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Pteridium aquilinum performance is driven by climate, soil and land-use in South-western Asia

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Abstract:	Growing anthropogenic impacts on natural and semi-natural ecosystems have created a network of degraded sites throughout the world. These disturbed ecosystems are often colonized by invasive plants such as Pteridium aquilinum , which is one of the most widespread plants worldwide. In northern Iran, P. aquilinum is often found invading newly-created habitats formed after anthropogenic disturbance. This study aimed to assess the relationship between P. aquilinum performance and a range of environmental factors (soils, climate, topography, and land-use) in northern Iran. In fifteen sites dominated by P. aquilinum, that spanned the regional distribution of P. aquilinum , we measured its cover, density, and biomass. P. aquilinum was found to occur in a variety of land-uses including abandoned agricultural lands, degraded forests, and upland rangelands. The performance of P. aquilinum varied significantly between the sites and it performed better in a moderate-Mediterranean climate. Variation partitioning confirmed the importance of climate followed by soil and land-use in explaining the performance of P. aquilinum . Topographic variables did not show any significant effect on P. aquilinum . Both temperature and rainfall affected P. aquilinum performance. Density was correlated positively with early-spring rainfall whereas biomass and cover were found to have positive correlation with temperature. There was also a gradient of soil texture/pH/N/P influencing P. aquilinum . Frond density and biomass were correlated positively with sand content, N and P, but negatively with pH, lime and bulk density. Thus, soil conditions alongside temperature in spring and early summer could explain P. aquilinum cover, but for density, rainfall in early spring was the most important factor, suggesting that in northern Iran P. aquilinum performance appears to be intermediate compared to responses reported

	for temperate (temperature-controlled) and tropical climates (rainfall-controlled).
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Pteridium aquilinum performance is driven by climate, soil and land-use in South-western Asia

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Abstract

Growing anthropogenic impacts on natural and semi-natural ecosystems have created a network of degraded sites throughout the world. These disturbed ecosystems are often colonized by invasive plants such as *Pteridium aquilinum*, which is one of the most widespread plants worldwide. In northern Iran, *P. aquilinum* is often found invading newly-created habitats formed after anthropogenic disturbance. This study aimed to assess the relationship between *P. aquilinum* performance and a range of environmental factors (soils, climate, topography, and land-use) in northern Iran. In fifteen sites dominated by *P. aquilinum*, that spanned the regional distribution of *P. aquilinum*, we measured its cover, density, and biomass. *P. aquilinum* was found to occur in a variety of land-uses including abandoned agricultural lands, degraded forests, and upland rangelands. The performance of *P. aquilinum* varied significantly between the sites and it performed better in a moderate-Mediterranean climate. Variation partitioning confirmed the importance of climate followed by soil and land-use in explaining the performance of *P. aquilinum*. Topographic variables did not show any significant effect on *P. aquilinum*. Both temperature and rainfall affected *P. aquilinum* performance. Density was correlated positively with early-spring rainfall whereas biomass and cover were found to have positive correlation with temperature. There was also a gradient of soil texture/pH/N/P influencing *P. aquilinum*. Frond density and biomass were correlated positively with sand content, N and P, but negatively with pH, lime and bulk density. Thus, soil conditions alongside temperature in spring and early summer could explain *P. aquilinum* cover, but for density, rainfall in early spring was the most important factor, suggesting that in northern Iran *P. aquilinum* performance appears to be intermediate compared to responses reported for temperate (temperature-controlled) and tropical climates (rainfall-controlled).

Keywords: Biological invasion, Bracken, Hyrcanian flora, invasive species, deforestation

Introduction

Increasing anthropogenic impacts on semi-natural and natural ecosystems have created a network of degraded sites across the world (Rejmanek 1989; Pysek et al. 2002). When these natural habitats are disturbed by human activity one of the most frequent problems is replacement of native species by invasive exotic species (Vitousek 1994). However, native species can be as competitive as invasive aliens, and can also expand into new habitats or increase their biomass or cover at the expense of others (Marrs and Watt 2006; Marrs et al. 2013). There are many factors influencing successful plant invasion, including safe sites for establishment and resource availability for growth and reproduction (Brym et al. 2011), although nowadays disturbance is becoming a key factor affecting invasion potential (Alpert et al. 2000; Domenech and Vila 2006). Unfortunately, most recent disturbances are associated with human activities (e.g., cultivation, grazing and deforestation; Hansen and Clevenger 2005; Alday et al. 2010). It is well known that plant invaders usually outcompete many native plants, leading to a decreased local plant species diversity (Vila et al. 2006; Hejda et al. 2009), increased ecosystem productivity and altered nutrient cycling rates (Liao et al. 2008), which together can influence negatively both ecosystem services and human well-being (Ehrenfeld 2010). Where invasive plants alter nutrient regimes, it is usually correlated with faster growth rates and greater biomass production compared to native species from the same habitats, and these increases can then accelerate decomposition rates and soil nutrient cycling (Allison and Vitousek 2004). Apart from threatening the conservation of native communities and ecosystem integrity (Vitousek et al. 1996), invasive species may induce significant economic costs (Pimentel et al. 2000).

Pteridium aquilinum (L.) Kuhn (bracken) is considered a major invasive species worldwide (Marrs and Watt, 2006). Although originally a woodland species, it has expanded its range to occupy many types of disturbed ecosystems (Marrs and Watt 2006). Its success is attributed to the production of a dense frond canopy with tall fronds and high biomass that produces dense shade (Marrs and Watt 2006; DeLuca et al. 2013), along with a large rhizome system containing considerable reserves of carbohydrates and frond-producing buds (Le Duc et al. 2003; DeLuca et al. 2013). As *P. aquilinum* invades, there can also be a deep litter layer (Marrs and Watt 2006), which inhibits colonization by other species (Lowday and Marrs 1992; Ghorbani et al. 2006). Collectively, the summer frond biomass and deep litter layer cause problems for agriculture, livestock grazing, and forestry (Roos et al. 2010; Levy-Tacher et al. 2015).

Climate, soil, and topography have been shown to be important factors controlling *P. aquilinum* distribution and performance (Marrs and Watt 2006). In temperate climates, low temperatures, especially frosts, are critical in limiting both *P. aquilinum* distribution and the length of the frond growing season (Marrs and Watt 2006). In contrast under tropical climates rainfall is the most important driving variable (Portela et al. 2009). Topography also appears to affect performance; *P. aquilinum* commonly colonizes steeper slopes on south and south-westerly aspects at high altitude (Hughes and Aitchinson 1986), but aspect is less influential at low altitudes (Lloyd 1972). *P. aquilinum* can survive in wide range of soil types with a wide range of soil physico-chemical conditions (Marrs et al. 2000; Marrs and Watt 2006). The soil profile is important because it is related to both aeration and water supply; although, *P. aquilinum* can grow on shallow soils, it grows better on deep soils in dry or humid sites (Watt 1976). It cannot tolerate waterlogging (DeLuca et al. 2013), because its rhizomes are unable to tolerate low oxygen concentrations that occur in waterlogged soils (Whitehead and Digby 1993). Thus, *P. aquilinum* is absent from waterlogged areas, surviving only in areas which are irregularly wet (Roberts et al. 1980; da Silva and Silva Matos 2006). *P. aquilinum* can grow over a wide pH range; but at pH extremes fronds are smaller and less abundant (Marrs and Watt 2006). There is usually a large organic matter content in the surface soil horizon below *P. aquilinum* because of the absence of effective mixing agents in most *P. aquilinum*-dominated communities (Marrs and Watt 2006). *P. aquilinum* litter is an effective contributor to soil organic matter (Anderson and Hetherington 1999), altering the soil environment creating an inorganic N-rich environment that is favorable to its growth and development (DeLuca et al. 2013; Milligan et al. 2018).

P. aquilinum is a part of Hyrcanian flora but currently it is regarded as a persistent and aggressive weed causing problems in various ecosystems of northern Iran (Khoshravesh et al. 2010). It has invaded several newly-created habitats after anthropogenic disturbance brought about by intensive grazing, change in land-use from pasture and forest, fire events, and land abandonment of cultivated areas (Adabi 2015; Ghodskhah Daryayi et al. 2013). Currently, almost nothing is known about the performance of this native invasive species in this region. Thus, understanding the way that *P. aquilinum* performs in different environmental situations will be of great benefit in developing effective strategies for its management and/or control. *Pteridium aquilinum* can expand into different conditions, defined by the site-dependent factors, like soil, climate, topography or land-use, all of which are likely to contribute to its current success. In this paper, therefore, we measured *P. aquilinum* performance (frond morphological variables) and a range of environmental factors (soils, climate, topography, land-use) across the known distribution of *P. aquilinum* in northern Iran with the aim of identifying the most important environmental factors (soil, climatic, topography, land-use) controlling *P. aquilinum* performance.

Materials and methods

Study sites

This study was conducted in Mazandaran Province, north of Iran (23,833km², 35º 47' - 36º 35' N and 50º 34' - 54º 10' E, Fig.1) located in the Hyrcanian ecoregion along the southern coast of the Caspian Sea and the north slope of the Alborz mountains. In a primary survey, the presence of *P. aquilinum* was detected in 120 sites. From this large pool, we selected 15 sites in seven regions including Ramsar (R), Marzanabad (M), Chamestan (C), Babol (B), Zirab (Z), Farim (F), and Hezar Jarib (H, Fig.1). These 15 sites were selected because: i) *P. aquilinum* was present at least in an area greater than 1ha (range, 2–42 ha); and, ii) they represent a wide altitudinal range from 650 to 2400 m above sea level, different land-uses, and climatic conditions (Table 1). The selected *P. aquilinum* stands were found in abandoned agricultural lands (AL, 8 sites), invaded rangelands (IR, 5 sites), plantation forest (PF, 1 site), and a deforested site (DF, 1 site). Sites near the Caspian Sea had a climate defined either as moderately-humid (3 sites) or moderate-Mediterranean (7 sites) with hot and humid summers, and mild, wet winters with little frost (Noroozi and Korner, 2018). Five sites in the Alborz mountains had a Semi-arid-very-cold climate; at these sites the weather is colder, frost is common, winters are long, and summers are short and dry. Annual mean rainfall ranges from 977 mm to 425 mm, with higher rainfall at the lowest elevations (Table 1).

P. aquilinum sampling

Samples were collected in the summer of either 2017 or 2018. At each site a standardized protocol was used to sample the main *P. aquilinum* area. Depending on the extent of the *P. aquilinum* stand, a minimum of one and a maximum of 14 transects, were sampled, distancing them at least 5m apart, and avoiding the borders; each transect was 50 or 100m long and was located randomly in the stand. Ten sample plots (1×1m) were placed every 5 or 10m on each transect. *P. aquilinum* performance was recorded in each of the 1m^2 plots. In total, we sampled 415 plots in 15 sites (10-100 plots per site). *P. aquilinum* cover (%) was estimated visually, the number of fronds (density, number per m^{-2}) was counted, and thereafter, all fronds were cut near soil surface, dried and weighed (dried biomass, g m^{-2}).

Soil sampling

Soil samples were collected from each plot on each transect using a soil auger (diameter = 7cm, depth = 30cm) beneath the litter layer. In the laboratory, the soil samples were air-dried and sieved to pass a 2 mm mesh. Soil texture (proportions of clay, sand and silt) was analyzed using the Bouyoucos-method (Day 1965). Then, the following soil chemical properties were measured: soil pH and electrical conductivity (EC) using a conductivity meter in a 1:2.5 soil/deionized water slurry (Allen 1989); total nitrogen concentration using the Kjeldahl-method (Bremner and Mulvaney 1982); available phosphorus concentration using the Olsen method (Olsen and Sommers 1982); total organic matter and total carbon concentration using the Walkley-Black method (Walkley 1947), and carbonate concentration by acid neutralization and titration (Allen 1989).

Topographic data

On each transect the elevation and geographic co-ordinates of each plot was recorded using a Global Positioning System (Garmin GPS MAP 64S, Belgium), and plot slope and aspect were also measured using a clinometer and compass, respectively. Heat load index, a value that reflects the average temperature in the environment, was calculated using aspect and slope variables (McCune and Keon 2002). The index ranged from 0 to 1; values close to 1 indicate a warmer temperature (usually south-west facing slope) and values close to 0 show cooler temperatures (usually north-east facing slopes).

Climatic data

Climate data were provided by the Meteorological Organization of Iran from the nearest recording stations to the study sites, thus, climate data is at site level (Table 1). We extracted climate variables including 24-hour rainfall, mean temperature, and minimum and maximum temperatures for January to July 2017 (7 months, 28 variables). A Principal Components Analysis (PCA) was performed to extract the most important variables. The first axis (PC1) was correlated with minimum temperature of March (TminMar) and April (TminApr), mean temperature of July (TmJul), and the second axis (PC2) with 24-hours rainfall of February (R24Feb), March (R24Mar), April (R24Apr), and May (R24May).

Statistical analysis

All statistical analyses were performed in R statistical environment (3.5.1 R Core Team 2019). *P. aquilinum* performance in seven regions were compared using linear mixed effects model (‘lme’ function, Pinheiro et al. 2020) for biomass with a Gaussian error distribution and (‘glmer’ function, Bates et al. 2015) for density and cover with a Poisson distribution; in both types of models regions were included as a fixed factor and transects nested within sites were included as random variables. A PCA using the ‘rda’ function was applied and the most important environmental variables were identified using the ‘adonis’ function (Permutational Multivariate Analysis of Variance; PMAV, “vegan” package, Oksanen et al. 2018). The regions and sites were then displayed on the PCA biplots as bivariate standard deviational ellipses using the ‘ordiellipse’ function. The 15 sites were also shown in PCA biplot classified according to climate.

From the geographic coordinates of the sampling sites, we assessed the effect of spatial autocorrelation by extracting Principal Coordinates of Neighbor Matrices (PCNM; Borcard and Legendre 2002) with the ‘pcnm’ function (Oksanen et al. 2018). Variation partitioning with function ‘varpart’ (Oksanen et al. 2018) was carried out on two datasets (PCNM+climate+soil+land-use and PCNM+climate+soil+topography). To describe the relationship between *P. aquilinum* variables and environmental variables we used a Principal Components Analysis (PCA) and *P. aquilinum* variables were passively fitted over the ordination using the ‘envfit’ function. The climate variables were included in a PCA after standardization. Finally, to have a clear description of the changes in *P. aquilinum* performance we fitted a response surface model (i.e. gam model) over the ordination space for each variable to identify trends of change (Alday et al. 2017).

Results

P. aquilinum performance

The mixed effects model showed a significant effect of regions on *P. aquilinum* density (R^2 marginal = 9.84), biomass (R^2 marginal = 6.64), and cover (R^2 marginal = 9.44). *P. aquilinum* frond density ranged from 6 to 84 fronds m^{-2} with the highest median in Babol (B) and Farim (F) and the lowest in Hezarjarib (H, Fig. 2a). The median for frond biomass ranged from 371.1 (H) to 719.8 g m^{-2} (F) while there was a much greater range in biomass (447.6-1755.8) in lowland sites (Z, Fig. 2b). Cover was more than 75% in all invaded sites, and 100% in region Z (Fig. 2c). These differences between the seven regions were confirmed by PMAV analysis (F=7.42, p-value=<0.001, R^2=0.18).

The first PCA axis (PC1) explained 64.10% and axis 2 (PC2) 20.84% of the total variation in *P. aquilinum* performance. Four regions (Z, B, M, and F) are located in left side of the ordination correlated with high *P. aquilinum* performance while C, R and H are located in the right side of ordination associated with low *P. aquilinum* performance (Fig. 3a, b).

The ellipses of all sites based on their climate showed that the two sites with semi-arid-very-cold climate (Fi and T) were placed in the upper-left quadrant associated with greater performance (Fig. 3c). Most of the sites with a Moderate-Mediterranean climate were located in the middle and left side of the ordination space showing high *P. aquilinum* performance, although ST was an exception being located at the positive end of axis 1 with lowest performance (Fig. 3d) and in the moderately-humid- climate Dl and H showed greater performances than EK (Fig. 3e).

Variance explained by environmental factors

Variation partitioning showed that environmental variables explained more variation in *P. aquilinum* performance than spatial variables (Fig. 4) and that the amount of variation explained by climate, soil, and land-use (Fig. 4a) was greater than that by climate, soil, and topography (Fig. 4b). The complete set of spatial (PCNM) and environmental variables (climate, soil, and land-use) explained 39.2% of the variation in *P. aquilinum* performance data (Fig. 4a). The sole effect of climate was 7.2% (p-value<0.001) whereas land-use and soil alone explained 4.3 and 3.4% of variation in *P. aquilinum* performance, respectively (Fig 4a). Space and soil had the greatest shared variation in *P. aquilinum* performance (4.6%, R^2=10.3, p-value<0.001), while the rest of the shared variation was less than 3% (Fig. 4a).

Response of *P. aquilinum* to soil

The first two principal components in PCA analysis of soil properties explained 52.18% of the total variance with axis 1 accounting for 30.93% of the variation were correlated positively with sand, N, P, K, and moisture and correlated negatively with bulk density and pH (Fig. 5a). Axis 2 explained 21.25% of the variation and was found to be correlated positively with lime, EC, and pH and negatively with moisture and sand (Fig. 5a).

Individual sites based on the type of land-use were significantly different with respect to soil parameters (PMAV, F-value=14.53, R^2=0.51, p-value<0.001). For example, abandoned arable land sites (SCH, VZO, TR, ST, H, SB, VGV, EK) located in the left side of ordination were correlated with less fertile soil with a high pH, lime content and bulk density (Fig. 5b). In contrast, most rangeland sites (T, FI, SG, F) were in the middle and right side of ordination correlated positively with N, P, K concentrations and moisture. The deforested site (DL) and plantation forest (NG) had fertile soils (Fig. 5b).

When *P. aquilinum* performance were fitted over the soil PCA, significant correlations were found for biomass (R^2=0.07, p-value<0.01) and density (R^2=0.16, p-value<0.01, Fig. 6), but not for cover (R^2=0.02, p-value=0.19). Biomass and frond density were related to nutrient concentrations, moisture and sand content. The fitted isolines were linear, increasing towards right side of the ordination (Fig. 6a, b).

Response of *P. aquilinum* to climate

The first two principal components of the PCA for climate explained 46% and 41% of *P. aquilinum* variation, respectively. Axis 1 was correlated positively with R24Mar, R24May and R24Apr and negatively with TMJul, TminApr, and TminMar (Fig. 7a). Axis 2 was correlated positively with R24Feb, R24Mar, R24May, and R24Apr. The deviational ellipses indicated significant differences between sites with respect to climate (PMAV, F=7.43, R^2=0.18, p-value<0.001). According to PCA axis, sites Z, F, H, and R showed a positive correlation with TMJul (Fig. 7a). Sites M, B, and C had a correlation with R24Apr, R24May, and R24Mar (Fig. 7a).

Significant correlations were found between all *P. aquilinum* performances and the climate variables; biomass (R^2=0.45, p-value=0.01, Fig. 7b), density (R^2=0.035, p-value =0.03, Fig. 7c) and cover (R^2=0.85, p-value<0.001, Fig. 7d). There was a clear positive correlation of biomass and cover with TMJul, TMinMar and TminApr in left side, but density was correlated with R24May, R24Apr, and R24Mar (Fig. 7c, d). All *P. aquilinum* performances showed non-linear isolines in response to climate variables (Fig. 7c, d, e).

Discussion

Our findings confirmed that both environment and land-use are important determinants for *P. aquilinum* performance in northern Iran. The amount of variance explained by both environmental and spatial components was 39.2%. Space alone explained most variation (13%), followed by climate (7.2%), land-use (4.3%), and soil (3.4%). Topography alone had little influence on *P. aquilinum* performance, partly because, as expected, its shared variance with climate was high (6%). However, 61% of the variation in *P. aquilinum* performance was not explained, but this is similar to results reported in other ecological studies (Vandvik and Birks 2002; Truchy et al. 2019; Kirk et al. 2019). Such large fractions of unexplained variance may be due to the unmeasured complex interaction between abiotic and biotic factors or large fractions of randomness and noise in the data (Moller and Jennions 2002; Fischer 2019). What is important is that the small amounts of variation accounted for are significant and important from an invasion-control perspective (Marrs et al. 2011).

We provided evidence of *P. aquilinum* expansion in several types of land-uses in northern Iran, from nutrient-poor soils in abandoned arable lands to nutrient-rich soils in rangeland and disturbed woodland. These infested ecosystems are in an early successional stage (Marrs et al. 2000) with high resistance and resilience to any restoration effort (Alday et al. 2013), causing ecological problems for land managers, foresters and rangers. It is interesting to highlight that these results showed that land-use accelerates bracken expansion, and this is consistent with other findings worldwide (Pakeman et al. 2000; Hartig and Beck 2003; Suazo et al. 2015; Ssali et al. 2017; Jean Baptiste et al. 2019). Our field observations showed that there was little to no natural regeneration in the deforested site dominated by *P. aquilinum*, probably due to shading and the deep litter layer, as both of these variables are known to inhibit seed dispersal, seed bank dynamics, and seed germination and establishment (Ghorbani et al. 2006; Gallegos et al. 2015; Ssali et al. 2018). In the plantation forest, *P. aquilinum* prevented coniferous saplings from growing as it competes for soil nutrients and water (Dolling 1996; and Gaudio et al. 2010). Moreover, summer rangelands in Iran have been abandoned recently because of *P. aquilinum* infestation, as the plants and soil seed bank beneath *P. aquilinum* stands have a poor grazing value and a low restoration potential (Adabi 2015; Khalili Narani 2017).

P. aquilinum responses to climate variables

In northern Iran, temperature and rainfall, which are both linked to elevation, were important drivers of *P. aquilinum* performance. At this regional scale, most of the sites with a Moderate-Mediterranean- climate showed high *P. aquilinum* performance. Overall, the present study suggest that our sites had an intermediate position between temperate climates where rainfall is deemed not to limit *P. aquilinum* performance, although it can affect frond height and density (Marrs et al. 1998; Marrs and Watt 2006) and tropical regions where rainfall appears more important than temperature for controlling *P. aquilinum* (Portela et al. 2009). In temperate regions, Marrs and Watt (2006) suggested that an oceanic climate was most favorable for *P. aquilinum* as frond production was restricted under continental climates, because of frond sensitivity to frost. Indeed, frost controls the length of growing season in temperate conditions through frond death in both early-spring and autumn (Watt 1954; Marrs and Watt 2006; Pakeman et al. 1994). Our study showed that the mean and minimum temperatures of January to July and maximums of January and February affected *P. aquilinum* biomass and frond cover at the beginning of the growing season in sites with elevation under 1000 a.s.l. In other words, temperature was more important than rainfall for *P. aquilinum* biomass and cover during spring and early summer. This agrees with Pakeman and Marrs (1992) who predicted that where frost is a rare occurrence a warm climate will produce a higher biomass. However, frond density appeared to be controlled by spring rainfall (R24May and R24Apr) rather than temperature, which may be linked to greater rainfall at higher elevations.

P. aquilinum responses to soil variables

It is well known that *P. aquilinum* can grow in a wide range of soil types (Watrud et al. 2003; Marrs and Watt 2006; DeLuca et al. 2013). In this study the most important soil variables correlated with *P. aquilinum* performance were soil texture and nutrient concentrations. Soil texture via soil bulk density was important, possibly through effects on moisture availability and soil aeration, both of which affect root/rhizome distribution and hence plant performance (DeLuca et al. 2013). The soils under *P. aquilinum* also had relatively high phosphorus concentrations, possibly because root leachates promote inorganic phosphate mobilization (Bhat et al. 2016). We also detected a gradient in both soil pH and nitrogen concentration. Here, soil pH had a negative relationship with frond density. So even though *P. aquilinum* can persist on soils with a pH between 2.8 and 8.6, it usually occurs, as in our study [pH range, 5.9-7.2], on acidic to neutral soils (Marrs et al. 2000; Marrs and Watt 2006; Adabi 2015; Milligan et al. 2018). Another reason could be that sandy soils are more acidic because of the relatively low clay content and hence reduced cation adsorption capacity and increased leaching potential (Adabi 2015). In contrast, we found low biomass and densities in soils with a high pH [pH_{max} = 7.2] and Ca status. The presence of *P. aquilinum* in less fertile soil with a high pH, mainly in abandoned land, is consistent with Suazo et al. (2015), who showed that *P. aquilinum* was absent from fields with soils of high fertility, but abundant on less fertile soil with the same land-use change history. Correspondingly, *P. aquilinum* prospers particularly on open sites with acid, infertile soils where it has competitive advantage by reducing mineral nitrogen through uptake and frond growth (da Silva and Silva Matos 2006; Griffiths and Filan 2007) and internal recycling (Marrs et al. 2007; Tipping et al. 2019).

Invasive species, like *P. aquilinum*, are well known to influence nitrogen cycles (Bardon et al. 2018; DeLuca et al. 2013). Essentially, where *P. aquilinum* has a large biomass and litter production, it adds a large amount of organic matter, hence, carbon and nitrogen to the soil (Maynard et al. 1998). Similar patterns are described in our study, where soil nitrogen was greatest in plots with high frond density, cover, and biomass. This is consistent with DeLuca et al. (2013) who showed that in an acid soil woodland under NH_4^+-N fertilization, soils under *P. aquilinum* had consistently greater soil NO_3^-N and NH_4^+-N concentrations compared to soils under *Calluna vulgaris*. They suggested that *P. aquilinum* has developed a strategy to increase soil inorganic N in acid soils for its growth and development. Increased nitrogen availability in *P. aquilinum* stands may reduce the potential for other native species re-establishment in the short-term, but may also result in improved fertility for the long-term establishment of favorable or native plant species (DeLuca et al. 2013). The soil nitrogen cycle may also be stimulated by enhanced nitrification, especially important in acidic soils (Der et al. 2009; Keersmaeker et al. 2013).

Conclusions

The remarkable result of our study was the presence of *P. aquilinum* in sites covering a range of soil conditions, climatic and topographic variables, and land-uses. Temperatures in spring and early summer coupled with soil conditions were important in explaining *P. aquilinum* cover, but for density, rainfall in early spring was the most important predictor. Our main conclusions about *P. aquilinum* performance with respect to the environmental gradients in northern Iran relates to three major factors: (1) the soil texture changes from sandy soils with high nitrogen and phosphorus concentrations and low pH with greatest frond density and biomass through to soils with low nitrogen and phosphorus but high pH with lower frond density and biomass, (2) rainfall in early spring which increases frond density, and (3) spring and early summer temperatures which impacts frond biomass and cover. Finally, this study showed that *P. aquilinum* has a great potential to invade natural ecosystems in northern Iran as it responded positively to a range of environmental factors under different disturbances. Several recent changes in land-use practice have been responsible for changes in the performance and extent of *P. aquilinum* in our study area. We found *P. aquilinum* a major problem in the lowlands where it is not economic or possible to grow crops and has a low value for livestock grazing. These areas had a history of conversion from forest to arable land in the past. However, there is now a serious threat for upland rangelands as *P. aquilinum* is also spreading into these areas. The spread of this fern could potentially lead to further land abandonment. Thus, these findings have great benefit in initiating the development of an effective strategy for land management under *P. aquilinum* invasion. Further studies are necessary to understand the causes and mechanisms behind this invasion and assess appropriate weed control and land restoration methodologies.

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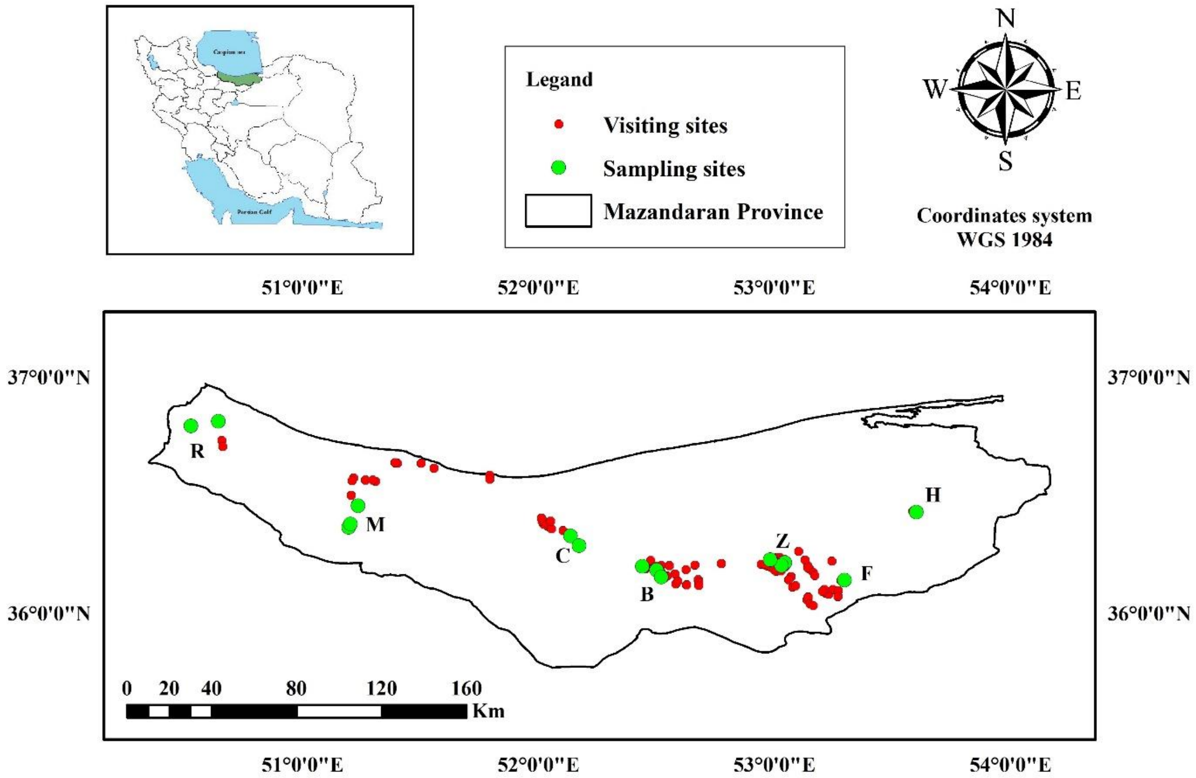

Fig. 1 The distribution of primary-survey (red) and sampling (green) sites dominated by *P. aquilinum* in Mazandaran Province in northern Iran

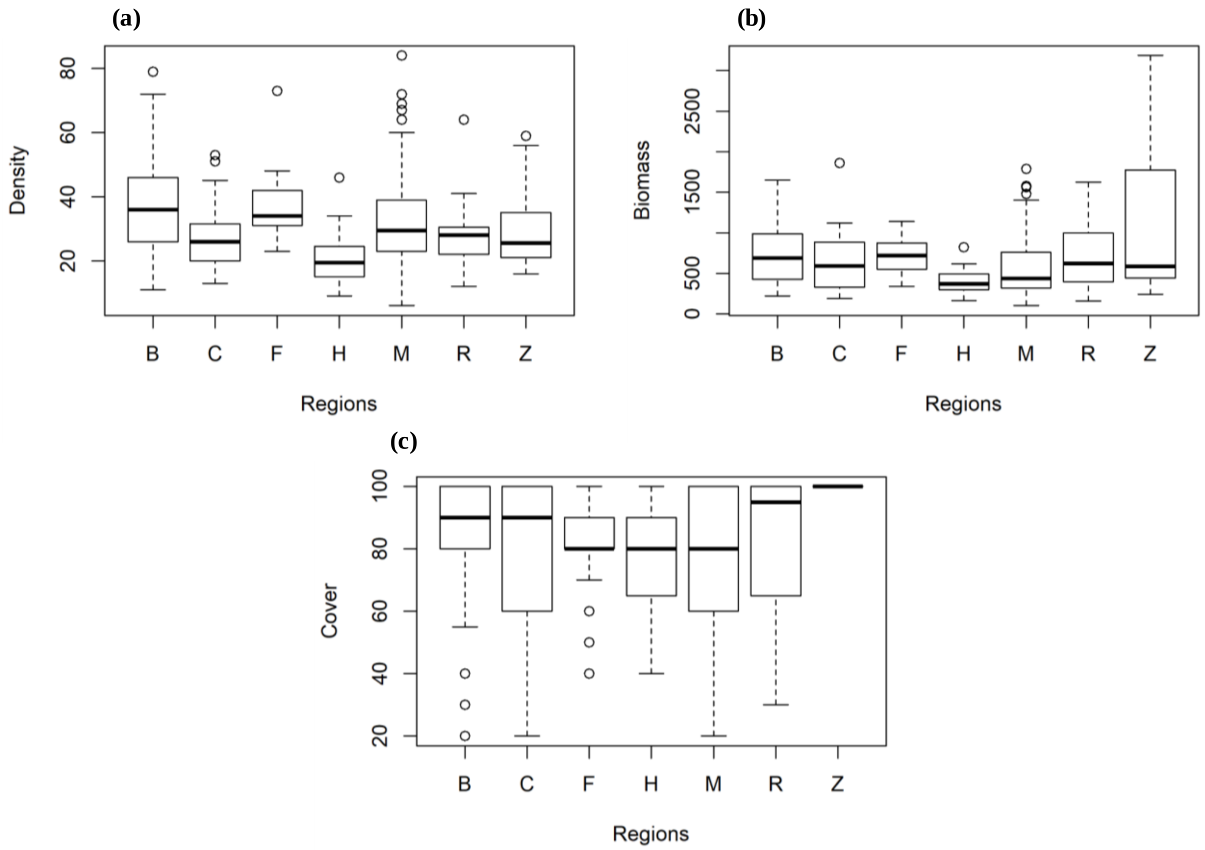

Fig. 2 Boxplot of *P. aquilinum* performance variables: (a) density, (b) biomass and (c) cover in seven regions (codes in Table 1) in Mazandaran province, northern Iran.

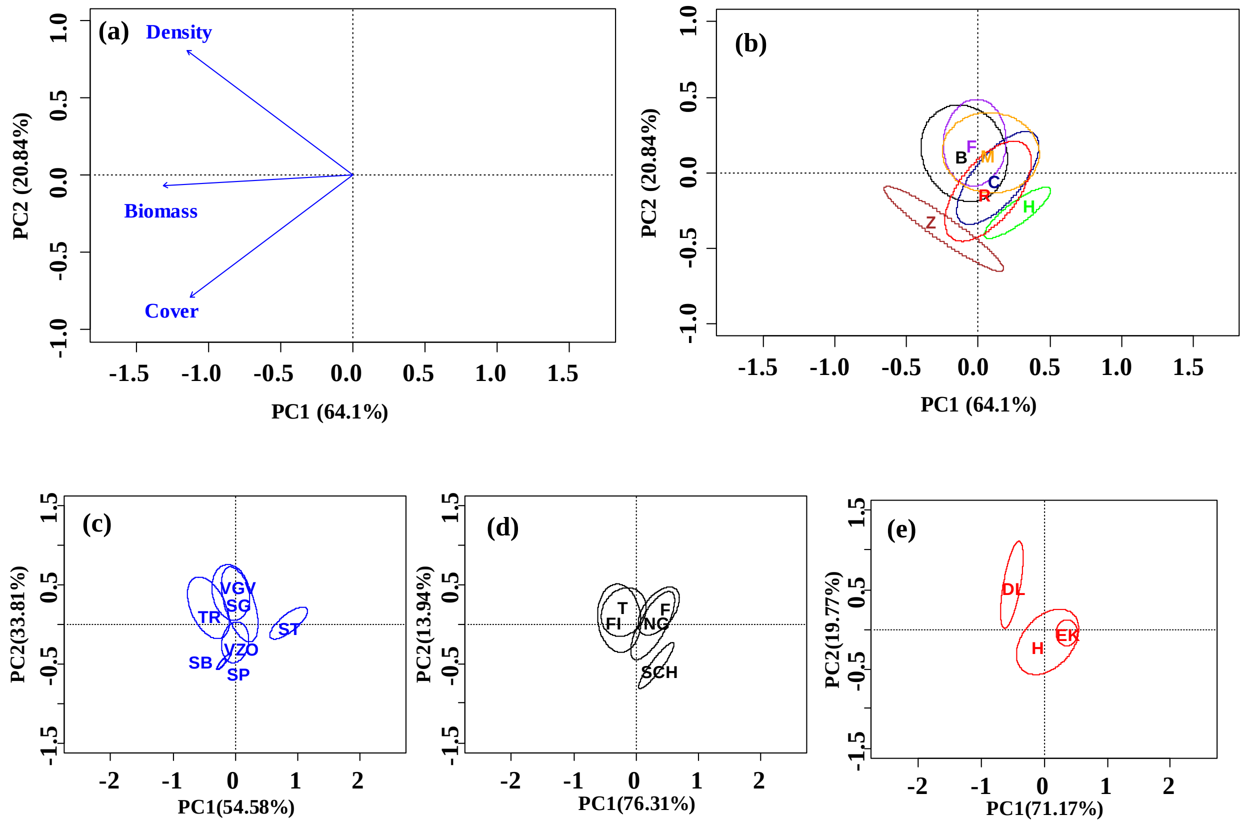

Fig. 3 Principal Component Analysis (PCA) of *P. aquilinum* performance in Mazandaran province, northern Iran and its relationships to regions and sites displayed as standard-deviational ellipses: (a) direction and strength of the three *P. aquilinum* performance variables (biomass, $\log_e(x)$; density, sqrt (x); cover, $\log_e(x)$); (b) seven regions; and 15 sites plotted in three groups according to climate (c) semi-arid-moderate/very cold, (d) moderate-Mediterranean, and (e) moderate-humid.

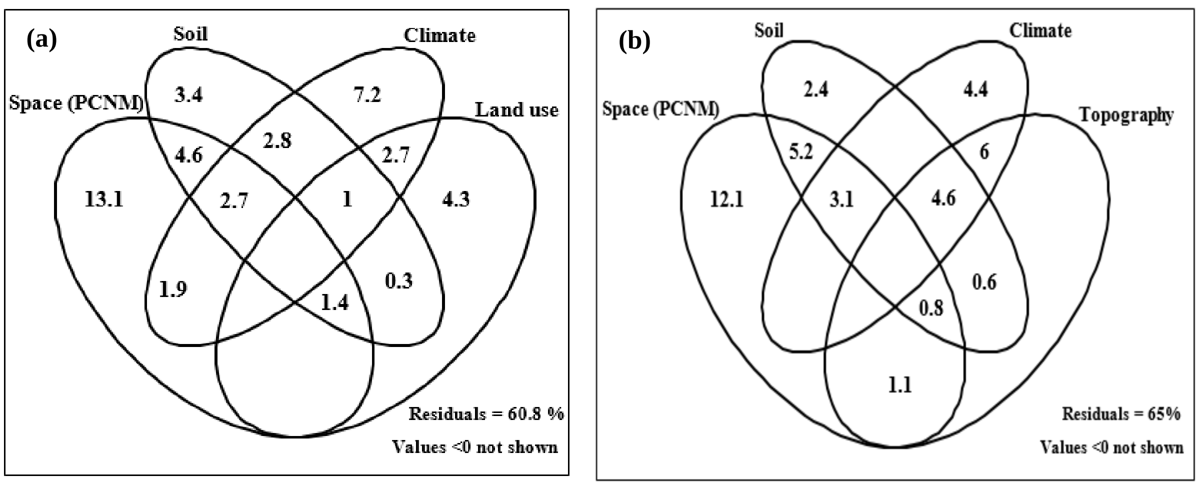

Fig. 4 Proportions of variance explained by soil, climate, land-use, topography, and spatial autocorrelation (space) on *P. aquilinum* performance in Mazandaran province, northern Iran. Values are the proportion contributed to overall R^2 by each fraction.

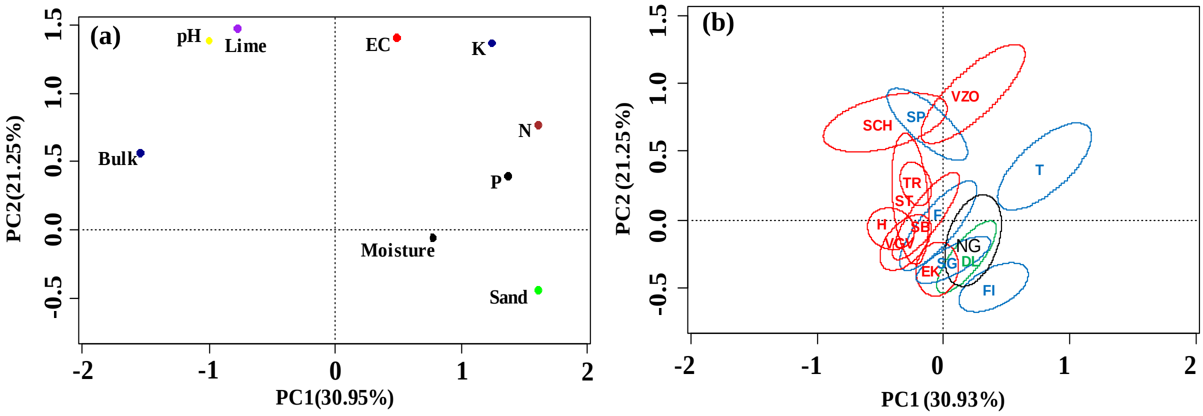

Fig. 5 Principal Component Analysis (PCA) of soil properties (**a**) in sites with different land-uses (codes in Table1), (**b**) invaded by *P. aquilinum* in Mazandaran Province, northern Iran.

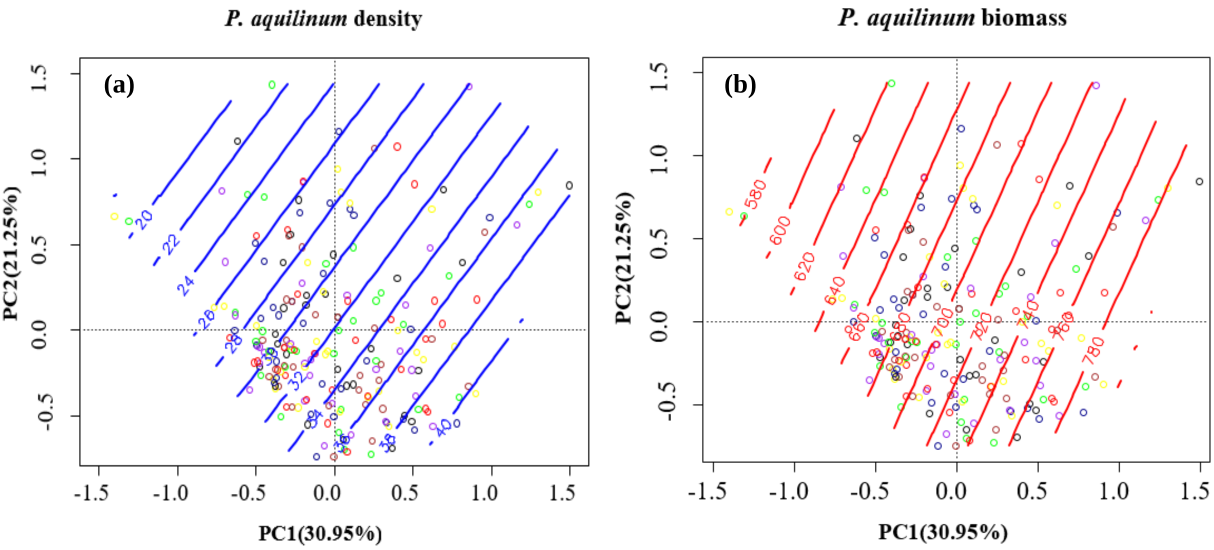

Fig. 6 Principal Component Analysis (PCA) of soil properties and *P. aquilinum* performance. Colorful points present soil parameters in Figure 5: (a) Isolines representing the *P. aquilinum* density (sqrt (x)) and (b) biomass ($\log_e$ (x)) on the first two axes of PCA ordination of soil variables in Mazandaran Province, northern Iran.

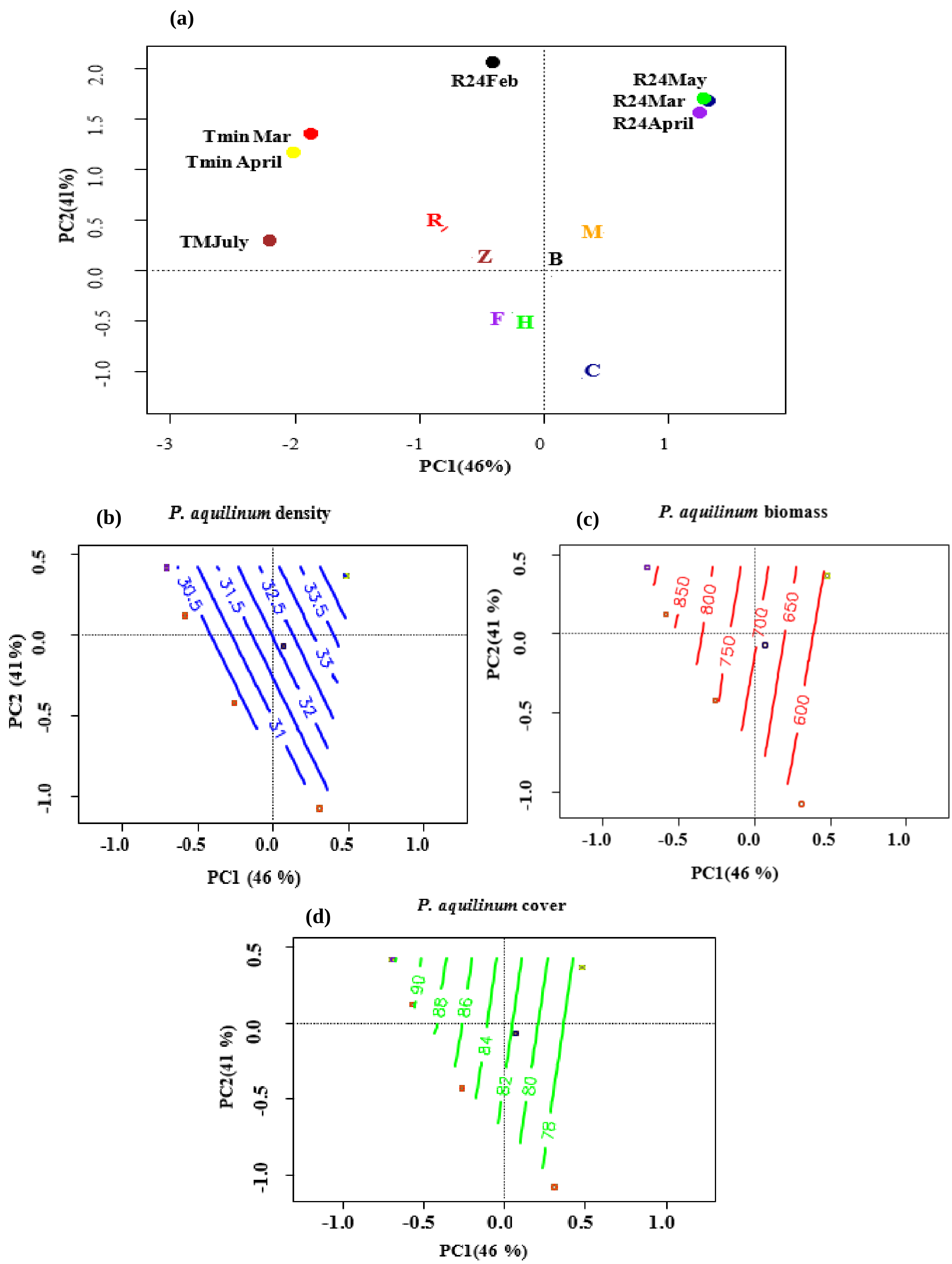

Fig. 7 PCA analyses of climate and *P. aquilinum* performance: (a) climate variables and invaded habitats, (b) Isolines representing the *P. aquilinum* density, (c) biomass, and (d) cover on the first two PCA axes.

Table 1 Detailed description of sampling sites dominated by *P. aquilinum* in Mazandaran Province, northern Iran. Land-use includes abandoned agricultural land (AL), invaded rangeland (IR), plantation forest (PF) and deforestation (DF)

Regions	Sites	Geographical co-ordinates	Area (ha)	No. of transect	No. of plots	Mean temperature (ºC)	Mean rainfall (mm/year)	Elevation (m a.s.l.)	Land-use	Meteorological station (Distance to site (km))
Babol (B)	Tiar (Tr)	36°10'45.58"N 52°29'56.71"E	22	2	20	12	526	1600	IR-AL	Alasht (30 km)
	Sangchal (SG)		17	2	10					
	Filband (Fi)		42	4	60					
Chamestan (C)	Vaz Olia (VZO)	36°16'52.39"N 52°10'13.45"E	1.5	1	10	11	304	2100	AL- PF	Baladeh (30 km)
	Nogme (NG)		13.7	2	25					
Hezar Jarib (H)	Sochelma (SCH)	36°25'38.41"N 53°34'29.59"E	7.6	4	20	12.5	512	1400	AL	Kiasar (20 km)
Marzan Abad (M)	Haris (H)	36°21'55.40"N 51°11'46.23"E	12	14	100	11	544	1900	IR- AL	Siahbishe (18 km)
	Foshkor (F)		11.1	4	20					
	Tale (T)		11	5	30					
Ramsar (R)	Dalkhani (Dl)	36°48'33.10"N 50°38'31.09"E	6.8	2	20	17.5	1170	1500	DF- AL	Ramsar (10 km)
	Ekrasar (EK)		6.7	2	20					
Farim (F)	Vergine Va (VGV)	36°8'11.51"N 53°17'44.64"E	6.6	2	30	12.5	512	800	AL	Kiasar (25 km)
Zirab (Z)	Porkola (SP)	36°11'58.23"N 53°1'33.13" E	5.3	4	15	16	564	650	AL-IR	Polsefid (9 km)
	Matehkola (ST)		4.2	1	15					
	Bahmanan (SB)		2.2	1	20					

Dear Dr Petr Dostál

Editor-in-Chief FG

On behalf of all co-authors I would like to thank you for the valuable comments on our revised manuscript (FOLG-D-20-00022R1). We have taken all suggestions as follow.

We are looking forward to hearing from you.

Yours faithfully,

Jamshid Ghorbani

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COMMENTS TO THE AUTHOR:

l. 201: effect of region on three indices of performance: I do not understand why you provide an explained variance for fixed effect only (marginal R2) in case of density and cover, but explained variance for fixed and random effects (conditional R2) in case of biomass. Please, provide marginal R2 for biomass as well.

Answer: The whole analyses were checked and Marginal R^2 was replaced for biomass.

References: Please, check the format of References in FG and correct (no numbering).

Answer: This was done.