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RESEARCH ARTICLE

Does pollen form follow function? Effects of stigma type, pollination mode and habitat on pollen morphological traits

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Abstract

1. Pollen grains display striking morphological diversity, yet the ecological drivers underlying this variation remain poorly understood.
2. We tested whether pollen morphology reflects adaptation to pollination mode, habitat moisture and stigma type, three ecological factors that impose selective pressures on pollen dispersal, desiccation tolerance and hydration dynamics.
3. We analysed 13 morphological traits for 1151 Central European angiosperm species using phylogenetic regression models. Traits included pollen size and dispersal units, number and type of apertures, coatings and both external and internal features of the exine.
4. Insect-pollinated species produced larger, coated grains with thicker exine layers and more reticulate ornamentation, while wind-pollinated species had smaller, smoother grains with thinner walls and more frequent Ubisch bodies. Species from wetter habitats were more likely to disperse pollen in clumps and showed distinct ornamentation patterns, but several traits hypothesized to reflect harmomegathic responses (e.g. aperture number, furrows, opercula) showed no moisture dependence. Stigma type also influenced pollen form: dry-stigma species had more coatings, thicker exine and more frequent opercula, while wet-stigma species had larger, thinner-walled grains with non-perforate ornamentation.
5. *Synthesis*. Our results support the idea that pollen morphology is functionally adaptive and shaped by distinct phases of pollen performance: dispersal, environmental exposure and stigma interaction. These findings highlight the potential of trait-based approaches for understanding reproductive strategies in angiosperms.

KEYWORDS
function, moisture, morphology, pollen, pollination, stigma, trait

1 | INTRODUCTION

Angiosperm pollen grains display remarkable morphological diversity, varying widely in size, shape, surface ornamentation, wall stratification and the number and arrangement of apertures. This highly taxon-specific diversity has been traditionally used in plant systematics, paleoecology and aerobiology (Erdtman, 1952; Halbritter et al., 2018). However, the relationship between pollen morphology and its ecological functions remains poorly understood (Mander, 2016; Matamoro-Vidal et al., 2016). Bridging this knowledge gap could provide critical insights into how pollen traits influence plant reproductive success, dispersal strategies and adaptation to diverse environmental conditions.

Pollination is an essential step in plant reproduction. Mature pollen grains are released or removed from the anthers and transferred to a conspecific receptive stigma by abiotic (wind and water) and biotic (various groups of animals) vectors, where they hydrate, germinate and produce pollen tubes. Consequently, the conditions under which pollen is transported, received and germinated exert selective pressure on pollen grain morphology to secure successful pollination (Faegri & van der Pijl, 1979; Pacini, 2000; Proctor et al., 1996). To begin with, pollen morphology has been suggested to be shaped by major pollination strategies. In wind-pollinated (anemophilous) plants, the pollen packaging, size, shape and surface sculpturing was hypothesized to improve the pollen aerodynamics and reduce its setting velocity cumulatively resulting in greater dispersal distances of the air-borne pollen (Furness, 2007; Niklas, 1985; Osborn et al., 1991). Specifically, wind-pollinated plants tend to have isolated, comparatively smaller, lightweight, smooth (psilate), dry, pollen grains of spherical shape (Faegri & van der Pijl, 1979). Further, pollen in some wind-pollinated species also shows a tendency toward fewer apertures, a trait that minimizes water loss during aerial exposure (Ackerman, 2000; Hall & Walter, 2011). Contrastingly, animal-pollinated (zoophilous) plants, often produce pollen in large aggregations facilitated by pollenkitt—a sticky, lipid-based compound that promotes pollen clumping (Pacini & Hesse, 2005). High pollen loads on stigmas in zoophilous species drive intense pollen competition, selecting for traits that promote rapid pollen germination. Larger pollen grains and those with more apertures are associated with faster tube growth (Humphrey & Ossip-Drahos, 2018). Additionally, highly complex pollen wall patterns with various decorations on the surface (e.g. spines, ridges, warts and papilla) might enhance adhesion to animal bodies or improve pollenkitt accommodation (Lynn et al., 2020). Such surface features may also function in separating charged pollen grains from floral structures or pollinators (Chaloner, 1986).

Desiccation represents another significant selective pressure shaping pollen morphology, as pollen grains undergo repeated hydration–dehydration cycles throughout their life cycle. Typically, pollen matures in a liquid environment within the anthers, dehydrates before dispersal and rehydrates upon contact with the stigma. Additional hydration–dehydration phases may also occur during pollen presentation or dispersal, depending on the relative humidity of the surroundings (Franchi et al., 2011; Heslop-Harrison, 1979). Harmomegathy, the ability of pollen grains to undergo reversible morphological changes in size and shape in response to hydration and dehydration, has been suggested to be a key adaptation that prevents wall collapse during rapid volume fluctuations (Wodehouse, 1935). This process involves retraction (bending) of the pollen wall during dehydration and extension (stretching) during hydration (Božič & Šiber, 2020). It is a complex mechanism influenced by several morphological traits, with apertures playing a central role (Matamoro-Vidal et al., 2016). In aperturate pollen, elastic apertures fold inward as pollen dehydrates, sealing off the thinnest and most vulnerable parts of the wall, thus reducing water loss (Banks & Rudall, 2016; Božič & Šiber, 2020). Similar protective behaviours are observed in some species with loose exine ornamentation patterns and thin exine layers (Katifori et al., 2010). Additional structural adaptations may further enhance desiccation resistance and prevent wall rupture during hydration–dehydration cycles. These include opercula (i.e. lid-like structures covering apertures; Furness & Rudall, 2003), collumellate or granular wall architectures that resist tensile and compressive forces, respectively (Banks & Rudall, 2016) and prominent sculptural elements, such as club-shaped clavae, which prevent mirror buckling in desiccated pollen (Katifori et al., 2010). Pollenkitt, a lipid-based compound, could also play a role by sealing the pollen surface and minimizing water loss (Pacini & Hesse, 2005). Finally, the dispersal of pollen grains in aggregated units (e.g. pollen dispersal units) was suggested to reduce desiccation risk by limiting the exposure of individual grains to drying conditions (Franchi et al., 2011).

The initial stages of pollen-pistil interactions—pollen adhesion to the stigma and subsequent germination—also impose additional selective pressures on pollen morphology (Edlund et al., 2004). In species with dry stigmas, pollenkitt could facilitate adhesion and, together with a comparatively higher number of apertures and/or thinner exine, is expected to promote faster pollen rehydration by enhancing contact with the stigma surface (Heslop-Harrison, 1979; Pacini & Hesse, 2005). In contrast, species with wet stigmas tend to exhibit pollen grains with fewer apertures and thicker exine, as the grains are directly exposed to stigmatic fluids upon landing and may experience rapid volume expansion. To mitigate the risk of mechanical damage caused by abrupt swelling, pollen grains in such species are expected to be larger, as larger grains are likely to swell more slowly than smaller ones, with a given amount of water having a proportionally smaller effect on their volume (Prieu et al., 2016).

Although the relationships between pollen morphology and its functional roles are intuitive, they have been rarely tested in a formal framework (Mander et al., 2021; Wang & Dobritsa, 2018). Existing studies often focus on a single driver of pollen morphology—such as pollination mode (e.g. Ackerman, 2000; Osborn et al., 2001) or habitat conditions (Ejsmond et al., 2011)—and are frequently limited to specific taxonomic groups (e.g. Ferguson & Skvarla, 1982; Osborn et al., 1991; but see Mander et al., 2021). Importantly, most studies fail to account for phylogenetic relatedness among species, despite evidence that pollen morphology is non-randomly distributed across phylogenies (Erdtman, 1952; Halbritter et al., 2018), and this can distort the results if it remains unaccounted for. This limitation makes it challenging to disentangle ecological adaptations in pollen form from patterns inherited through common ancestry.

Here, we address these gaps by formally testing drivers of pollen trait variation. We analysed a comprehensive dataset of 13 pollen traits capturing functional aspects of pollen dispersal, desiccation tolerance and hydration dynamics for 1151 European angiosperm species. Based on functional interpretations from the palynological literature, we formulated three core hypotheses (H1-3) that connect pollen morphology and anatomy to pollination mode, habitat moisture and stigma type:

> **H1.** *Pollination mode acts as a selective force on pollen traits related to dispersal efficiency.*

We predict that wind-pollinated species should exhibit traits that enhance aerodynamic dispersal and minimize water loss during exposure, such as dispersal of single pollen grains of smaller size, smoother surface ornamentation, fewer apertures, thin pollen walls and minimal coatings. In contrast, insect-pollinated species are expected to produce larger grains with complex ornamentation, more apertures, thicker walls and sticky surface coatings (e.g. pollenkitt), which aid in adhesion to pollinators and support rapid germination on stigmas under high pollen competition. In addition to the traits specified in H1, we also examined several morphological features not directly included in our predictions but potentially relevant to pollen function: furrow type, porate apertures, presence of opercula and Ubisch bodies (Table 1; Figure 1).

> **H2.** *Habitat moisture acts as a selective force on pollen traits related to desiccation resistance.*

We predict that species from drier habitats should exhibit traits that reduce water loss and promote structural integrity during hydration–dehydration cycles, such as the dispersal of relatively large, coated pollen grains in clumps, with fewer apertures, the presence of furrows (or pores) and opercula, and thicker pollen walls with columella. In contrast, species from wetter habitats, where the desiccation risk is lower, are expected to show reduced expression or absence of these features, for example, smaller pollen grains with smooth surfaces, more apertures, absence of furrows or opercula, and thinner walls lacking columella. In addition to the traits specified in H2, we also examined the role of various exine ornamentation types and Ubisch bodies in water balance and structural functions (Table 1; Figure 1).

> **H3.** *Stigma type acts as a selective force on pollen traits related to hydration and germination dynamics.*

We predict that species with dry stigmas should exhibit traits that promote adhesion and controlled pollen hydration, such as the presence of sticky surface coatings and a higher number of apertures. In contrast, species with wet stigmas are expected to produce larger pollen grains with fewer apertures (preferably furrows if present) and thinner walls, traits that reduce the risk of rupture during rapid rehydration in the presence of stigmatic fluids. In addition to the traits specified in H3, we also examined whether other pollen structures, such as pollen dispersal unit, opercula and exine ornamentation vary with stigma type and potentially contribute to hydration control and mechanical stability (Table 1; Figure 1).

2 | MATERIALS AND METHODS

2.1 | Pollen trait data

We focused on the Central European angiosperm flora due to its long history of botanical research, which has produced extensive information on pollen morphology and plant ecology relevant to this study. Pollen trait data were obtained from PalDat, the world's largest open-access database for palynological data (www.paldat.org; PalDat, 2000 onwards). PalDat is maintained by the Division of Structural and Functional Botany at the University of Vienna (www.botanik.univie.ac.at/sfb) and supervised by AutPal, the 'Society for the Promotion of Palynological Research in Austria' (https://autpal.jimdofree.com/). PalDat provides detailed descriptions of pollen morphology and anatomy, complemented by high-quality images captured using high-resolution light and electron microscopy. The database primarily focuses on European plant species but also includes representatives from other regions of the world. As of 03.01.2025, it contains over 36,000 pollen images covering approximately 4500 species from 1800 genera.

For this study, we extracted 13 morphological traits from the PalDat database, describing pollen dispersal units, presence of pollen coatings, pollen size, aperture number and shape (furrowed or porate), presence of opercula and Ubisch bodies, exine thickness and ornamentation (reticulate, sculptured or perforated exine), and presence of columellae in the exine (Table 1). Prior to analysis, the dataset was partially transformed and supplemented with additional pollen trait data. Because the PalDat database contained information on pollen coatings for a comparatively small number of species, we extracted additional trait data from published literature (Halbritter et al., 2018; Hesse, 1979a, 1979b, 1979c, 1980; Pacini & Hesse, 2005). Pollen size, available in PalDat as an ordinal categorical variable, was converted into numeric values by calculating the mean for each category: very small (<10 μm)—6 μm, small (10–25 μm)—18 μm, medium (26–50 μm)—38 μm, large (51–100 μm)—75 μm and very large (>100 μm)—150 μm.

In the PalDat database, pollen grains are classified into seven categories based on the number of apertures, ranging from inaperturate (no apertures) to hexaaperturate (6 apertures). Pollen grains with more than six apertures are grouped into the 'hexaaperturate' category. To determine the exact number of apertures for species in this category, we analysed equatorial-view images from the PalDat database. We counted the visible apertures in each image and doubled the count to account for those not visible. This approach was applied to 113 species in the dataset.

Species with elongated apertures, defined by a length-to-width ratio greater than 2, were classified as having furrows. These apertures positioned either equatorially (colpus) or distally (sulcus) function as structural infoldings that support pollen wall stability during significant volumetric changes. In contrast, species with porate apertures—characterized by their more circular shape and placement either at the equator or evenly distributed across the pollen grain—were treated as a separate group. We assumed that porate apertures

TABLE 1 Overview of the 13 pollen morphological traits analysed in this study, with their proposed functions and predicted associations with pollination mode, habitat moisture and stigma type.

Trait		Definition	Trait data used in the analysis	Trait availability
Pollen dispersal unit		The unit in which pollen is dispersed from the flower	Binary: 0—pollen dispersed as single grains (monads), 1—pollen dispersed in groups of two or more pollen grains (e.g. tetrads, pollinia)	100%
Pollen coatings		Various organic compounds (pollenkitt, primexine matrix, tryphine, elastoviscins and viscins threads) typically produced by the tapetum, deposited on the exine and/or within exine cavities of pollen grains and connecting pollen grains	Binary: 0—pollen grain surface has no coatings, 1—pollen grain surface is covered by an organic compound (e.g. pollenkitt, tryphine) that facilitates adhesion of pollen grains	23%
Pollen size		The length of the pollen largest diameter as measured using a light microscope	Numeric, µm	100%
Aperture number		Apertures are regions on the pollen wall characterized by a morphological and/or anatomical deviation from the surrounding wall, typically involving a reduction or absence of the exine, the outer layer of the pollen wall	Numeric	99%
Furrow sensu lato (synonyms: elongated aperture, furrow, infolding, colpus)		A type of aperture characterized by a longitudinal groove or depression, typically extending along the surface of the pollen grain	Binary: 0—pollen has no furrows, 1—pollen with furrows	100%
Porate aperture		A type of aperture in the pollen wall that is more or less circular, positioned either equatorially or distributed regularly over the surface of the pollen grain	Binary: 0—pollen has no porate apertures, 1—porate apertures are present in the pollen wall	100%
Operculum ('lid'; a part of exine covering an aperture)		A distinct, delimited exine structure that covers an aperture in a pollen grain	Binary: 0—absent, 1—present	61%
Ubisch bodies ('orbicules'; polymorphic sporopollenin-element produced by the tapetum)		Polymorphic sporopollenin elements produced by the tapetum, typically found on the inner wall of anthers or attached to the surface of pollen grains	Binary: 0—absent, 1—present	52%
Exine ornamentation	The pollen surface features and patterns present on the exine	Reticulate exine surface (i.e. presence of network-like structures on pollen wall surface, for example, brochate or striate pollen)	Binary: 0—absent, 1—present	99%
		Sculptured exine (i.e. presence of ornamental elements protruding from exine; e.g. spines, clubs, warts)	Binary: 0—absent, 1—present	99%
		Perforated exine (i.e. pollen wall with holes less than 1 µm in diameter)	Binary: 0—absent, 1—present	99%
Exine thickness		The width of the exine, the outer layer of the pollen wall	Numeric, µm	85%
Columellae		Vertical rod-like supports under the tectum, the outermost layer of the exine	Binary: 0—absent, 1—present	80%

Note: Definitions for pollen traits are adapted from (Halbritter et al., 2018). All pollen traits, except for exine thickness and columellae presence (Beug, 2021), were sourced from the 'PalDat' database (www.paldat.org). 'Trait availability' refers to the proportion of species (out of 1151, representing 100%) for which we could obtain pollen data. Data on habitat moisture and pollination mode were available for all the species.

Function		
Facilitating dispersal	**Protection against desiccation during dispersal (harmomegathy)**	**Hydration on stigma**
Single pollen grains of wind-pollinated species are lighter and set out in the air slowly. Dispesal of pollen grains in groups increase success of relatively specific/targeted insect pollination (Furness, 2007; Niklas, 1985; Osborn et al., 1991)	Dispersal in packages protect single pollen grains (usually recalcitrant) from desiccation (Franchi et al., 2011)	Role unclear
Pollen coatings enhance pollination success in insect-pollinated species as they attract pollinators by odour, pollen organization and providing digestible reward for pollinators. Also, it enables better pollen adhesion to insect bodies (Ackerman, 2000; Dobson & Bergström, 2000; Furness, 2007; Niklas, 1985; Osborn et al., 1991; Pacini & Hesse, 2005; Timerman et al., 2014; Whitehead, 1983)	Pollen coatings protect pollen grains from desiccation in dry habitats. In wet habitats, pollen coatings might protect pollen grains from pathogens (Pacini & Hesse, 2005)	Pollen coatings facilitate pollen adhesion to dry stigma and its rehydration upon it (Edlund et al., 2004; Heslop-Harrison, 1979; Pacini & Hesse, 2005)
Small pollen size reduces setting velocity and thus increase the dispersal distances in pollen of wind-pollinated species (Ackerman, 2000; Faegri & van der Pijl, 1979; Furness, 2007; Niklas, 1985; Osborn et al., 1991; Tejaswini, 2002; Whitehead, 1983)	Plants from dry habitats should have larger grains as they are more resistant to sudden changes in pollen grain volume due to desiccation (Ejsmond et al., 2011)	Plants with wet stigma should have larger pollen grains as they are less responsive to fast swelling (Edlund et al., 2004; Heslop-Harrison, 1981; Pacini & Hesse, 2005; Prieu et al., 2016)
Small number (or lack) of apertures allow for reduced water loss in wind-pollinated species before and during dispersal. Pollen of insect-pollinated species should have a larger number of apertures, because of high pollen loads (i.e. higher competition among germinating pollen grains) deposited on the corresponding stigmas (number of apertures is positively correlated with pollen germination speed). (Ackerman, 2000; Hall & Walter, 2011; Humphrey & Ossip-Drahos, 2018)	Small number (or lack) of apertures prevent water loss in dry habitats. Alternatively, apertures present in pollen wall in large numbers allow for more efficient folding during exposure to dry air (Matamoro-Vidal et al., 2016)	Pollen grains of dry-stigma species have a relatively high number of apertures, to facilitate pollen rehydration. Contrastingly, wet-stigma species have no or a few apertures to prevent pollen wall breakage during relatively fast hydration (Heslop-Harrison, 1979; Pacini & Hesse, 2005)
Furrows support pollen wall stability during strong dehydration of wind-dispersed pollen before and during dispersal	Furrows are beneficial in dry habitats because they support strong changes in pollen grain volume during desiccation. Alternatively, pollen grains in dry habitats might lose water through furrows, thus mainly wetland species should possess this trait	Furrows can support fast changes in pollen grain volume during hydration at wet stigma
Similar to furrows. The differences among the corresponding groups are expected to be less pronounced, as furrows provide much more flexibility to the pollen wall due to their large size and longitudinal orientation		
Operculum should enhance adaptive advantage or furrows and porate apertures to pollen grains as it allows for better regulation of pollen water status (Furness & Rudall, 2003)		
The role of Ubisch bodies is not fully established. Theory suggests that Ubisch bodies could contribute to the reduction of clumping, thereby enhancing the dispersal efficiency by, for example, wind (Huysmans et al., 1998). Additionally, they might assist in the attachment of pollen to pollinators' bodies		
The functional role of reticulate pollen wall surface is not fully understood. Presence of a 'net' made of sporopollenin around the pollen grain could provide more stability to the pollen wall during harmomegathic changes of the pollen grain volume. Thus, we expect this trait to be more prominent in wind-pollinated, dry-stigma species occurring in dry habitats		
Smooth (psilate surface) improves aerodynamic properties of wind-dispersed pollen grains. Ornamented pollen gets attached easier to the pollinators because of the electrostatic forces and better storage of pollen surface coatings that also aid aggregating pollen into larger clumps (Chaloner, 1986; Faegri & van der Pijl, 1979; Furness, 2007; Lynn et al., 2020; Niklas, 1985; Osborn et al., 1991)	Prominent sculptural elements on pollen surface prevent mirror buckling when pollen is desiccated (Katifori et al., 2010)	Unclear
Similar to furrows and pores. The differences among the corresponding groups are expected to be less pronounced, as pores are much smaller and less flexible than furrows and pores (Edlund et al., 2004; Heslop-Harrison, 1981; Pacini & Hesse, 2005)		
Thinner exine in pollen of wind-pollinated species to reduce pollen grain weight. Lower pollen mass increases setting velocity and thus positively affects pollen dispersal distances by wind (Ackerman, 2000; Furness, 2007; Heslop-Harrison, 1979; Lee, 1978; Niklas, 1985; Osborn et al., 1991; Whitehead, 1983)	Thick exine can be advantageous in dry habitats as it protects against rapid desiccation. Alternatively, thinner exine is more flexible and thus can help to accommodate pollen grain volume changes in dry habitats (Katifori et al., 2010)	Shorter hydration times on wet stigma should select for thin exine as it allows for rapid germination (Edlund et al., 2004; Heslop-Harrison, 1979; Pacini & Hesse, 2005)
Collumelate structures provide additional flexibility to pollen grain walls that can be advantageous when pollen experiences rapid changes in its volume (e.g. in wind-pollinated, dry-stigma, xerophilic species; Furness & Rudall, 2003)		

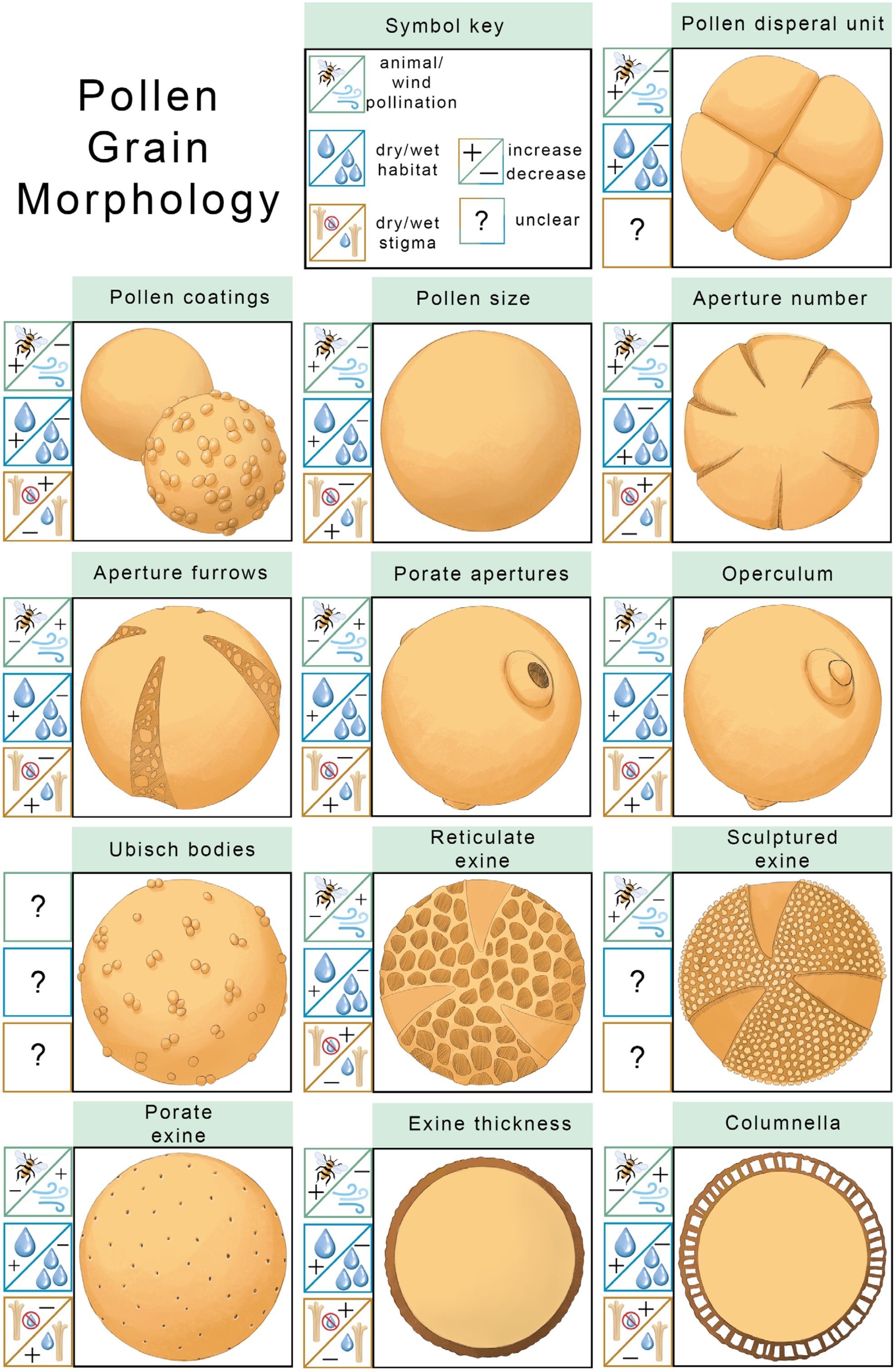

FIGURE 1 Conceptual overview of hypothesized functional relationships between pollen morphological traits and three selective factors: Pollination mode, habitat moisture and stigma type. Each panel illustrates one of the 13 pollen traits analysed in this study, along with predicted trait responses (increase, decrease, no effect, no pattern or unclear) to differences in pollination mode (insect vs. wind), habitat soil moisture (dry vs. wet) and stigma type (dry vs. wet). Predictions are based on published functional hypotheses and compiled in Table 1. Symbols indicate the expected direction of trait-environment associations, while question marks denote uncertainty in functional relevance. Illustrations depict trait morphology schematically and are not drawn to scale.

provide less flexibility to the pollen wall due to their size and uniform distribution.

To classify the diverse range of pollen surface features and patterns observed under a scanning electron microscope—collectively referred to as 'exine ornamentation' (Halbritter et al., 2018)—we grouped species into three broad categories:

1. Reticulate exine, characterized by network-like structures on the pollen wall surface (e.g. brochate or striate patterns).
2. Sculptured exine, distinguished by ornamental elements such as spines, clubs or gemmae and warts protruding from the exine (e.g. bacculate or clavate patterns).
3. Perforate exine, defined by the presence of pores or holes less than 1 μm in diameter in the pollen wall.

Notably, some species exhibit ornamentation features that span multiple categories. For example, the pollen of *Viburnum lantana* (Adoxaceae) is classified as both reticulate and perforate due to its network-like and perforated surface patterns. In such cases, we treated ornamentation as polymorphic and included both trait states in the dataset. Polymorphic species were retained in the analysis by assigning them both states, and these were treated appropriately in models that accommodate multi-state traits.

Data on exine thickness and the presence of columellae were obtained from Beug (2021), based on measurements and observations of acetolysed pollen samples. For species without specific data on exine thickness, average values were estimated using measurements from multiple congeneric species.

2.2 | Species characteristics data

Species habitat moisture was inferred using Ellenberg ecological indicator values for soil moisture (Ellenberg & Leuschner, 2010), which range from 1 (xeric habitats) to 12 (submerged and floating aquatics). These values, developed for Central European flora, reflect the duration and severity of drought stress likely experienced by plants during growth and flowering (Schaffers & Sýkora, 2000). To reduce confounding effects related to plant stature and vertical microclimatic gradients, we restricted the dataset to herbs and shrubs. Pollen presentation height could strongly influence exposure to wind, turbulence and air humidity (Geiger, 1961), and including trees would have introduced systematic differences in pollen dispersal environment unrelated to the ecological factors tested here. This restriction allowed us to focus on pollen traits under broadly comparable near-ground atmospheric conditions.

Next, all species in the dataset were classified as either wind- or insect-pollinated using the BioFlor database (Klotz et al., 2002). Ambophilous species, that is, those pollinated by both wind and animals, were excluded from the study. Furthermore, each species was categorized by stigma type (dry or wet) following Heslop-Harrison (1981), who noted that stigma type is typically conserved at the family level. We therefore assigned stigma type uniformly across all species within a family based on this assumption. While this approach may overlook intra-familial variation, it allowed consistent and tractable trait coding across >1000 species.

2.3 | Data analysis

We web-scraped the entire PalDat database on 01.01.2021 and matched it against species for which Ellenberg indicator values for soil moisture were available. This filtering resulted in a final dataset of 1151 angiosperm species, spanning 500 genera and 96 families most typical for Central Europe. Although this represents less than one-fourth of all angiosperm families, our sample includes representatives from all major clades (e.g. monocots, eudicots, magnoliids) and thus ensures a relatively broad phylogenetic coverage (File S1).

To test the association between pollen traits and ecological predictors while accounting for phylogenetic relatedness, we used phylogenetic generalized linear models implemented in the *phylolm* package (Tung Ho & Ané, 2014). This regression approach was chosen because it accounts for phylogenetic relatedness among species (Paradis & Claude, 2002). Closely related species are more likely to share similar traits than distantly related ones, leading to non-independence of data (risk of pseudo-replication) and potential violations of statistical assumptions in comparative analyses that do not account for such autocorrelation (Revell et al., 2008). Binary traits (e.g. presence/absence of pollen coating or operculum) were modelled using the 'logistic MPLE' method with a binomial error distribution and the Count-based traits (e.g. number of apertures) were modelled using the 'Poisson GEE' method with a Poisson error structure. For continuous traits such as exine thickness, we used models with Gaussian error structure.

The pGLM analyses were based on a phylogeny derived from a large European flora (Durka & Michalski, 2012). Differences in pollen trait values between species with different pollination modes and stigma types were assessed using post-hoc Tukey tests ($p < 0.05$). To improve functional fit, pollen size and exine thickness were ln-transformed prior to analysis. Since exine thickness is positively correlated with pollen size (Lee, 1978), the latter was included as a predictor in the exine thickness model. Model assumptions were checked by inspecting residuals with the *DHARMa* package (Hartig, 2024).

All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022).

3 | RESULTS

The final dataset analysed encompassed 1151 species across 500 genera and 96 families. Among these, 136 species (12%) are wind-pollinated, while the remaining 1015 species (88%) are insect-pollinated. Most of the species, 865 (75%), possess dry stigmas (File S1). This dataset spans the full range of habitat moisture conditions, from dry sandy grasslands to permanently flooded aquatic habitats, with most species found in mesic conditions (File S2).

Data for most pollen traits were available for over 80% of the species in the dataset (Table 1). Information on operculum presence–absence was available for 61% of the species, as this trait occurs only in specific taxa (Furness & Rudall, 2003). Presence–absence data for Ubisch bodies were available for 52% of the species, while pollen coating data were the most limited, covering only 23% of the dataset (File S1).

3.1 | Pollination mode

The phylogenetic generalized linear models revealed statistically significant differences in several pollen traits between wind- and insect-pollinated species (Table 2). Insect-pollinated species had significantly larger pollen grains than wind-pollinated species (back-transformed means: 38.9 µm vs. 30.6 µm, respectively; Figure 2c).

Pollen coatings were more prevalent among insect-pollinated species (0.89 ± 0.05) than wind-pollinated species (0.31 ± 0.09; Figure 2b). Insect-pollinated species also exhibited a significantly thicker exine (back-transformed means: 1.72 µm vs. 1.35 µm, respectively; Figure 2g), more frequent reticulate ornamentation (0.20 ± 0.09 vs. 0.04 ± 0.03; Figure 2e), and a lower frequency of Ubisch bodies (0.42 ± 0.22 vs. 0.65 ± 0.16; Figure 2d). No significant differences between pollination modes were found in pollen aperture number, number of pollen grains per dispersal unit or presence of columella. Additional traits not included in the a priori hypothesis—furrow type, porate apertures and operculum—also showed no significant differences between wind- and insect-pollinated species.

3.2 | Habitat moisture availability

We identified several statistically significant associations between habitat moisture and pollen traits, with patterns differing between wind- and insect-pollinated species (Table 2).

In insect-pollinated species, increasing habitat moisture was associated with smaller pollen grains (slope = −0.006 ± 0.002, $p < 0.05$; Figure 2c) and a higher frequency of clumped pollen dispersed in units (slope = 0.34 ± 0.07, $p < 0.05$; Figure 2a). No significant relationship with habitat moisture was found for pollen coatings in either pollination mode.

Traits related to apertures and wall architecture—including aperture number, furrows, porate apertures, opercula, wall thickness and columella—did not show significant responses to habitat moisture in either pollination mode (Table 2).

TABLE 2 Effects of pollination mode, habitat moisture and stigma type on 13 pollen morphological traits of 1151 Central European species as determined from phylogenetic generalized linear models (model estimates and their standard errors).

	Pollination mode				Stigma	
	Difference between the groups (i.e. model intercepts)		Response to moisture gradient (i.e. slopes of the regression lines)			
Trait	Wind	Insect	Wind	Insect	Dry	Wet
Pollen dispersal unit	0.02 ± 0.01 a	0.01 ± 0.01 a	−0.001 ± 0.10 n.s.	0.34 ± 0.07 *	0.01 ± 0.01 a	0.04 ± 0.01 a
Pollen coatings (presence–absence)	0.31 ± 0.09 a	0.89 ± 0.05 b	0.12 ± 0.17 n.s.	0.02 ± 0.10 n.s.	0.89 ± 0.05 a	0.70 ± 0.14 b
Pollen size (µm)	30.6 ± 1.22 a	38.9 ± 12.82 b	−0.004 ± 0.006 n.s.	−0.006 ± 0.002 *	38.9 ± 1.17 a	46.1 ± 1.8 b
Aperture number	3.42 ± 3.13 a	2.08 ± 2.38 a	0.01 ± 0.04 n.s.	−0.03 ± 0.02 n.s.	2.08 ± 2.38 a	1.17 ± 1.83 a
Furrow (presence–absence)	0.86 ± 0.15 a	0.86 ± 0.15 a	- 0.05 ± 0.09 n.s.	0.01 ± 0.02 n.s.	0.86 ± 0.15 a	0.87 ± 0.16 a
Porate apertues (presence–absence)	0.12 ± 0.15 a	0.12 ± 0.15 a	0.04 ± 0.08 n.s.	0.04 ± 0.03 n.s.	0.12 ± 0.15 a	0.12 ± 0.15 a
Operculum (presence–absence)	0.26 ± 0.15 a	0.16 ± 0.15 a	−0.18 ± 0.14 n.s.	−0.03 ± 0.04 n.s.	0.16 ± 0.15 a	0.03 ± 0.04 b
Ubisch bodies (presence/absence)	0.65 ± 0.16 a	0.42 ± 0.22 b	−0.35 ± 0.11 *	0.03 ± 0.03 n.s.	0.42 ± 0.22 a	0.45 ± 0.24 a
Exine ornamentation (presence–absence)						
Reticulate exine	0.04 ± 0.03 a	0.20 ± 0.09 b	0.40 ± 0.15 *	−0.04 ± 0.04 n.s.	0.20 ± 0.09 a	0.13 ± 0.08 a
Sculptured exine	0.03 ± 0.04 a	0.06 ± 0.07 a	−0.35 ± 0.26 n.s.	0.12 ± 0.10 n.s.	0.06 ± 0.07 a	0.06 ± 0.07 a
Perforated exine	0.39 ± 0.09 a	0.33 ± 0.06 a	0.07 ± 0.08 n.s.	−0.07 ± 0.03 *	0.33 ± 0.06 a	0.50 ± 0.07 b
Exine thickness (µm)	1.35 ± 0.39 a	1.72 ± 0.48 b	−0.001 ± 0.001 n.s.	−0.001 ± 0.001 n.s.	1.72 ± 0.48 a	1.45 ± 0.39 b
Columella (presence/absence)	0.94 ± 0.04 a	0.95 ± 0.03 a	0.33 ± 0.30 n.s.	−0.05 ± 0.07 n.s.	0.95 ± 0.03 a	0.94 ± 0.04 a

Note: Different letters indicate significant differences between two groups ($p < 0.05$; Tukey post-hoc test). Asterisks indicate regression slopes significantly different from zero ($p < 0.05$).

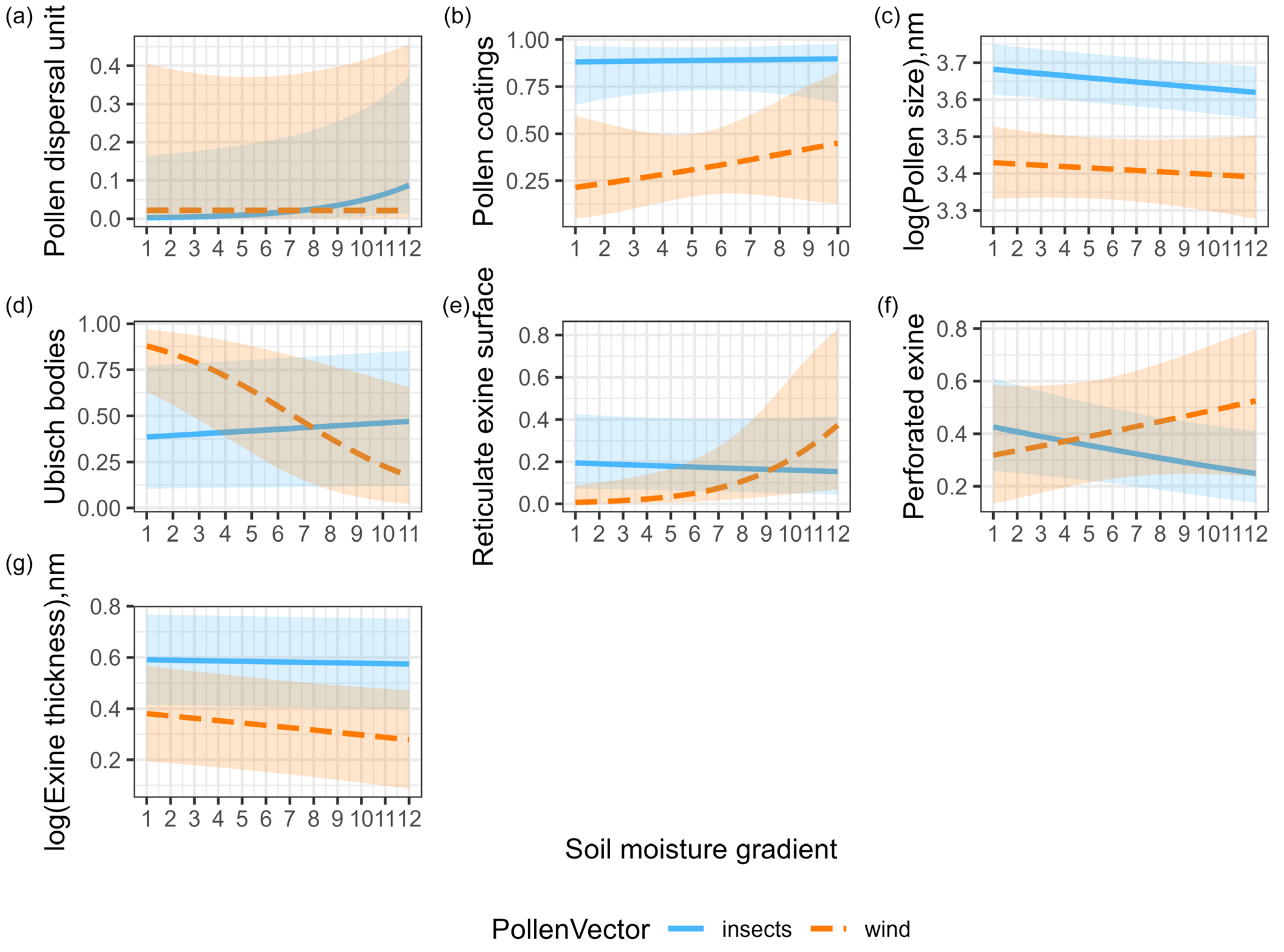

FIGURE 2 Variation in selected pollen traits along the habitat moisture gradient for wind- and insect-pollinated species, based on phylogenetic generalized linear models (only statistically significant results, $p < 0.05$). Traits include: (a) probability of pollen being dispersed in clumps, (b) probability of pollen coatings on the pollen surface, (c) pollen size, (d) probability of Ubisch bodies on the pollen surface, (e) probability of a reticulate exine surface, (f) probability of a perforate exine surface and (g) exine thickness (log-transformed). Soil moisture gradient expressed in Ellenberg ecological indicator values. Shaded areas represent 95% confidence intervals.

Among the additional traits examined, wind-pollinated species showed a significant decrease in the frequency of Ubisch bodies along the moisture gradient (slope = −0.35 ± 0.11, $p < 0.05$; Figure 2d), and a significant increase in reticulate exine ornamentation (slope = 0.40 ± 0.15, $p < 0.05$; Figure 2e). In insect-pollinated species, increasing habitat moisture was associated with a reduced frequency of perforate exine ornamentation (slope = −0.07 ± 0.03, $p < 0.05$; Figure 2f).

3.3 | Stigma type

Our analysis revealed statistically significant differences in several pollen traits between species with dry and wet stigmas (Table 2). Species with dry stigmas produced significantly smaller pollen grains (back-transformed means: 38.9 μm vs. 46.0 μm, respectively; Figure 3b) and exhibited a higher frequency of pollen coatings (0.89 ± 0.05 vs. 0.70 ± 0.14; Figure 3a). Dry-stigma species also had thicker exine layers (back-transformed means: 1.72 μm vs. 1.45 μm; Figure 3e) and a higher probability of possessing opercula (0.16 ± 0.15 vs. 0.03 ± 0.04; Figure 3c). In contrast, species with wet stigmas were more likely to exhibit non-perforate exine ornamentation (0.50 ± 0.07 vs. 0.33 ± 0.06; Figure 3d).

No significant differences were observed in pollen dispersal units, aperture number, presence of furrow or porate apertures, Ubisch bodies or other pollen surface ornamentation types.

4 | DISCUSSION

Our study reveals clear associations between pollen morphology and plant interactions with abiotic and biotic environments. Traits such as the ability to be dispersed in clumps, the presence of pollen coatings, pollen size, operculum, Ubisch bodies, various exine ornamentation types and exine thickness exhibit non-random patterns among species differing in pollination mode, habitat soil moisture

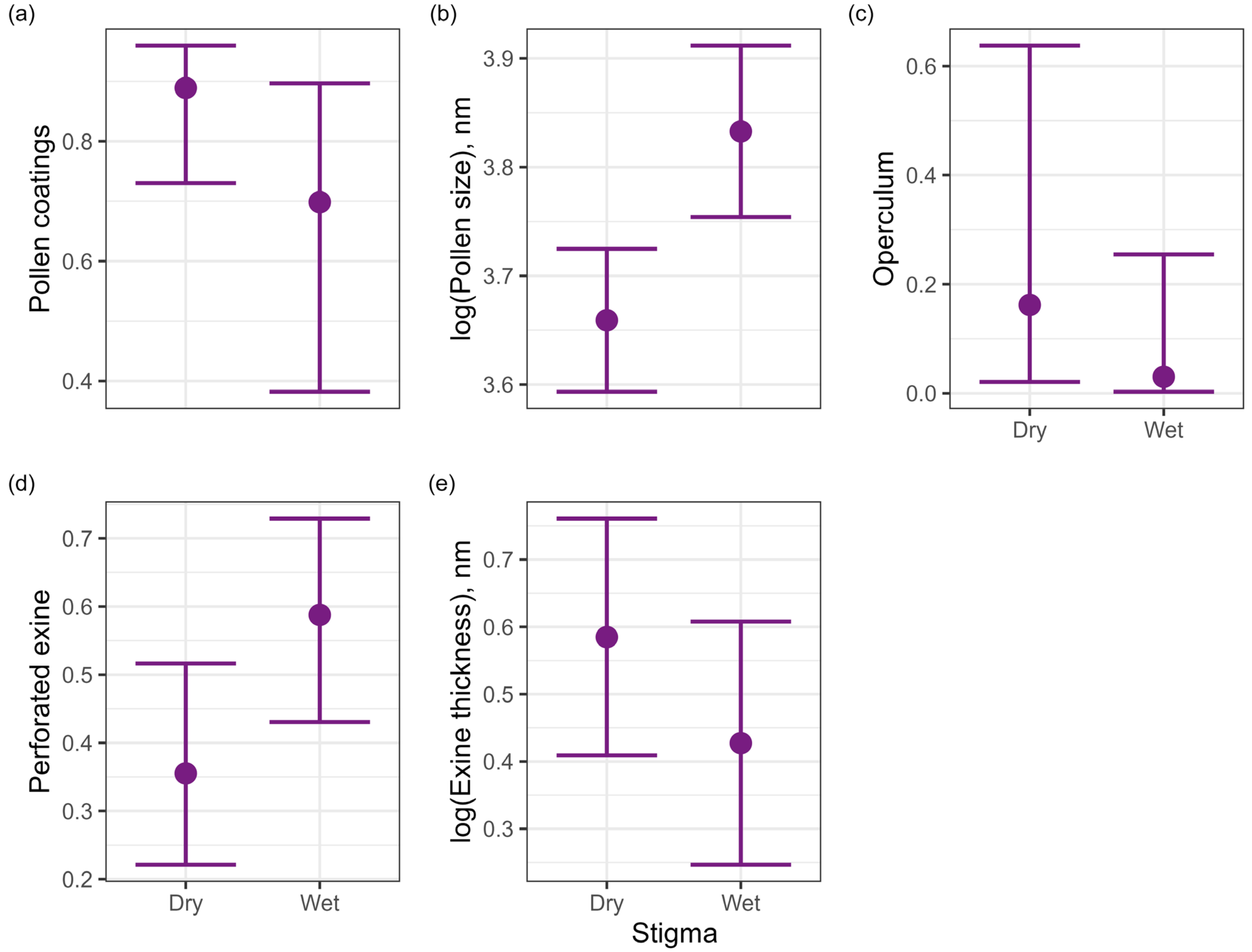

FIGURE 3 Differences in selected pollen traits between species with dry and wet stigmas, based on phylogenetic generalized linear models (only statistically significant results [$p < 0.05$] are shown). Error bars represent 95% confidence intervals. Traits include: (a) probability of pollen coatings on the pollen surface, (b) pollen size, (c) probability of operculum on the pollen surface, (d) probability of a perforate exine surface and (e) exine thickness (log-transformed).

and stigma type. These findings underscore the functional significance of these traits in plant reproduction and reaffirm that pollen form follows function, with specific traits being associated with particular pollination modes and environments (Franchi et al., 2011; Heslop-Harrison, 1979; Mander, 2016).

4.1 | Pollination mode acts as a selective force on pollen traits related to dispersal efficiency

Pollen morphology differed systematically between wind- and insect-pollinated species, supporting the hypothesis that pollination mode acts as a selective force on traits related to dispersal efficiency. Insect-pollinated species were more likely to produce larger pollen grains with thicker and reticulate exine and frequent occurrence of pollen surface coatings such as pollenkitt. The presence of pollen coatings in insect-pollinated species has been associated with improved pollen adhesion to pollinator bodies and reduced loss during grooming, due to the formation of cohesive pollen clumps that increase the likelihood of efficient delivery of multiple grains to multiovulate ovaries of zoophilous species (Dobson & Bergström, 2000; Pacini & Hesse, 2005; Timerman et al., 2014). Larger grain size has been shown to correlate with increased germination rates and faster pollen tube growth, thereby supporting reproductive success under conditions of intense pollen competition common in zoophilous species (Humphrey & Ossip-Drahos, 2018; Tejaswini, 2002). The significantly thicker exine in insect-pollinated species further provides essential structural stability and protection against mechanical stress during physical manipulation by pollinators and repeated hydration–dehydration cycles (Heslop-Harrison, 1979; Lee, 1978).

By contrast, wind-pollinated species exhibited traits consistent with selection for enhanced aerodynamic performance and reduced desiccation risk during aerial transport that usually occurs over much longer distances as compared to insect-pollinated species. These included smaller grain size, thinner exine without ornamentation and absence of pollenkitt. Smaller, smoother grains are known to reduce settling velocity, increasing the potential dispersal distance of airborne pollen (Ackerman, 2000; Niklas, 1985; Whitehead, 1983). Thinner exine walls may contribute to lower pollen mass, further supporting aerodynamic efficiency and may be sufficient in species where physical protection is less critical than in animal-mediated systems. Additionally, wind-pollinated species showed a higher frequency of Ubisch bodies (small, sporopollenin-based structures on the surface of the tapetum-derived pollen wall), which have been hypothesized to limit pollen clumping and promote the release of individual, free-floating grains (Huysmans et al., 1998). This supports the idea that Ubisch bodies contribute to maintaining pollen dispersibility by minimizing adhesion among grains in wind-dispersed taxa.

No significant differences between pollination modes were observed for several traits included in the hypothesis, including aperture number and number of pollen grains per dispersal unit. Similarly, additional traits not originally included in the hypothesis—furrow type, porate apertures, operculum and columella—also did not differ between wind- and insect-pollinated species. These results suggest that some widely used pollen morphological and anatomical features used in palynological classification may not consistently reflect ecological differentiation at the level of broad pollination syndromes. Alternatively, our broad trait categorization (e.g. binary traits for furrow apertures or columella) and pollination mode might have been too coarse to capture more nuanced selective pressures on pollen morphology. In particular, using aperture number may have masked important functional variation, as such data do not account for trait size relative to pollen grain surface—an aspect likely critical for pollen flexibility, hydration dynamics and dispersal efficiency (Katifori et al., 2010; Prieu et al., 2016; Wang & Dobritsa, 2018). Consequently, future studies should incorporate quantitative measurements (e.g. aperture-to-grain surface ratios) and refine pollination mode classifications to better assess the functional significance of these traits. In particular, distinguishing among different pollinator groups rather than relying on broad pollination syndromes may reveal finer-scale adaptations in pollen morphology. Integrating biomechanical or physiological experiments would further clarify how structural traits translate into functional performance under different dispersal scenarios.

4.2 | Habitat moisture selects pollen traits related to desiccation resistance

Previous research has suggested that habitat moisture should strongly influence pollen morphology by selecting for traits that optimize desiccation resistance under various air humidity levels pollen grains can experience during presentation and dispersal (Franchi et al., 2011; Heslop-Harrison, 1979; Wodehouse, 1935). Specifically, traits such as fewer apertures, the presence of furrows or pores, opercula and thick exine walls with columellate or granular architecture have been proposed to reduce water loss and improve structural stability during hydration–dehydration cycles (Banks & Rudall, 2016; Božič & Šiber, 2020; Furness & Rudall, 2003; Katifori et al., 2010; Matamoro-Vidal et al., 2016). Surface coatings such as pollenkitt may further minimize water loss by sealing the pollen surface (Pacini & Hesse, 2005), while aggregated dispersal units could reduce desiccation risk by shielding individual grains from direct exposure (Franchi et al., 2011). Our results provided only partial support for these predictions. Among insect-pollinated species, those from drier habitats produced significantly larger pollen grains, which may promote desiccation resistance by reducing the surface-area-to-volume ratio and slowing rehydration (Prieu et al., 2016). Contrary to our prediction, clumped pollen dispersal was more frequent in insect-pollinated species from wetter habitats. This pattern may reflect reproductive strategies adapted to lower pollinator abundance or visitation frequency in aquatic settings (indicator values of 10–12 correspond to aquatic environments; Figure 2a), where transferring larger pollen loads in fewer visits could increase reproductive success (Murail et al., 2025). Although we found no significant association between pollen coatings and habitat moisture—likely due to limited data coverage for this trait (available for only 23% of species)—we speculate that clumped pollen in aquatic species may be facilitated by sticky surface compounds such as pollenkitt. In addition to their role in pollination, these coatings could help reduce pollen loss to splash water during pollen presentation. Finally, among additional traits not explicitly included in our hypothesis, wind-pollinated species from drier habitats had a lower frequency of perforate exine ornamentation, a trait that may help maintain structural integrity under dry conditions (Božič & Šiber, 2020; Katifori et al., 2010).

Surprisingly, our findings did not support the hypothesis that habitat moisture influences key pollen traits associated with harmomegathy. Traits such as aperture number, furrows, pores and opercula showed no significant relationship with habitat moisture, despite long-standing assumptions about their role in desiccation tolerance (Franchi et al., 2011; Heslop-Harrison, 1979; Wodehouse, 1935). This unexpected result may partly reflect limitations of our binary classification of the pollen traits, which may obscure important variation in their functional expression (see above). Additionally, the selective pressures shaping harmomegathic responses may act at finer microenvironmental scales than those represented by our dataset. The ecological indicator value for soil moisture used in our study reflects the overall environmental conditions a plant experiences throughout the growing season, whereas pollination typically occurs under the most favourable conditions for fertilization, when drought stress is low. For instance, species from dry sandy grasslands often flower in early spring, when soil moisture and air humidity around the flower remain relatively high. Also, the timing of flowering and pollen dispersal (e.g. seasonality, daily fluctuations in humidity) were not explicitly considered, though it likely affects pollen function. Therefore, future studies should incorporate more precise environmental data reflecting the actual conditions pollen experiences during dispersal and pollination, such as microclimatic humidity or direct measurements of floral microenvironments. Bridging this ecological gap with real-time studies of pollen performance under natural humidity regimes will help disentangle correlations from causation in trait-environment relationships (van der Kooi et al., 2019; Williams et al., 2016). Applying such approaches across diverse habitats and floras, especially in tropical or arid regions, will also be essential to assess the generality of patterns detected for the Central European flora.

4.3 | Stigma type selects pollen traits related to hydration and germination dynamics

Our study identified stigma type as a functionally significant driver of pollen trait variation, providing one of the first broad-scale, phylogenetically informed tests of its impact on pollen morphology. In agreement with our expectations, pollen from dry-stigma species was more frequently coated with sticky surface compounds such as pollenkitt. These coatings likely promote effective adhesion to the relatively dry stigma surface and facilitate controlled hydration, two critical prerequisites for successful germination in the absence of free stigmatic fluid (Edlund et al., 2004; Heslop-Harrison, 1981; Pacini & Hesse, 2005). In addition, dry-stigma species produced significantly smaller grains with thicker exine walls and a higher likelihood of possessing opercula. These traits likely enhance mechanical stability and delay hydration until compatible interactions with the stigma are established (Banks & Rudall, 2016; Lee, 1978). In contrast, species with wet stigmas presenting a continuous film of stigmatic fluid produced larger pollen grains with a lower frequency of perforate exine ornamentation, thereby confirming our hypothesis. These traits may promote rapid and uniform hydration upon contact with the wet stigma surface, while minimizing structural risk of rupture due to uncontrolled water uptake (Edlund et al., 2004; Pacini & Hesse, 2005). The significantly thinner exine observed in wet-stigma species likely further supports accelerated germination in fully hydrated pollen grains. Cumulatively, these findings demonstrate that stigma type exerts a measurable influence on specific pollen traits related to adhesion and hydration control. These post-dispersal interactions complement the selective pressures imposed by dispersal mode and environmental conditions, underscoring the complex and multi-phase nature of pollen adaptation in flowering plants.

However, despite these clear differences, we found no significant variation in several other traits predicted to vary with stigma type, including aperture number, aperture morphology (furrows or pores), Ubisch bodies, pollen dispersal units or columella. This absence of pattern may be attributed to the strong evolutionary conservation of pollen traits across angiosperm lineages. Evolutionary history itself can strongly shape pollen morphology and may constrain the extent to which ecological selection can modify certain traits. Several pollen characters, particularly aperture number and aperture architecture, are deeply conserved across angiosperm lineages and often exhibit strong phylogenetic signal (Furness & Rudall, 2003; Wang & Dobritsa, 2018). Consequently, the absence of ecological associations for some traits in our analyses may reflect evolutionary constraint rather than a lack of functional relevance. Recent macroevolutionary analyses of pollen morphospace indicate that pollen diversity is structured by lineage-specific developmental trajectories and historical contingency, with many clades occupying restricted regions of morphospace over long evolutionary timescales (Jardine et al., 2022). Jardine et al. further proposed that the comparatively narrow function of pollen—successful transfer of male gametes—may reduce selection for continued morphological experimentation within lineages, thereby reinforcing phylogenetic conservatism in certain traits. Together, these insights suggest that functional adaptation in pollen morphology operates within boundaries imposed by evolutionary history, with ecological selection acting more readily on some trait dimensions than on others that are developmentally or phylogenetically canalized.

4.4 | Study limitations and avenues for future research

Despite the broad taxonomic coverage and phylogenetic regression analyses employed here, several limitations constrain the scope and generality of our findings. First, our analysis is restricted to herbaceous and shrubby species of the Central European flora and therefore does not capture pollen trait syndromes characteristic of woody plants, particularly canopy-forming trees. Tree species experience fundamentally different dispersal and humidity regimes due to greater pollen release height and stronger wind exposure, which may select for distinct pollen morphologies (Geiger, 1961; Niklas, 1985). Consequently, our conclusions should be interpreted as applying primarily to low-stature angiosperms in temperate ecosystems. More broadly, the study focuses on a temperate subset of global angiosperm diversity. Although the Central European flora spans a broad gradient from dry lowland habitats to alpine environments, it lacks Mediterranean, polar and tropical systems, where pollen is exposed to more extreme thermal and desiccation stresses (Franchi et al., 2011; Heslop-Harrison, 1979). Pollen trait syndromes associated with long-term viability under severe drought, heat or freezing conditions are therefore likely underrepresented, and the generality of our findings beyond temperate floras remains to be tested.

A further limitation concerns the uneven availability and coarse resolution of several pollen traits in existing databases. Traits such as pollen coatings, opercula and Ubisch bodies are documented for only a subset of species in PalDat, reducing statistical power to detect ecological associations, while many characters were necessarily treated in a simplified, often binary form. Although such simplification captures major functional distinctions relevant to dispersal and exposure (Ackerman, 2000; Furness, 2007), it may obscure functionally important variation and partly explain the absence of ecological associations for some traits (Wang & Dobritsa, 2018).

For example, extreme pollen packaging systems such as pollinia and massulae (most prominently found in orchids) exhibit additional wall adaptations that cannot be adequately described using broad trait categories. These systems are rare in the Central European flora and fall outside the scope of a comparative, trait-based analysis, but their functional morphology warrants targeted, lineage-specific investigation.

More generally, current large-scale palynological datasets remain strongly biased toward morphological descriptors, whereas physiologically important pollen traits, such as desiccation tolerance, longevity, hydration kinetics, cell wall plasticity and the biochemical composition of the pollen coat, are rarely available at the species level (Franchi et al., 2011; Pacini & Franchi, 2020). This imbalance limits our ability to link pollen morphology directly to performance across dispersal and post-dispersal environments and underscores the need to integrate comparative trait analyses with physiological measurements and microclimatic data at the scale of pollen presentation and dispersal (Geiger, 1961). Incorporating quantitative descriptors of aperture geometry and wall biomechanics would further enable more mechanistic tests of long-standing functional hypotheses (Katifori et al., 2010; Prieu et al., 2016).

Finally, pollen morphology is shaped not only by ecological selection but also by intrinsic developmental and biophysical processes that may constrain or bias the range of phenotypes available to selection. Experimental and theoretical work has shown that aspects of exine architecture can emerge through self-assembly processes during wall formation, driven by colloidal interactions and physicochemical properties of sporopollenin deposition (Hemsley et al., 1994; Hemsley & Gabarayeva, 2007). More recent biophysical models demonstrate that diverse pollen wall patterns can arise from modulated phase separations in the primexine, generating ornamentation without requiring direct selection on individual structural features (Radja et al., 2019). Together with evidence for strong phylogenetic conservatism in several pollen traits (Furness & Rudall, 2003; Jardine et al., 2022), these findings indicate that functional adaptation in pollen morphology operates within boundaries imposed by developmental and evolutionary constraints.

AUTHOR CONTRIBUTIONS

Sergey Rosbakh and Massimo Nepi conceived the idea and designed the methodology. Sergey Rosbakh and Maximilian Pichler compiled the pollen trait dataset and analysed it. Sergey Rosbakh wrote the manuscript with inputs from all authors.

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CONFLICT OF INTEREST STATEMENT

Sergey Rosbakh is an Associate Editor of '*Journal of Ecology*', but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70290.

DATA AVAILABILITY STATEMENT

Please add the in-text citation for example, the data used for the analysis and associated R-code are available at Zenodo: https://zenodo.org/records/15115700 (Rosbakh, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

File S1. Data availability for plant characteristics and pollen traits across the phylogeny of 1151 Central European angiosperm species included in the study.

File S2. Distribution of 1151 Central European angiosperm species included in the study along the habitat moisture gradient.

File S3. Species composition, pollen trait coverage and data availability for 1151 Central European angiosperms.

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