four fixed effects that are known to be relevant predictors of fern distribution: (1) orientation (categorical; reference level: east-oriented streams); (2) cover of the tree layer (continuous, as %); (3) moss cover (continuous, as %); (4) soil sediment size (categorical; reference level: soil with even distribution of soil granulometric classes). We found no multicollinearity ($r < |0.5|$; VIFs < 3) between covariates. Continuous explanatory variables were scaled to improve model convergence and allow comparing the relative importance of each predictor.

For each full model, we performed a model selection according to the information-theoretic approach. Each model evaluated, including a different combination of predictors, could represent a different, biologically meaningful a priori hypothesis (Harrison et al. 2018). All the possible combinations between predictors were ranked and weighted from the full model (number of models run per full model: $2^4 = 16$, where 4 is the number of predictors). The null model was also included, to allow comparing model performance relative to a fixed baseline (Mac Nally et al. 2018). Model selection was performed using the minimum Akaike's Information Criterion corrected for small samples (AICc: Burnham and Anderson, 2002), a metric which considers both model parsimoniousness and goodness of fit (Aho et al. 2014). We followed the 'nesting rule' to avoid retaining overly complex models (Harrison et al. 2018), thus we did not select models with ΔAICc ≥ 2 with respect to the best model (the model with the lowest AICc value), and models with an AICc value greater than any simpler alternative. We achieved either a set of top-ranked models or a single best model for each response variable. For each model, the weight, meaning the probability that a given model is the best model, was standardized within the subset of selected models. Selected models are reported in the Supplementary material (Tables S1–S11). For each best model, we estimated coefficients of predictors, 95% confidence intervals and variance of random effects from the top-ranked, namely the best model. The effects of predictors were assessed by checking whether 95% confidence intervals of coefficients overlapped 0. Best models were validated by checking residual patterns (Zuur et al. 2009). We performed model selection and GLMMs through the R packages *MuMIn* (Bartoń 2012) and *glmmTMB* (Brooks et al. 2017), respectively.

Considering that positive or negative association between pairs of fern species may arise from similar or opposite responses to environmental factors, we tested potential interspecific associations in abundance using Spearman's correlation on the number of ramets recorded in sampling plots.

Results

The most frequent and abundant ferns were *Athyrium filix-femina* and *Polystichum setiferum* (Table 2), both occurring in 52 plots, with 277 and 327 total ramets, respectively. A representative scheme of how ferns occurred in streams is reported in Fig. 2.

Top-ranked models explaining abundance and presence of ferns are summarised in Table 3 (see Tables S12–S21 of the Supplementary material for more details). Fern
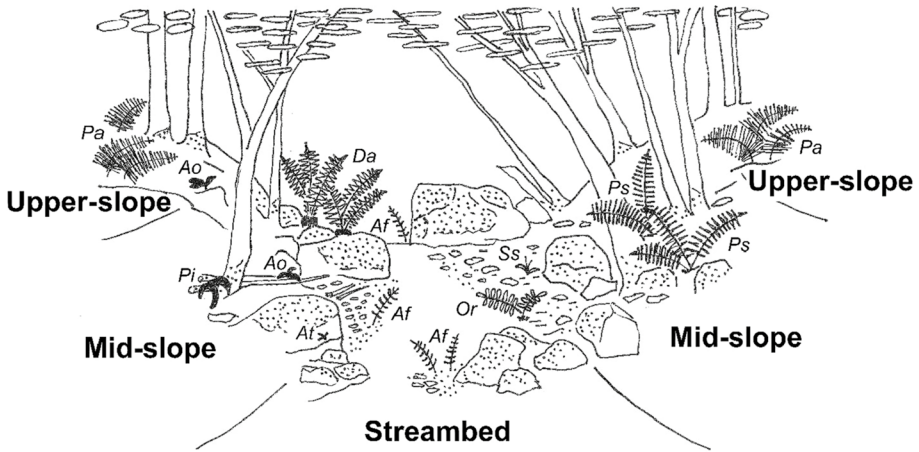
Fig. 2 Scheme of the main fern species distribution in north-oriented streams: *Asplenium onopteris* (Ao), *Asplenium trichomanes* (At), *Athyrium filix-femina* (Af), *Dryopteris affinis* (Da), *Osmunda regalis* (Or), *Polypodium interjectum* (Pi), *Polystichum setiferum* (Ps), *Pteridium aquilinum* (Pa), *Struthiopteris spicant* (Ss). *Dryopteris borreri* is not represented in the scheme because it seems to replace *D. affinis* in south-oriented streams. Image credits: M. Landi

responses to potential environmental drivers were often species-specific, with most of them responding to soil sediment size.

For five fern species, including *Asplenium onopteris*, *A. trichomanes*, *Dryopteris affinis*, *Polypodium interjectum*, and *P. setiferum*, ramet abundance increased in large-grained soils or decreased in fine-grained soils, either for at least one of the life stages or for the total ramets (Fig. 3). *D. borreri* abundance, on the other hand, decreased at sites with large-grained soils (Fig. 3d), although such decrease did not occur when vegetative and generative ramets were considered separately.

Abundance of three fern species responded to moss cover either for one of the life stages or for the total ramets: *D. affinis* and *P. setiferum* ramets increased with increasing moss cover (Fig. 4a, b), whereas *P. aquilinum* ramets decreased with increasing moss cover (Fig. 4c).

Abundance of *D. affinis* and *P. interjectum* also depended on orientation, with *D. affinis* ramets decreasing in south-oriented streams (Fig. 5a) and *P. interjectum* ramets decreasing in north-oriented streams (Fig. 5b).

Two fern species showed life stage-specific effects on ramets abundance (Table 3). For *D. affinis*, vegetative ramets decreased in fine-grained soils, while generative ramets increased with moss cover. In *P. interjectum*, vegetative ramets decreased in north-oriented plots, whilst generative ramets increased in large-grained soils.

Compared to models predicting fern abundance, models predicting probability of fern presence generally provided consistent results, although the effect of soil sediment size often disappeared for some species (Table 3). Apart from *A. onopteris*, whose presence probability decreased in fine-grained soils, the presence probability of four fern species was determined by stream orientation or moss cover. The probability of presence for *A. trichomanes* increased in south-oriented plots, while that of *D. affinis* decreased in south-oriented plots. The probability of presence for *P. interjectum* decreased in north-oriented plots. Moss cover increased the probability of *A. filix-femina* presence.

Table 3 Summary of results achieved by top-ranked GLMMs predicting population-level responses of fern species. "↗"=Increasing effect (green); "↘"=Decreasing effect (red); "–"=No effect. "NA"=Not available due to convergence issues. For more details on GLMMs results, see Tables S12–S21 of the Supplementary material

Species	Abundance of vegetative ramets	Abundance of generative ramets	Species presence	Species abundance
Asplenium onopteris	↗ large-grained soils	–	↘ fine-grained soils	↗ large-grained soils ↘ fine-grained soils
Asplenium trichomanes	–	↗ large-grained soils	↗ S-oriented streams	↗ large-grained soils
Athyrium filixfemina	–	–	↗ moss cover	–
Dryopteris affinis	↘ fine-grained soils	↗ moss cover	↘ S-oriented streams	↘ fine-grained soils ↘ S-oriented streams
Dryopteris borreri	–	–	–	↘ large-grained soils
Osmunda regalis	–	–	–	–
Polypodium interjectum	↘ N-oriented streams	↗ large-grained soils	↘ N-oriented streams	↘ N-oriented streams
Polystichum setiferum	↘ fine-grained soils ↘ large-grained soils ↗ moss cover	–	–	↘ fine-grained soils ↗ moss cover
Pteridium aquilinum	–	NA	–	↘ moss cover
Struthiopteris spicant	–	–	–	–

The best selected models predicting fern community indices are reported in Table S22 of the Supplementary material. Community-level responses were mainly conditional on soil sediment size. Although the number of fern species occurring in each plot was not influenced by any predictor, both Chao-1 richness and Shannon index of diversity decreased in fine-grained soils, indicating a higher fern richness and diversity in soils characterized by mixed- or large-grained soils (Fig. 3g). Consistently, Simpson's dominance index increased in fine-grained classes of soil granulometry (Fig. 3h). Moreover Chao-1 index increased and Simpson's index decreased with moss cover (Fig. 4d), suggesting an association between fern richness and moss cover.

Concerning potential interspecific interactions, we found only positive associations between fern species. Abundance of *A. filix-femina* was positively correlated to those of *Osmunda regalis* and *Struthiopteris spicant* ($r_S = 0.50$ and $r_S = 0.48$, respectively; $P < 0.01$).

Fig. 3 Effect of soil sediment size (granulometry) on population (**a–f**) and community (**g–h**) responses of ▶ ferns. Dot and error bar depict observed mean and standard error. Only fern responses significantly influenced by soil sediment size are reported. Asterisk denotes when the abundance is referred to as generative ramets
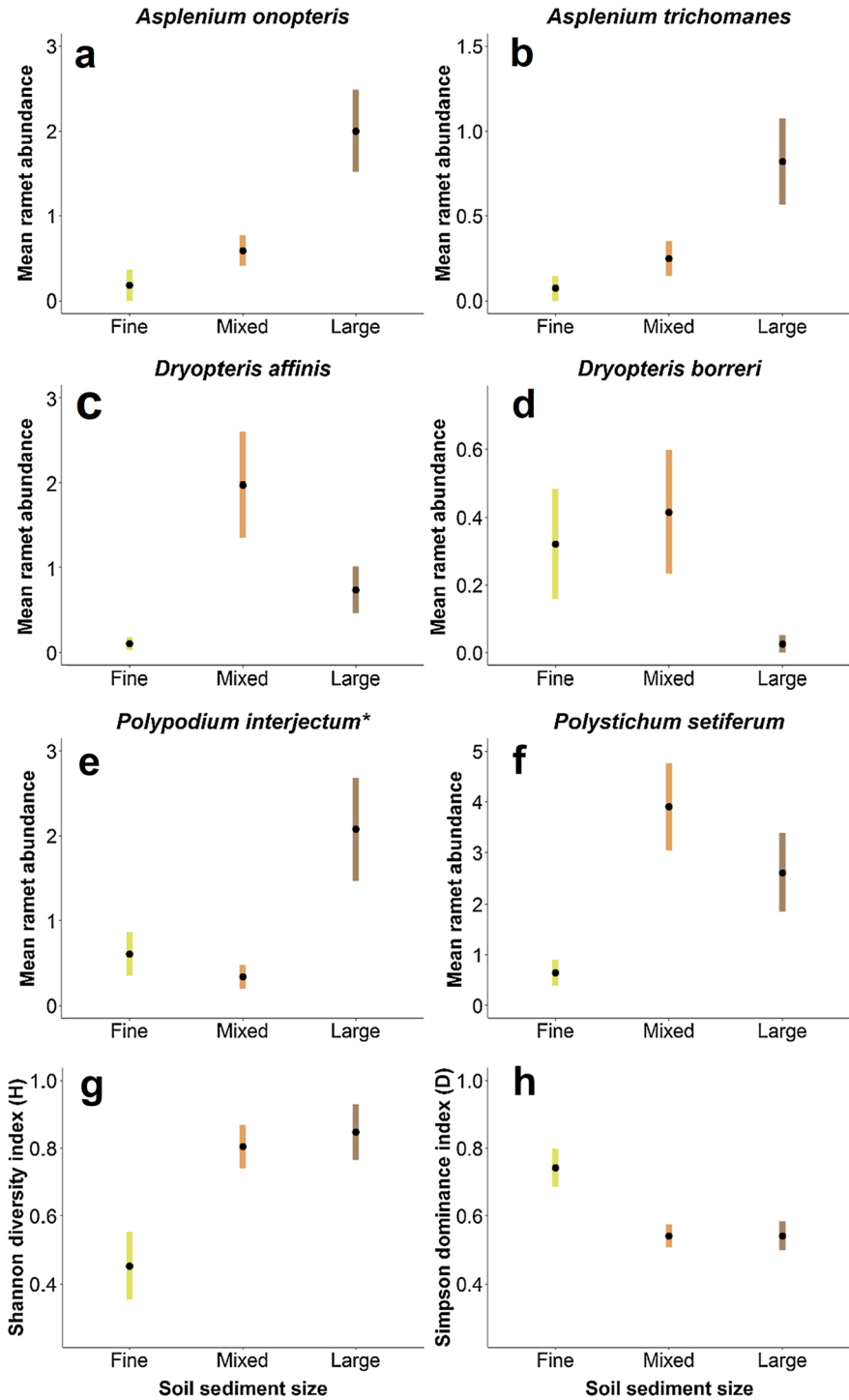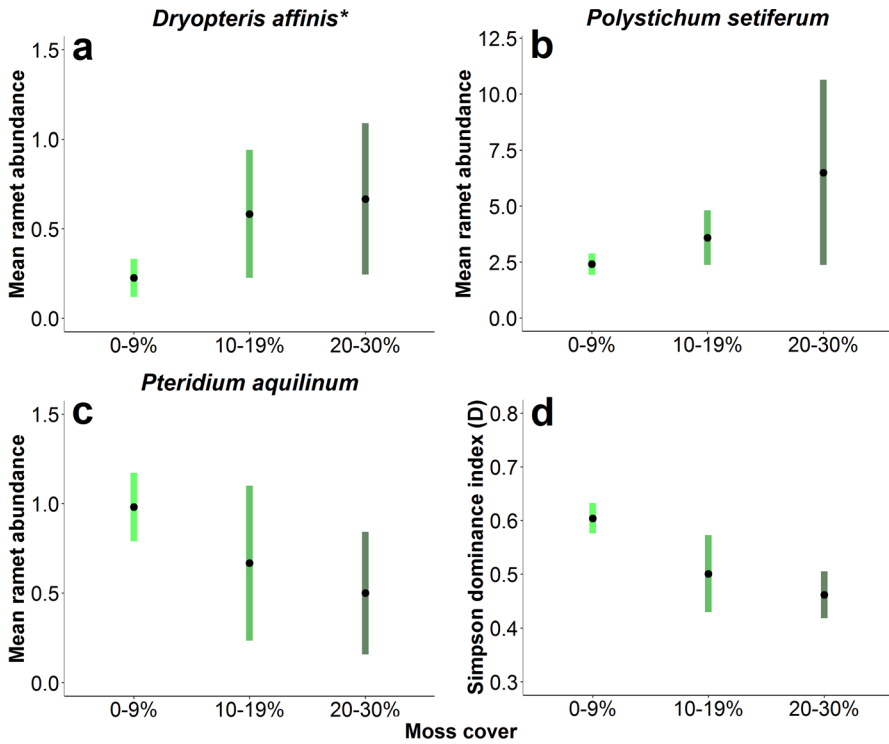
Fig. 4 Moss cover effect on population (**a–c**) and community (**d**) responses of ferns. Dot and error bar depict observed mean and standard error. Only fern responses significantly influenced by moss cover are reported. Moss cover was grouped in three classes arbitrarily to improve graphical interpretation. Asterisk denotes when the abundance is referred to as generative ramets

Also, abundance of *S. spicant* showed a weak, albeit significant, association to that of *O. regalis* ($r_S = 0.35$; $P < 0.01$). All other correlations were weaker and not significant.

Discussion

We disentangled environmental factors driving population- and community-level responses of ferns in a riparian *Alnus glutinosa* forest habitat to understand whether fern species can be used as an ecological indicator group in this habitat. We found that fern diversity and distribution were mainly influenced by soil granulometry and, to a lesser extent, orientation of the streams and moss cover. Compared to previous studies, our work expanded the number of fern species analysed in the same habitat. We first discuss population- and community-level specific responses. Then, we focus on the potential role of fern indication at the habitat level.

Population-level responses

The abundance of different sporophyte demographic life stages, i.e. juvenile, vegetative adult, generative adult and senescent, can be influenced by different environmental
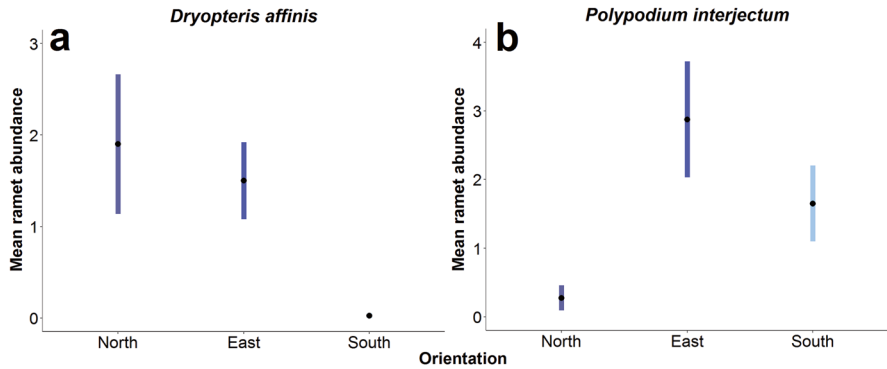
Fig. 5 Effect of sampling-plot orientation on population responses of ferns. Dot and error bar depict observed mean and standard error. Only fern responses significantly influenced by orientation are reported

variables (Cinquemani Kuehn and Leopold 1993; Rünk et al. 2006). Our results showed that the use of vegetative and generative life stages can be informative of the populations´ ecological conditions.

For *Osmunda regalis*, we found more vegetative ramets compared to the generative ramets. This agrees with previous findings showing stable populations with a higher proportion of generative adults growing prevalently in spring swamp habitats and lower canopy cover, whereas a few sporophytes reached the generative adult stage in stream habitats (Landi and Angiolini 2011). This is likely due to water flow disturbance and higher canopy. Generally, the high availability of water in the soil supports the occurrence of *O. regalis* in the streambed. However, the streambed is more unstable compared to the mid-slope and upper-slope, being more influenced by the water flow. Therefore, it is likely that the growth of the sporophyte to the generative adult stage is negatively influenced by flood disturbance than other fern species, e.g. *Athyrium filix-femina. Osmunda regalis* has a very prominent epigeogenous rhizome and a non-elastic rachis of the fronds that is negatively affected by rolling rocks and debris (Landi and Angiolini 2011). We did not find any predictors correlated with the abundance of ramets for *O. regalis*. This suggests that favourable characteristics for the development of the sporophyte in stream habitats are lacking, e.g. peaty soil, or they vary little, e.g. low light availability.

Abundances of *O. regalis* and *Struthiopteris spicant* in sampling plots were positively associated but did not depend on any investigated predictor, suggesting their preferential occurrence in other habitats, e.g. forest swamps. Consistently, in a demographic study on *S. spicant* its abundance increased with moisture, being most successful in poorly drained forest swamps (Cousens 1981). In addition, this species has been associated with the abundance of *O. regalis* in the spring swamps of central Italy (Landi and Angiolini 2008, 2011).

In the investigated streams, *A. filix-femina* is one of the most abundant fern species and one with the highest number of generative ramets. This finding agrees with the fact that *A. filix-femina* grows in a great variety of habitats such as marshes, ponds and lakes, streams and humid woods. In Central Europe and in Mediterranean regions, it is often found in shady environments (Douda 2010; Haou and Bélair 2020; Pignatti et al. 2017). However, *A. filix-femina* preferentially occurs in the streambed according to a previous study on fern abundance and frequency on different elevations in stream channels (Greer et al. 1997). The correlation coefficient indicated that *A. filix-femina* is positively associated with *O. regalis* and *S. spicant,* as it shares its habitat with them. Accordingly, they are confined

to streambeds in hilly streams. Furthermore, these fern species are constantly present in the forests of the alliance *Osmundo regalis–Alnion glutinosae* (Landi and Angiolini 2010). The presence of *A. filix-femina* depended on moss cover, very abundant in the shady and humid environments of the streams. Therefore, it is likely that the numerous generative ramets produce a high number of spores. Also, *A. filix-femina*'s more "herbaceous-like" consistency and a generally smaller size compared to other fern species, e.g. *O. regalis* and *Dryopteris affinis* s.l., permits A. *filix-femina* to more easily colonize the streambed habitat and to better cope with flood disturbance. A smaller frond with a more herbaceous-like aspect, being also more flexible, has the advantage of having less resistance to waterpower. Therefore, damages to fern rachides are less likely. Our results support a wide ecological niche for this species, in agreement with the variety of humid environments where it lives, especially if placed in relation to the other ferns of our study.

D. affinis decreases in fine-grained soils. This suggests that the species is negatively affected by the sedimentation processes and flood disturbance. In addition, the increase of generative ramets with moss cover and the decrease of the species in south-oriented streams indicates the species prefers humid and cool habitats. Our results are consistent with the presence of *D. affinis* group on the north-oriented slopes of Harz Mountains of Germany (Bär et al. 2020), in the ancient woodlands of England (Rackham 1980), but also with the greater adaptation of *D. affinis* to moderately shaded habitats.

Our data shows that *D. affinis* was more frequent in our streams than *D. borreri*. Further, no environmental variable that predicted *D. affinis* abundance was relevant in the model for *D. borreri*. Both species fall within the *D. affinis* group. This is the first study that has investigated the ecological differences between these two entities. *D. affinis* was negatively affected by fine-grained soils and *D. borreri* by large-grained soils. Therefore mixed-grained soils can be colonized by both species. However, the lower number of predictors in the model for *D. borreri*, might indicate its wider ecological amplitude compared to *D. affinis*. This latter species prefers more humidity and is more shade-tolerant. The attribution of species or subspecies rank has been widely discussed and perhaps not yet resolved (Fraser-Jenkis 1980; Marchetti 2004; Pignatti et al. 2017). Our study supports the distinction between these two entities also from the ecological niche perspective. In addition, the results showing their ecological differences are consistent with the much wider distribution in Europe of *D. borreri* compared to *D. affinis* (Pignatti et al. 2017; PoWO 2019).

In the streams investigated here, *Polystichum setiferum* was the most abundant fern species and the most frequent along with *A. filix-femina*. Both species increased in abundance with moss cover. Similarly to *D. affinis*, *P. setiferum* abundance decreased in fine-grained soils, but it was not affected by stream orientation. Previous studies found *P. setiferum* growing on calcareous sands on ditch banks, and in moderately sunny habitats (Bremer 1995; Lo Gullo et al. 2010). Such ecological characteristics suggest that, as *D. affinis*, *P. setiferum* is negatively affected by the sedimentation processes, but it can grow in habitats with more variability in light and soil chemistry.

We rarely found fronds of *Pteridium aquilinum* with spores (<2% of the total ramets). The establishment via spores of this species is relatively uncommon and vegetative reproduction is the main strategy of colonization and expansion (Watt 1969; Marrs and Watt 2006). The streams investigated in this study have cool temperatures and low daily temperature range. This is due to the shorter duration of the solar radiation, greater humidity maintained by the continuous water flow and to the denser tree canopy cover, where we also detected an abundant growth of mosses (Landi et al., 2009). Such conditions for *P. aquilinum* are unfavourable because in our study area the species prefers forests prone to summer fires and drier soils fully exposed to daylight (Karst et al. 2005; Marrs and Watt

2006; Ershova 2010). *P. aquilinum* has been frequently recognized as a dominant colonizing species of fire disturbed areas (Johnson 2001; Silva and Silva Matos 2006; Gallegos et al. 2015), while in our study area fires rarely reach the streams.

The three species *Asplenium trichomanes*, *A. onopteris* and *Polypodium interjectum* can grow on ground and other substrates as rocks and bark of dead trees. Our results showed that *A. trichomanes* establishment is favoured in southern orientation and in large-grained soils. Such results are consistent with the increase of juvenile sporophytes in open habitats, its remarkable acclimation to different light conditions, and its preference for growing on vertical rocks or boulders (Bremer 2004; Haou and Bélair 2020; Jermy and Page 1980; Page 1977; Vasheka et al. 2019). Furthermore, a greater presence of stones and boulders at the sites decreases the competition with other herbaceous species. Thus, generative fronds growth is favoured. Our results for *A. onopteris* showed this species mainly prefers large-grained soils but can also grow on mixed-grained soils. Compared to *A. trichomanes*, it might be possible that *A. onopteris* occupies different soil sediment sizes. Lastly, our results showed that *Polypodium interjectum* is positively affected by the presence of mixed-grained soils, favouring generative life stages, while it decreases in the cooler north-oriented streams.

The fern species we excluded from the statistical analysis were rare or not very frequent in the hilly areas of central Italy, because they live in warmer (*P. cambricum*), or cooler areas (*D. dilatata*), or are preferentially basiphilous (*A. scolopendrium*). On the other hand, *Equisetum telmateia* is frequent in Italy, but typically present in lower parts of the streams, marshy areas and rivers on sandy or clay soils (Roberts 1980; Marchetti 2004; Pignatti et al. 2017). Therefore, in the upper parts of the streams, usually shady and rocky, the species presence is not favoured.

Community-level responses

Numerous fern species (e.g. *Athyrium filix-femina*, *Dryopteris affinis* group, *Osmunda regalis*, and *Struthiopteris spicant*) are good indicators of riparian alderwoods of the alliance *Osmundo regalis–Alnion glutinosae* in Europe (Landi and Angiolini 2010). This community requires high moisture, meso-oligotrophic waters, acid reaction soils and waters that drain through the ground. As suggested by the Simpson index, sites with fine-grained soils support more homogeneous fern communities, i.e. communities dominated by one or few species. This agrees with the Chao-1 and Shannon indices which suggested a lower fern diversity on fine-grained soils. At the community level, this represents a hint that fern communities are governed by soil granulometry. In streams, the presence of fern species and the distribution of their life stages are not random, rather their presence and abundance are driven by the environmental variability of the habitat, with ferns being abundant in some streams and absent in others. When considering the abiotic characteristics of the streams, the variability of the soil granulometry is linked to the distance from the water flow (streambed, mid-slope and upper-slope), and to the flood disturbance. The main direction of the streams favours species growing under different conditions with cooler environments on north-oriented streams, and sunny and warmer environments on south-oriented streams. However, it is important to recall these environmental conditions are not necessarily linked to habitat conservation status. Furthermore, the higher moss cover retains moisture and might promote spore germination, likely explaining why moss cover favours richer and less homogeneous fern communities. The association between fern richness and moss cover was detected through the Chao-1 index, which gives more weight to rare species.

Thus, it is also possible that moss cover would primarily positively impact rare fern species, because the habitat quality is better. Other studies highlighted the association between these two groups as both groups are dependent on a film of water on the under-surface of the gametophyte (Pharo et al. 1999). Fern species with abundant vegetative and generative sporophytes in turn reflect the continuity of different water dynamics, humidity, and transport of debris. Fern presence and abundance might have benefited from these factors.

Habitat quality assessment

Ferns allowed us to draw conclusions about an overall good ecological status of the investigated habitat, namely residual alluvial forests, a priority habitat of conservation concern (Natura 2000 code 91E0). Our study further confirms the importance of the ecological indication role of ferns (Della and Falkenberg 2019; Silva et al. 2018). Particularly, we stress their role as early-warning species for environmental changes in the 91E0 habitat (Bonari et al. 2021). An advantage in using ferns as indicators is that they are perennial organisms. Accordingly, most of the fern species evaluated in this study have a distinctive underground stem (rhizome) that each year resprout adventitious roots and stems. They can thus be considered long-living species that are informative on long-term changes of the habitat. Therefore, their presence can be interpreted as a response to a stable habitat, though characterized by a hydrological discontinuity. In our study area, the abundance of ferns in well-preserved stream forest habitat with a high canopy cover can be appraised as good indicators of the ecological status of riparian alderwoods. In our plots, canopy cover was generally high (median = 85%). Some of the investigated ferns are sensitive to changes in soil moisture. Those that increase with moss cover are generally more hygrophilous and could therefore be considered as indicators of good habitat status (e.g. *Dryopteris affinis*). On the contrary, those species that are less hygrophilous and are favoured by more open forest canopy could indicate habitat worsening (e.g. *Polystichum setiferum*). Accordingly, we suggest that when the presence of ferns with vegetative and generative sporophytes reflects the different water dynamics and moisture degrees, they can be used as indicators of the ecological habitat integrity. Further, we stress the importance of soil granulometry for habitat quality as it can indicate appropriate environmental conditions of the habitat. Finally, we suggest that an added valuable element for future habitat monitoring is the use of the different fern life stages as they might inform on different ecological characteristics and species requirements.

Conclusions and implications for conservation

We studied the ecology of several fern species, their populations and communities occurring along streams in a natural forest habitat of European priority importance. We conclude that ferns can help us appraise about the ecological conservation of this habitat. In natural streams across forests, on acidic or sub-acidic soil, the distribution of fern species varies according to the soil sediment characteristics, orientation and moss cover. We also found that growth of the generative life stage compared to the vegetative adult might benefit from different ecological characteristics for certain fern species.

Our study deepened the understanding of fern ecology at fine scale in riparian alderwood forests and provides valuable information for the elaboration of future conservation

strategies of fern species that are of conservation interest. We highlight the importance of studying ferns at the population-, community-, and habitat-level to better understand their ecology and use them, along their life stages, as early-warning species in habitat monitoring.

Alnus glutinosa-dominated riparian forests are characterized by a fern-rich understory often made up of small fragments but in an overall good conservation status. From the conservation perspective, this habitat deserves to be protected by anthropogenic disturbances that may alter the soil sedimentation and moss cover. Threats include all modifications of the natural hydrology as streambed interventions, water uptake and eutrophication, of which some of the studied species are sensible to and can be therefore used as early-warning species. Forest roads and plantations are also to be avoided as they may imply habitat modifications and thus a general deterioration in the ecological quality of the habitat.

Declarations

Conflict of interest Authors have no conflict of interest to declare.

Ethical approval Plant names agree with the International Code of Nomenclature for algae, fungi, and plants.

Animal research Not applicable.

Consent to participate Not applicable.

Consent to publication All authors agreed with the content, gave explicit consent to submit, and they obtained consent from the responsible authorities at the institute/organization where the work has been carried out, before the work is submitted.

Plant reproducibility Not applicable.

Clinical trials registration Not applicable.

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