The colors of heath flowering – quantifying spatial patterns of phenology in Calluna life-cycle phases using high-resolution drone imagery

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Abstract

Recent developments in high-resolution ecosystem mapping using unmanned aerial vehicles (UAV) open up promising perspectives for the monitoring of fine-scale vegetation patterns and ecological functioning. In this study, we examine the potential of UAV imagery to track the structural composition and related phenological traits of the dwarf shrub Calluna vulgaris on a former military training area. On a European Natura 2000 heathland site, habitat management is shown to be evaluated on the basis of flowering dynamics and reproductive recovery as a proxy of functional changes that are generated after fire destruction. In particular, we utilize true color camera information and digital surface models to determine the spatiotemporal evolution of Calluna life-cycle phases and flowering phenology 2 years after controlled burning. A stepwise methodological framework is presented that extracts Calluna pixels, spatially separates juvenile and mature life-cycle phases, differentiates between generative and vegetative shoot extension and finally quantifies proportions of flowers, fruits and vegetative growth in two consecutive peak flowering periods. We show that Calluna life-cycle phases can be spatially differentiated in pioneer, building and mature phases in UAV imagery. In the juvenile phase, regeneration from germination is low (<10%) and sprouting from the stem base dominates recovery patterns after fire management. The study further reveals that the distribution of flowering and fruiting during peak flowering time is spatially heterogeneous with high variations between years. In the fire unaffected mature phase, proportions of flowers and fruits are reduced indicating a decrease in reproductive capacity of unmanaged Calluna stands. A phenological phase shift is detected from flowering to fruiting that is related to an increase of Calluna growth height. The study shows that the functional patterns of growth and reproduction can be mapped for heathland ecosystems using simple true color drone cameras.

Introduction

Plant phenology as a manifestation of the temporal change of growth and reproduction in the plant life-cycle has been recognized as an ecological key indicator of ecosystem processes and dynamics. In particular, variations within phenophases such as flowering time and length are regarded as fingerprints of climate change (e.g. Root et al. 2003; Menzel et al. 2006; Cleland et al. 2007; Körner and Basler 2010), biodiversity loss (Wolf et al. 2017), extreme weather events (Rich et al. 2008; Jentsch et al. 2009) and geographical time-space phenomena and biotic interactions in general (Fenner 1998; Schwartz 2003). In that respect, the production of leaves, flowers and fruits is directly affected by climate and nutrient gradients (Brun et al. 2003; Seghieri et al. 2009; Cardoso et al. 2012), plant community composition...
(Feinsinger 1987), the distribution and preferences of pollinators and seed predators (Levin and Anderson 1970; Bosch et al. 1997; Elzinga et al. 2007) and the intra-annual amount of available energy, particularly in temperate zones and higher latitudes. The direct link between phenological aspects and various ecosystem properties enables the prediction of long-term development trends and enhances the understanding of ecological systems (Pau et al. 2011). For this reason, phenological phase characterization can act as a key component for the monitoring and assessment of habitat management and ecological restoration in applied nature conservation (Pywell et al. 2003; Morellato et al. 2016; Buisson et al. 2017). However, interactions between plant life-history events and phenological traits are complex and are also controlled by phylogenetic constraints (Kochmer and Handel 1986). Further research is required in order to specify landscape-specific responses of small-scale patterns of phenophase variability that are not influenced by broad-scale geographic gradients.

Spatial patterns of plant phenology are successfully described by means of remote sensing, which mainly uses medium to coarse spatial resolution satellite data (250 m to 8 km) with a high temporal resolution. Due to spatial resolution constraints, most existing studies have thereby focused on large-scale patterns of spatiotemporal vegetation dynamics (e.g. Garonna et al. 2014; Hamunyela et al. 2013; Heumann et al. 2007; Karkauskaite et al. 2017; Ma et al. 2013; Piao et al. 2006; Ricotta and Avena 2000; Wang et al. 2016). Only a few studies present regional-based plant phenology mapping (1 m–30 m pixel size), which is used for the quantification of browning trends in boreal forests (Sulla-Menashe et al. 2018), early detection of tree disturbances (Latifi et al. 2018), monitoring agro-ecosystems (Lobell et al. 2003; Pan et al. 2015) or evaluating green-up shift (Debinski et al. 2000; Fisher et al. 2006; Vrieling et al. 2017). In most cases, multi-temporal spectral phenology curves are indirectly used for habitat type discrimination (Forster et al. 2011; Féret et al. 2015), tree species identification (Dymond et al. 2002; Hill et al. 2010), crop type classification (Peña-Barragán et al. 2011; Forster et al. 2012) or estimation of floristic diversity (Vina et al. 2016). Detailed phenophase delineations are limited in satellite imagery in which spectral signatures spatially point to vegetation vitality that can solely be related to aspects of greening and senescence in aggregated pixels. In fact, it has been shown that fine-scale phenological variations are mainly driven by individual species distributions that cannot be mapped with recent satellite imagery (Klosterman et al. 2018). This is because the spatial resolution of open earth observation data does not allow for the identification of single plants and their individual components such as leaves or blossoms. A distinct differentiation between leaf emergence, flowering and fruit formation at the species level is, however, essential for assessing the ecological implications of spatial phenophase variability. Recent developments in sensor technology mounted on unmanned aerial vehicles (UAV) open up promising potentials for detailed ecosystem investigations (Anderson and Gaston 2013; Díaz-Delgado et al. 2019). For the first time in research history, the structure of ecological entities can be quantified from individual plants down to the leaf scale. While this new level of information has been studied for species level classification in natural habitats (e.g. Laliberte et al. 2010; Fraser et al. 2016; Michez et al. 2016; Lu and He 2017), only few investigations have been made into the mapping of plant phenological traits (Berra et al. 2016; Klosterman et al. 2018).

This study aims to develop a UAV-based method for quantifying spatial patterns of flowering phenology for the dwarf shrub heath species Calluna vulgaris (L.) HULL (henceforward referred to as Calluna) on a former military training area in northeast Germany. Dominant stands of Calluna form a habitat type that is protected by the European habitat directive within the Natura 2000 network (EU, 1992). Characterized by Calluna communities as their most widespread vegetation, heathlands are considered to be one of the main anthropo-zoogenic landscapes in Europe since the end of the 18th century (Gimingham and De Smidt 1983; Webb 1998). Nowadays, heathland areas are dramatically decreasing due to abandonment of use, nitrogen deposition and high vulnerability to climate change (Heil and Bobbink 1993; Diemont et al. 1996; Webb 1998; Fagúndez 2012). For this reason, active habitat management such as controlled burning, regular mowing and/or grazing is required in order to maintain Calluna and establish a favorable conservation status of the heathland ecosystem. Fire management in particular systematically creates a spatial continuum of different Calluna life-cycle phases (LCP) (Gimingham 1972). These comprise stages of seedling establishment and vegetative resprouting from post-fire recovery as well as unaffected mature stands (Matt Davies et al. 2010). Each LCP is thereby determined by characteristic phenological traits which evolve by natural succession. In order to monitor arising functional patterns for an ecological evaluation of the actual fire management success, this study presents a methodological framework for the spatial derivation of LCP-related phenology.

In this study, we aim to show that phenophase variability of Calluna can be mapped quantitatively in form of proportions of vegetative shoots, flowers and fruits using high-resolution UAV imagery captured by a simple RGB-camera. Our study addresses the following questions:

a Can heterogeneous Calluna stands be spatially distinguished in UAV imagery according to different life-cycle phases? Can this technique be used to evaluate the success of fire management?
Can flowering phenology be quantitatively described on the basis of UAV RGB (red-green-blue) color values? What characteristic phenophase proportions can be derived for different Calluna stands?

What is the structure of spatially inherent phenological differences and what are the implications for site-specific ecological research?

This study provides a step-by-step procedure for deriving Calluna LCPs and quantifying related phenology within the flowering period for a spatially explicit mapping of phenophase proportions.

Materials and Methods

Study Area and Data

Landscape and habitat characteristics

The study area belongs to Kyritz-Ruppiner Heide, a former military training area in the northwest of the federal state of Brandenburg, Germany (Fig. 1). Situated within the North European Plain, it was predominantly formed by outwash sedimentation during the last glacial/interglacial transition period. As a consequence, the overall area of approximately 120 km² is covered by nutrient-poor, acidic sandy soils. This leads to Podzols under forested areas and acid Arenosols, Cambisols and Regosols with only a thin (<10 cm) humus layer in open land areas (IUSS Working Group, 2006). The area has an average altitude of 80 m NHN, an average annual air temperature of 8.3°C and an annual rainfall average of 560 mm. The vegetation is subject to seasonality of the temperate zone with a continental climate. During the decades of military use between 1952 and 1992, an intense disturbance regime of tree cutting, mechanical destruction of humus and vegetation layers, explosions and fires created wide open sandy landscapes. These were extensively populated by Calluna vulgaris dwarf shrub heather in natural succession. Today, the area is considered one of the largest unfragmented heathland areas in Europe and has

Figure 1. Study area and heathland show fields for the RGB mapping of flowering phenology on 12 September 2017; RGB color values for image pixels that include different phenological states of Calluna. RGB, red-green-blue.
been designated as a Site of Community Importance (DE2941302) under the European Natura 2000 network directive, which foresees the protection of the heathlands as its own habitat type (HT 4030; EU, 1992).

**UAV imagery**

UAV images were captured on 12 September 2017 and 10 September 2018 using a fully autonomous DJI Phantom 4 Pro drone with an integrated gimbal-mounted camera that recorded the reflected solar spectrum onto a 8-bit Red-Green-Blue (RGB) filtered silicon-photodiode. Flight altitude was 80 m above ground level with an image overlap of 80% along and across track. An area of 15.93 ha (246 images) was covered in 2017 and 16.97 ha (268 images) in 2018, resulting in flight times of 39 and 41 min, respectively. In order to obtain a 3D point cloud based on internal GPS coordinates and matching points (Lowe 2004) in the image overlap, the image blocks were processed on the Pix4D cloud web server by applying a structure from motion (SfM) photogrammetry process chain (Strecha et al. 2008; Küng et al. 2011). A digital surface model (DSM) was subsequently interpolated on a triangulated irregular network on the basis of 3D point coordinates. Finally, the RGB image pixels were re-projected to the surface grid to derive geo-referenced orthomosaics with pixel sizes of 2.05 cm in 2017 and 2.12 cm in 2018, respectively. The image mosaics were co-registered using manually selected ground control points and finally clipped to the test area boundary shape (Fig. 1) covering 8.31 ha in total. In order to minimize color distortion caused by varying leaf transmittance and different surface types under sunlit/shadow conditions (Curran 1980; Leblon et al. 1996), the flights were conducted under fully stratus cloud coverage. In addition, an automated in-flight white balancing was performed.

**Test area and reference data**

The test area for the UAV overflight was situated in the south of Kyritz-Ruppiner Heide training area (53°3′8.49″N; 12°40′17.43″E). The vegetation is dominated by dwarf shrub heather (*Calluna vulgaris*) on a soil matrix that is partly covered by bryophytes (e.g. *Ceratodon purpureus, Polytrichum piliferum, Hypnum jutlandicum, Dicranum spp.*) and lichens (e.g. *Cladonia spp.*, *Cetraria spp.*). The heather is over layered by individual birch (Betula pendula) or Scots pine (Pinus sylvestris) trees. The heather coverage is irregularly interpenetrated by grass species (e.g. *Corynephorus canescens, Agrostis capillaris, Carex arenaria, Deschampsia flexuosa*), mainly in young stands. In early spring 2016, the area was managed by controlled burning in order to preserve *Calluna* dominance. Following destruction through fire management, young *Calluna* stands establish themselves via vegetative regeneration from the stem base and through seed germination. Burning has additionally left patches of old stands that were not affected by the fire and hence form dense patterns (see dark areas in Fig. 1) of closed canopies.

In September 2017 and 2018, the flowering phase of *Calluna* was sampled at the end of peak flowering period (25–50% flowering individuals) (Jentsch et al. 2009) on the dates of UAV overflight missions. In 2017, flowering was pronounced, resulting in a typical purple landscape facet. Following a dry period between May and July of the following year, flowering was significantly lower in 2018. In total, 67 individual *Calluna* plants and 30 background classes (soil, litter, bryophytes, lichens, grass) were mapped in the field. For *Calluna*, the percentage proportion of shoots stocked with flowers, fruits, buds, mixed flower-fruit as well as green shoots lacking any flowering phase was determined. Additionally, we digitized 477 *Calluna* individuals on 25 plots in the field in order to delineate boundaries between plants. Every plant and background entity was located on the geo-referenced ortho-mosaic. The final locations were digitized in form of spatial polygons covering the whole extent of the terrestrial sampling unit.

**Phenophase differentiation**

Phenophases were differentiated according to the proportions of three main phases at the shoot level of individual *Calluna* plants. The phenological extrema are therein defined as 100% where all shoots are fully stocked with A) flowers, B) fruits or C) only leaves. These three main phases can be characterized by distinct spectral signatures in the visual part of the solar-reflected spectrum (VIS: 350–700 nm) (Fig. 2). In particular, field spectroscopic measurements reveal that A) flowers maximize blue-red reflectance, B) fruits maximize red reflectance and C) leaves are dominated by green reflectance maxima. All possible variations of phenophase proportions between 0 and 100% are consequently given through color transitions that vary within the Red-Green-Blue color space. This basic assumption was used to relate phenophase proportions mapped in the field to the image RGB color space that cover the same VIS wavelength area. The reference image colors were extracted as median RGB values covered by the \( n = 67 \) terrestrial polygons for *Calluna* individuals.

In order to represent maximum color chromaticity that can be related to phenophase characteristics, brightness effects caused by angular reflection (luminance) of incoming solar irradiation on rough surfaces (varying leaf angles, shadowing) need to be corrected in image pixels.
For that purpose, the brightness component of the 8-bit image RGB color cube (achromatic axis) (Fig. 1) was removed by normalizing every RGB grey value into an rgb chromaticity space:

\[
\begin{align*}
    r &= \frac{R}{R+G+B} \\
    g &= \frac{G}{R+G+B} \\
    b &= \frac{B}{R+G+B}
\end{align*}
\]

The resulting rgb color distribution of \( n = 67 \) reference plants can be mapped within a ternary diagram that represents a Maxwell color triangle with additive color proportions \( r + g + b = 1 \) (Fig. 2). Ternary diagrams are pseudo-3D representations that can be described by 2D Cartesian coordinates. On the basis of a Cartesian affine transformation, a reference color space was generated placing the rgb extrema (A–C) at the edges with \([x,y]\) coordinates of \((A[1,0], B[0,0], C[0,1])\). Chromaticity extrema were defined as the maximum distance between one color value and the others that represents the three main phenological phases in the reference samples. Finally, a regular grid with corner coordinates of lower right \([1.3,-0.3]\) and upper left \([-0.3,1.3]\) and a cell size of 0.01 was spanned over the final color space for predicting color transition between the reference samples.

For each reference sample, the fractional cover of flowers, fruits and vegetative shoots were modeled within the reference color space. A trend surface analysis (Gittins 1968; Agterberg 1984) was applied to describe the transition of each phenophase as a trend in the \(x,y\) plane. This was followed by a residual Kriging (Odeh et al. 1995; Hengl et al. 2007) to adjust the trend for residual variations. The residuals were modeled using variogram estimates used for an automated selection of an optimal variogram model (Hiemstra et al. 2009).

For prediction purposes, the RGB color transformation was applied to the UAV imagery data for both years using the same transformation model and RGB colors as derived for the reference samples collected in 2017. In order to reduce color-balancing effects that produce relative channel-specific variations of RGB grey values between 2017 and 2018, an empirical line correction was applied to 2018 imagery. For that purpose, manually selected reference points on stable bare ground pixels...
were regressed between data for both years. The resulting regression lines for each RGB channel were applied to the 2018 imagery in order to harmonize both color spaces.

Calluna life-cycle segmentation

Phenology characterization is based on phenophase proportions per plant unit area. Here, the LCP concept is an intrinsic plant unit which characterizes different age and growth states of Calluna (Watt 1955; Gimingham 1972). Age classes can be described as plant heights from a normalized digital surface model (nDSM) (see supplementary A.2.1) that indicate the temporal development of plant growth after burning. Pixel heights do not uniquely mark LCPs of plants since they are assigned to multiple branch and leaf layers. Hence, they represent complete height profiles of n-pixels (Fig. 3) that were segmented into spatial clusters to represent coherent plant units as LCPs. It was assumed that (1) single plants are determined by 3-dimensional conical height profiles of varying peak heights that intersect with adjacent profiles in valley structures and (2) closed canopies of same heights are additionally distinct through different canopy colors that represent varying phenophases of individual plants (Fig. 3). Canopy colors were clustered using a k-means unsupervised classification of phenophase proportions per pixel (input from section 3.1). The borders between clusters were digitized as line structures assigned to \( h = 30 \) cm and subsequently subtracted from the nDSM to provide enhanced valley structures. Finally, an inverse watershed algorithm implemented in the system for automated geoscientific analyses (SAGA) (Conrad et al. 2015) was applied to the enhanced nDSM to cluster spatial segments.

Watershed segments are concepts from geographical analyses of pixel topology in digital imagery (Beucher and Meyer 1992; Roerdink and Meijster 2000). Image segments are therein derived as basin clusters dived by linear watersheds. For each segment, the maximum height was determined and grouped into three height classes \( h_c \) that characterize Calluna LCP according to (Watt 1955): (1) pioneer phase \((h_c \leq 10 \) cm\) (2) building phase \((h_c > 10 \ cm \leq 39 \ cm)\) and (3) mature phase \((h_c > 39 \ cm)\).

Spatial statistics of Calluna flowering phenology

Phenophase proportions are based on median RGB values per LCP segment that are projected into the rgb reference color space for each respective phenophase category (proportions of flower, fruit and vegetative shoots). In order to determine the phenological status of a LCP segment, the three categories were assigned to the dominant phenophase expression. Single phenophase dominance was defined if one category exceeds the other two categories by \( >15\% \) proportion per LCP segment. The remaining plant units were determined by dominating phenophase transitions which were extracted as the maximum sum of two categories. In consequence, phenophase distribution can be described in six dominance expressions that characterize the main phenological aspect of a LCP segment (Fig. 4). The spatial distribution of dominant phenophase expressions were described for all LCP segments on the test field within each year for 2017 and 2018.

Results

Phenophase distribution

The proportion of flowers, fruits and vegetative shoots for reference plant samples shows distinct patterns of transition originating from the three defined corners of the reference color space (Fig. 5). Normalized color values of main rgb extrema indicate the dominance of one phenophase at the corner coordinates. An overlap of visible phenophase surfaces is directed towards the center of the rgb space where mixed rgb color proportions represent a coexistence of different phenophases per reference plant unit. Vegetative shoots reach a maximum of 80% of the proportion within the defined color space, since no plant was found across all reference samples that exhibited only vegetative shoots during 2017 sampling. The mean deviation between reference point proportions and the modeled grid values can be described using the root mean squared error (RMSE). The best surface fit is given for fruit proportion (RMSE = 11.69%) and vegetative shoots (RMSE = 12.18%). Due to an observed mixture between

Figure 3. nDSM height profiles of plant units in UAV imagery; pixel heights are not distinct, since they can be assigned to different plants (red line \( h_{\text{max}} \)); watershed definition for plant unit segmentation on the basis of two assumptions: (1) valley structures and (2) phenophase variations. nDSM, normalized digital surface model.
flowers and withered flower petals, a trend surface-based approximation of pure flowering parts is reduced in accuracy (RMSE = 14.89%).

For visualization purposes, an area of 12 × 10 m was selected that represents a typical distribution of pioneer and building phase Calluna on a soil matrix after fire management (Fig. 6 show field A). The soil is partly covered with crusts of lichens and bryophytes that are further layered with stones and branch residuals. Phenophase proportions are only mapped for pixels that were classified as Calluna in 2017 and 2018 (see supplementary A.2.2). Phenophase patterns represented as RGB pixel reflectance values show variation between both years of sampling, as well as within one sampling period.

In 2017, distinct spatial patterns of fully flowering shoots and fruits could be observed. Leaf signals of vegetative shoots are mostly overlapped with fruit phases, whereas fully flowering shoots exhibit a smaller amount of green reflectance. There are areas of uniquely dominating phases that represent pure pixels of leaf, flower or fruit reflectance. In 2018, the flowering phase is strongly reduced and the fruit phase disappears almost completely, as indicated by an overall increase in green shoot reflectance. An increase in bright bare ground pixels can additionally be observed due to a decrease of lichen and bryophyte cover following a dry period between May and July of 2018.

**Calluna life-cycle segments**

Plant unit segments are spatially aggregated height and color information that inherit structural and phenological traits of Calluna individuals. Structural traits are expressed as growth characteristics. The underlying assumption here is that during plant growth, the peripheral extension growth is expanded in consecutive LCPs. In consequence, small growth heights are correlated to small patch diameters leading to a decreased segment area which can be shown summarizing all mapped segments (Fig. 7). Thereby, the median segment area is significantly higher for increasing height classes that are finally assigned to Calluna LCPs.

In total, 356,131 spatially distinct LCP segments could be derived for the 8.31 ha test area. It could be shown that the number of LCP segments systematically deviated from the number of Calluna individuals that were digitized in the field. Within the segment area, the number of individuals is constantly underestimated by an average

![Figure 4](image_url). Phenophase dominance per life-cycle segment as used for spatial statistics of phenophase variability; corresponding terrestrial phenophase representation visualized by field photos.

![Figure 5](image_url). Trend surface-modeled transition of phenophase proportions on the basis of gridded rgb reference color space; iso-surfaces are based on phenophase proportions of reference points that represent median proportions of terrestrial plant samples.
rate of 45.81% with a standard deviation of 12.47%. This underestimation is defined as the averaged aggregation error that can be applied to the segment number to correct for the Calluna population size, resulting in approximately 650,000 Calluna individuals on the test site.

Phenological traits are mapped for each LCP segment in which the spatial distribution of the three modeled phenophase proportions are represented (Fig. 8 show field B). Here, heights are clearly discriminated between homogenous patterns of old stands and structural variations within young stands. The resulting segments reflect spatial variations in flowering phenology across all LCPs. Different phenological phases can emerge at the same time, as seen for segments with mixed phenophase proportions. Such mixtures are mostly formed by the coexistence of green shoots or flowers and fruits on different shoots. Nevertheless, the alteration of plants dominated by flowers or fruits is spatially more distinct. In particular, fully flowering plants are mainly clustered in northeast direction of deciduous trees, whereas the fruit phase is strongly related to mature stands. While segments that are mainly dominated by one phenological phase can be spatially visualized as phenophase dominance, transition areas forms mixed patterns of specific dominance expressions.

Spatiotemporal statistics

The phenology of Calluna significantly varies between the two sampling years (Fig. 9). In 2017, 56.6% of LCP segments were dominated by the generative phase (sum of fruit, flower and fruit-flower), whereas in 2018 only 5.7% of fruit dominance could be mapped. In general, the 2018 data shows a strong shift from generative to vegetative shoot extension, with no detectable flowering dominance. While flowers and fruits are still present, they are usually present alongside green shoots (46.7%), whereas in 2017 mixed stands are reduced (39.6%).

Phenophase statistics were separately generated for segments falling into consecutive height classes that represent Calluna LCP (Fig. 10). The generative phase reaches its...
peak in the pioneer (61.4%) and building phase (60.9%), whereas flowering is reduced during the mature phase (39.4%). Young stands are more likely to be dominated by purely flowering or fruiting shoots. A phenological phase shift appears between the pioneer phase, which is mainly characterized by flowering, and the building phase, where fruit formation has already been developed to a greater extent. Pioneer stands further exhibit slightly higher amounts of segments with purely vegetative shoot extension (4.6%). Between young and old stands there are two general visible trends that indicate (1) a decrease in generative dominance and (2) an increase in mixed proportions of fruit and vegetative shoot transition.

**Discussion**

**The distribution of Calluna life-cycle phases after fire management**

On the basis of aggregated height and shape statistics from UAV imagery, spatial segments of three different Calluna LCPs could be mapped on the test site. Two
years after fire management, the result shows an expected diversification and a restoration of early Calluna life-forms. In contrast, abandoned heaths are successively controlled by degradation processes which are characterized by a predominance of mature and degenerated Calluna phases (Miller and Miles 1970; Henning et al. 2017). In this case, the regeneration of Calluna after controlled burning is realized via seed germination or vegetative propagation. Generally, sprouting from the stem base of remaining plants after fire is known to create faster and vigorous shoot extension (Kayll and Gimingham 1965). However, the capacity of vegetative regeneration declines in plants older than 15 years at the time of burning (Lovat 1911; Kayll and Gimingham 1965), and seed germination is required for a dense rejuvenation. The effectiveness of fire management for the restoration of degenerated Calluna thus depends on the establishment of seedlings, which is additionally determined by characteristics of the implemented fires themselves (such as duration and temperatures), post-fire substrate type or soil moisture (Whittaker and Gimingham 1962; Grant 1968; Nilsen et al. 2005; Matt Davies et al. 2010).

On the test site, only 8.7% of the young individuals captured by LCP segments are estimated at <10 cm, indicating low rates of seed germination over two consecutive years. Most of the mapped LCP segments belong to the building phase (71.3%), while 20% of Calluna stands were not affected by the fire. It is important to mention that in this study the building phase mostly showed an early onset within the regeneration life-cycle after resprouting, whereas the pioneer phase is related to germination. In fact, during regeneration after burning the pioneer phase can be completely bypassed, while the building phase needs only 2 years to become established within primary life-cycle of Calluna (Gimingham 1988; Schellenberg 2017). In that respect, UAV imagery is capable of monitoring post-fire recovery dynamics for an evaluation of Calluna regeneration and rejuvenation success. To this end, height statistics of LCP segments are used to sequence regeneration forms, assuming different growth rates between seedlings (1–5 cm) and sprouting (up to 12 cm) per year (Bannister 1964; Lindholm 1980; Alonso et al. 2001).

**Phenology of Calluna life-cycle phases**

In the present case study, fire management lead to an increase in reproductive capacity of Calluna, which is characterized by a profuse flower and fruit production during the pioneer and building phases following a humid summer season in 2017 (Fig. 9). Dominant phenophase proportions clearly differ between mature phases that remained unaffected by fire management and young stands. In the mature phase, the dominance of flowering and fruiting shoots is reduced by over 20% and substituted by an increased vegetative shoot extension. This result reflects a common trend of mature Calluna stands in which reproduction is reduced and flowering zones along individual shoots become shorter due to the aging process (Miller and Miles 1970; Gimingham 1972; Legg et al. 1992). Miller 1979 shows that flower production increased up to 4–10 years following fire management, until complete ground cover was achieved. In the present study, reproduction is constant within the juvenile LCPs; however, there is a visible phase shift between flowering and fruit development. In the pioneer phase the flowering
phase appeared to be more dominant than during the building phase, while flowers were almost completely absent during the mature phase. In this case, the monotemporal UAV image acquisition does not allow for the distinction whether flower onset is late or whether flowering time is extended for young Calluna stands.

The fact that flowering onset or length is modified under individual structural traits such as LCP or reproductive origins has been described for herbaceous species (Sun and Frelich 2011). However, this phenomenon has not yet been discussed in literature for Calluna. There is evidence that functional responses such as flowering intensity of Calluna after nitrogen addition varies between different LCPs (Meyer-Grünefeldt et al. 2015a; Taboada et al. 2018). This creates a link between patterns of flowering and the distribution of functional diversity that has recently been gaining importance in ecological research, since the ecosystem conservation highly benefits from holistic biodiversity assessment that integrates functional aspects into phylogenetic and taxonomic approaches (Petchey and Gaston 2006; Devictor et al. 2010; Lausch et al. 2016). Applied nature conservation may thus benefit from further multitemporal UAV studies that examine the relationship between phenophase dynamics and functional traits in order to better characterize the ecological performance of Calluna after fire management.

**Spatiotemporal patterns of phenophase variations**

The distribution of Calluna flowering is spatially heterogeneous considering a snapshot in time during the phenological flowering cycle in 2017. It could be shown that flowering and fruiting phases spatially coexist with individual variations that cover the entire range of possible proportions between flowering, fruiting and vegetative shoots. The phenomenon of asynchronous flowering time has been addressed by various studies for co-occurring species, between populations and, to a lesser extent, between individuals of one species (e.g. Gross and Werner 1983; Primack 1985; Dieringer 1991; Devaux and Lande 2010). It can generally be stated that an evolutive diversification of flowering time increases the reproductive success of individuals due to a reduction in competition for pollinators (Waser 1979; Rathanck and Lacey 1985; Totland 1993), avoidance of herbivores and fruit predation (Fenner 1998) or in response to climatic constraints (Dieringer 1991; Hall and Willis 2006). It has been shown that plant populations inherit a sufficiently large amount of genetic variance which enables a rapid adaptation of flowering to varying local conditions (Burgess et al. 2007; Elzinga et al. 2007; Franks et al. 2007). However, existing processes and patterns of phylogenetic adaptation to form phenological variation by means of natural selection are still not clearly understood for natural populations (Kochmer and Handel 1986; Pors and Werner 1989; Ehrén 2015). Tracing spatial patterns of UAV plant unit phenology in time could contribute to a better understanding of phenological assortative mating by mapping mating opportunities. In that respect, research into the intensity, prevalence and consequences of mating between individuals within similar flowering times is still in its infancy (Fox 2003; Weis et al. 2005).

The methodology developed in this study can further be used to map spatial patch dynamics of flowering aspects that determine the availability of habitats for insect pollination. By this means, point measurements from field experiments can be enhanced towards spatially explicit information on selective pressure by pollination. Imaging spectroscopy has recently been applied to delineating different pollination types in grassland communities (Feihlauer et al. 2016), and peak flowering is used to discriminate plant species patches in UAV imagery (Cruzan et al. 2016). In that respect, a correlation of floral traits and abiotic factors such as soil fertility, water regime or shadowing effects has yet to be implemented for the detection of environmental constraints on flowering time. An overall determination of selective and environmental factors in their spatial configuration is further thought to potentially segregate non-adaptive patterns by chance factors to explain flowering variations after Ollerston and Lack 1992. Phenophase proportions per LCP segment derived in this study can therein be used as additional descriptors for individual fitness variations on the plant scale itself that are traceable over time. A critical debate about differences and entailing consequences of flower production per individual and its meaning for changes in reproductive capacity and plant growth under varying conditions in consecutive seasons is still ongoing (Obeso 2002).

While it was shown that plants with high allocation of reproductive energy are limited in vegetative growth (Harper 1977; Kay 1987; Snow and Whigham 1989), the implications for Calluna resilience patterns to weather extreme events, specifically drought in areas with limited humidity, are still unknown. In particular, the integration of LCP segments enables an enhanced multifactor assessment of heathland susceptibility to shifts in environmental conditions (Peñuelas et al. 2004; Fagúndez 2012; Meyer-Grünefeldt et al., 2015). In this study, phenophase proportions indicate that the reproduction of Calluna was strongly decreased (by 43.8%) in 2018 after a season with low rainfall (60 mm in May-July compared to 192 mm on a 60 year average basis). Most of the individuals developed no or very few flowers. Flowering and fruiting was only present in the upper 20% zone of the shoot. Here, the study reveals a general statement: there are individuals that flower under bad conditions and there are
individuals that do not flower under good conditions. However, no information on peak flowering shift, flowering duration and the distribution of small-scale habitat parameters was derived in this study. Therefore, arising implications for tracking individual fitness levels in consecutive seasons must be examined as part of follow-up studies using the proposed UAV methodology.

Conclusions

A novel method was developed to map the flowering phenology and spatial distribution of Calluna life-cycle phases on the basis of high-resolution UAV RGB imagery in a heathland 2 years after fire management. The generation of 3D point clouds enabled the segmentation of spatial units in order to allocate phenophase variation on the canopy level. Calluna patches were therein extracted using machine learning classification and object-based image segmentation. Segment heights and sizes were derived as structural traits that characterize Calluna LCP. Color information could subsequently be used to quantify the proportions of flowers, fruits and vegetative shoots for each LCP segments as additional phenological traits. Finally, dominant phenophase patterns were mapped in a spatially explicit manner and analyzed in its spatial configuration. The study delivers the following findings:

a1 UAV-derived spatial segments are capable of statistically representing Calluna life-cycle phases and inherent growth forms. Following fire management, regeneration patterns included germination and vegetative sprouting in particular.

a2 Typical patterns of heterogeneous Calluna stands can be distinguished for juvenile recovery in pioneer and building phases and for the mature phase that was unaffected by fire. In the juvenile phases, regeneration of Calluna mainly occurs through vegetative development of new shoots from old stem bases. Seedling establishment rate is low, as estimated <10% on the test site 2 years after fire.

b The distribution of flowering phenology represented through LCP segments is spatially heterogeneous. Flowering, fruit phase and vegetative propagation are highly interspersed with high variations between years.

c Juvenile phases exhibit significantly higher proportions of flowering and fruiting shoots in comparison to fire-unaffected mature stands. The pioneer phase exhibits higher proportions of flowering shoots, indicating a late flowering onset or an increased flowering time.

The study presents findings for two UAV images captured in the main flowering peak for 2017 and 2018, respectively. Further studies are required to map the temporal shift of flowering and fruiting phase over an entire vegetation period, or to track individual fitness levels over consecutive seasons. In that respect, the developed method has the potential to deliver information on how environmental constraints interact with structural and phenological traits to form functional types of Calluna which can be manipulated by habitat management. For the monitoring of evolving patterns of functional diversity, this study shows that simple RGB cameras mounted on UAVs are able to extract spatial variations of optical traits using in situ samples for calibration. In combination with spectral library information on optical plant traits, recent multi-spectral systems are seen to provide transferable calibration routines to implement recurring overflights and hence monitor the re-establishment of sustainable structures and biodiversity on heathlands.

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**Supporting Information**

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

**Figure S1.** Linear regression (red line) between extracted (nDSM) and measured (terrestrial) heights for \( n = 97 \) polygons; difference between regression line and diagonal (black line) indicates corrected shift distance.

**Supplementary Material.** Methodological framework description for UAV based Calluna life-cycle mapping and uncertainty evaluation.