

Spatial analysis of root hemiparasitic shrubs and their hosts: a search for spatial signatures of above- and below-ground interactions

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Abstract Root hemiparasitic plants take up resources from the roots of neighbouring plants, which they use for fuelling their own growth. While taking up resources from the hosts below-ground, they may simultaneously compete with the hosts for sunlight. Suppression caused by the parasitism could result in openings in the vegetation structure and increased mortality levels. On the other hand, the root hemiparasites may also be constrained by the hosts, restricting the parasites to a limited number of locations within a community. These vegetation alterations and location restrictions can be referred to as *spatial signatures* of the root hemiparasites. In order to search for such spatial signatures, we investigated a population of a predominant *Acacia* species in Australia co-occurring with established root hemiparasitic shrubs, using intensity estimates of the *Acacia* and

dead shrubs to be indicators of parasite populations. We find evidence that the root hemiparasitic shrubs, like herbaceous root hemiparasites, prefer growing at distances from neighbouring plants that fulfil resource requirements both below-ground and above-ground. Assuming that root hemiparasites are limited by their hosts, we present an optimal host density and distance to host hypothesis (‘Goldilocks hypothesis’) to account for such a vegetation pattern. Although mortality appeared to primarily result from intraspecific competition and shoot parasitism, the root parasitism could explain some of the mortality in open areas. It is likely that both processes occur simultaneously. In spite of differing annual and perennial life strategies among root hemiparasites, root parasitism across systems may follow these two general processes in the formation of vegetation patterns.

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Introduction

...[I]s the vegetation open because of the presence of the parasite, or is the parasite present because the vegetation is rather low and open? ter Borg (1985)

After several decades of research into root hemiparasites and hosts in natural vegetation, the conundrum of this chicken-and-egg question still stands. Root hemiparasites parasitise the roots of neighbouring plants to get access to water and mineral nutrients and can, in this way, have a substantial impact on the natural communities in which they grow (Press and Phoenix 2005; Pennings and Callaway 2002; Gibson and Watkinson 1992). Root hemiparasites also have autotrophic capabilities, but these are often lower than those of most hosts, making the parasites less competitive for sunlight (Tennakoon et al. 1997a; Stewart and Press 1990). For this reason, Matthies (1995) suggested that root hemiparasites tend to establish and grow more vigorously in relatively nutrient-poor, low-productivity communities than in nutrient-rich, high productivity habitats because they can better compete for sunlight and have relatively easy access to limited resources (Phoenix and Press 2005; Matthies 1995). The root-to-shoot ratio has also been shown to increase in some plants when they are attacked by root hemiparasites (Tennakoon et al. 1997b). Thus, root parasitism may serve two purposes for the root hemiparasite: providing it with mineral nutrients and water, while simultaneously suppressing the host's ability to compete for sunlight (Těšitel et al. 2010b).

Herbaceous root hemiparasites (especially in genus *Rhinanthus*, Orobanchaceae) have been studied in an attempt to unravel the above-ground competitive relationship between the root hemiparasites and their hosts, and potential host suppression. Soil mineral content and water availability may have profound effects on the above-ground interactions (Těšitel et al. 2015). Population density has a large impact on the successful establishment of root hemiparasites (Mudrak and Lepš 2010; de Hullu 1985). Similarly, distance from a host affects competition for sunlight (Keith et al. 2004; Těšitel et al. 2011). Root hemiparasitism reduces the biomass of many different host species in herbaceous communities, and the impacts are host-specific (Matthies 1995, 1996, 1997; Marvier

1996). Suppression of hosts may leave a spatial signature of higher mortality than expected under density-dependent mortality. For example, Atsatt and Strong (1970) found that the most beneficial hosts for the root hemiparasite *Castilleja exserta* were very susceptible to being killed from the parasitism. Several studies have used pot experiments to study the relationship between root hemiparasites and hosts (Davies and Graves 2000; Těšitel et al. 2010a; Matthies 1997). Such experiments usually do not take into account density-dependencies (Smith 2000), nor do they account for the observation that most root hemiparasites can parasitise multiple hosts simultaneously. These limitations lead to potential discrepancies between results obtained from pot cultures and natural communities. Spatial analysis of vegetation structure in natural communities may be more appropriate for identifying density-dependent phenomena and accounting for the multi-host strategy. Spatial analyses may also help answer the question of whether the vegetation is open due to the parasite, or whether the parasite managed to get a foothold because the vegetation was already low and open.

Due to more conservative feeding behaviours and lower transpiration rates, perennial hemiparasites may have lower host impacts compared to the herbaceous root hemiparasites (Těšitel et al. 2010b; Tennakoon et al. 1997a). Despite this, it has been found that woody root hemiparasites take up carbon heterotrophically from their hosts (Tennakoon and Pate 1996; Tennakoon et al. 1997b; Bell and Adams 2011), which can reduce growth of the hosts (i.e. host suppression). A natural population of a predominant woody host species and woody root hemiparasites in an established, low-nutrient system could prove useful in a search for spatial signatures of potential above-ground competition and below-ground suppression.

In order to search for such spatial signatures, we used the above-ground biomass densities and spatial densities for an abundant *Acacia* shrub together with two species of root hemiparasitic shrubs in a natural community. We recorded the positions of all dead shrubs within the study site to investigate density-dependent mortality and potential hemiparasite-induced mortality. We find evidence for the location of the root hemiparasites to likely follow an optimal (“just right”) strategy in terms of distance from the host and host density, i.e. not being too close to the

host to lose in the competition for sunlight, but not so far away that there will be too few compatible hosts in early phase of establishment. We name this the ‘Goldilocks hypothesis’ and compare it to the ‘host-quality hypothesis’ (Watson 2009), which predicts that host quality is a factor of paramount importance for the establishment and growth of a hemiparasitic plant.

Methods

Site description

The 1.1 ha (75 m × 145 m) site used for the analysis is located in a low-nutrient, low-productivity, semi-arid habitat in South Australia (Fig. 1). The predominant species within the site is the shrub *Acacia ligulata* A. Cunn. ex Benth. (dune wattle, Fabaceae), a widespread species in the southern part of Australia. Due to the volume and abundance of *Acacia ligulata* within the site, most of the above-ground biomass consists of this species. We considered this species to be a good indicator for spatial impacts by hemiparasites on hosts. Other species occurring in the site are *Sida petrophila* (rock sida, Malvaceae), *Senna artemisioides* nothosp *filifolia* (desert cassia, Caesalpiniaceae) and *Dodonaea viscosa* ssp. *angustissima* (sticky hopbush, Sapindaceae). The woody root hemiparasites within the site are *Santalum spicatum* (R.Br.) A.DC. (Australian sandalwood, Santalaceae) and *Exocarpos aphyllus* R.Br. (leafless ballart, Santalaceae). The hemiparasitic vine, *Cassytha melantha* R.Br. (large dodder-laurel, Lauraceae) is found in high densities in the northeast corner of the study site.

Data collection

The locations of all 2018 *A. ligulata* shrubs, irrespective of size, and 27 root hemiparasitic shrubs were recorded by either using a total station (M3, Trimble) or a high-accuracy GPS receiver (Pathfinder® ProXRT, Trimble). The horizontal accuracy was <0.3 m. To obtain locations for the few remaining shrubs not recorded by either of these two devices, we used measuring tape with at least two already location-determined shrubs as reference points. For each *A. ligulata* shrub and root hemiparasite, the height (h , in metres) and stem circumference

($stem_cir$, in centimetres) were recorded and crown volume ($crown_vol$) was estimated per decimetre using a measuring rod. Volumes (V) of the full shrubs were calculated by adding crown volume to the cone-estimated volume of the stem, $V = crown_vol + \pi/3 \cdot (\pi \cdot stem_cir/200)^2 \cdot h$. Locations of all dead shrubs within the site also were recorded, and it was detailed whether or not remnants of shoot hemiparasite *C. melantha* were attached.

Above-ground biomass allocation

The first spatial signature for which we searched was related to location restrictions, and we therefore investigated the locations of the root hemiparasites in relation to the above-ground biomass of the predominant host. The *A. ligulata* shrub volumes (calculated from height, stem circumference and crown volume estimates as above) were used for investigating the above-ground biomass allocation. A Gaussian kernel with a bandwidth (σ) set as the fifth root of the number of points according to Silverman (1986), i.e. $2018^{(1/5)} = 4.58$, was used for the smoothing. The smoothing interpolates the above-ground biomass values at the irregular spatial locations within the study site. For this task and two of the subsequent investigations, we used the `spatstat` package v1.46-1 (Baddeley and Turner 2005; Baddeley et al. 2015) for R v3.3.1 (R Core Team 2016).

Estimated intensities of *Acacia ligulata* and dead shrubs

In order to estimate the intensities of the *A. ligulata* relating to the locations of the root hemiparasitic shrubs, a function of the distances from hemiparasite locations was obtained. The *A. ligulata* intensities were first estimated using only locations (unmarked) and subsequently estimated using above-ground volumes (marked) as weights for all individuals in addition to their location. These intensity estimates were performed with the ‘`rho`hat’-command in `spatstat`.

The second spatial signature searched for was related to vegetation alterations, more specifically induction of mortality. Mortality may be density-dependent as a result of intraspecific competition (Kenkel 1988), which is also known as “self-

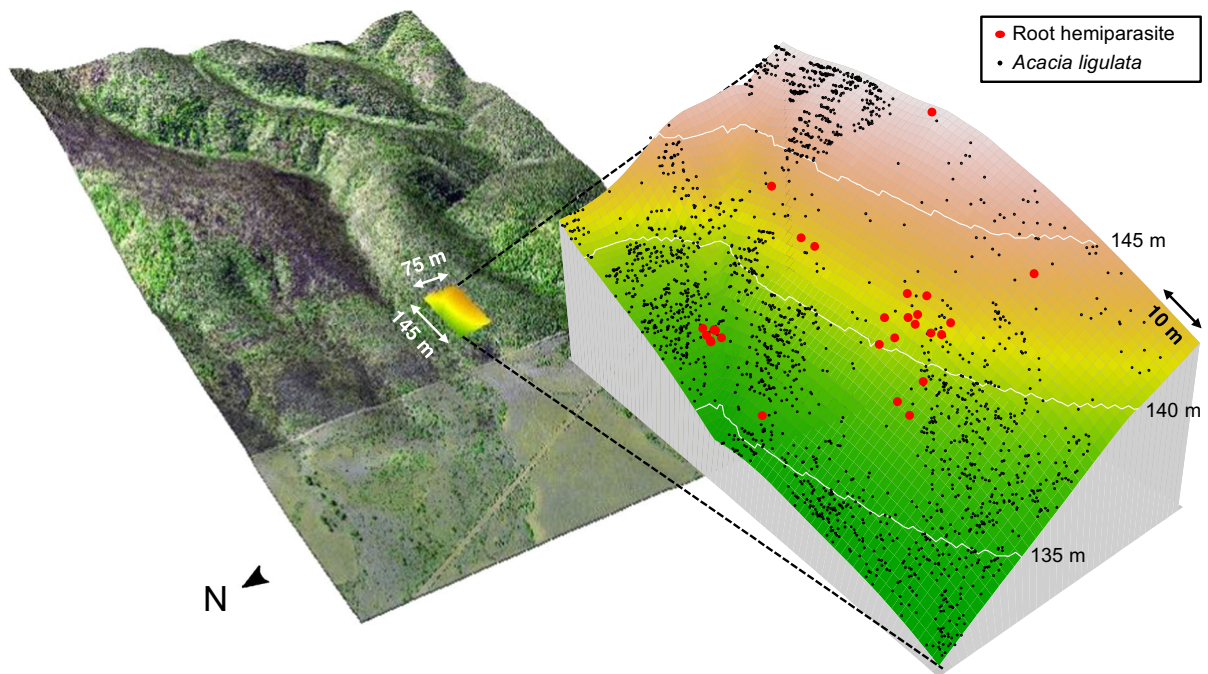


Fig. 1 Digital elevation model (DEM) of the Conservation Park and expansion of the study site, showing elevation and locations of *A. ligulata* shrubs (black discs) and root hemiparasitic shrubs (large red discs). (Color figure online)

thinning”. Mortality may also result from parasitism, either from root or shoot hemiparasites within the study site. Mortality may also result from many processes other than density-dependence or parasitism, but the two biotic processes were considered the most relevant within this study site. Therefore, in order to investigate density-dependence and shoot and root parasitism, the intensities of dead shrubs were plotted using a covariate combination of an *A. ligulata* density function and the aforementioned distance function of the root hemiparasitic shrubs. To obtain this plot, we used the ‘rho2hat’-command in *spatstat* with a Gaussian kernel, again with a bandwidth (σ) set to 4.58. It was used in combination with the ‘reweight’ method (Baddeley et al. 2012; Jones 1991), which nonparametrically estimates the intensity by use of the cumulative distribution function. To investigate the mortality within the study site potentially induced by the hemiparasitic vine, a dead shrub intensity plot was prepared where dead shrubs with *C. melantha* haustorial remnants were excluded (201 shrubs excluded, and 601 shrubs remaining). This plot was compared with the plot that included all dead shrubs. This method enabled us to further investigate

“self-thinning” and the potential impact from the root hemiparasites on mortality.

Mortality investigations using trivariate random labelling

To further investigate the mortality around the root hemiparasites in relation to the distance, a trivariate random labelling analysis was performed. The method makes it possible to test if qualitative marks (here ‘dead’ and ‘live’) are dependent on the distance r to an antecedent focal pattern (here ‘root hemiparasites’) by the use of a random labelling null model. Trivariate random labelling and how to calculate the summary statistic (i.e. probability) is described in greater detail elsewhere (Wiegand and Moloney 2014; Jacquemyn et al. 2010), but for our analysis it looked like:

$$p_{\text{rhp,dead}}(r) = \frac{\lambda_{\text{dead}}}{\lambda_{\text{dead}} + \lambda_{\text{live}}} \frac{g_{\text{rhp,dead}}(r)}{g_{\text{rhp,dead+live}}(r)},$$

where λ_{dead} and $\lambda_{\text{dead+live}}$ are the intensities of dead and all *A. ligulata* shrubs, respectively, and $g_{\text{rhp,dead}}(-r)$ and $g_{\text{rhp,dead+live}}(r)$ are the associated bivariate pair-correlation functions for estimating intensity

normalised neighbourhood densities a distance r away from the root hemiparasitic shrubs (subscript rhp). The potential mortality induced by the hemiparasitic vine could disrupt the analysis. Because of the potential disruption, prior to the analysis, an area of $30\text{ m} \times 75\text{ m}$ was excluded from the eastern part of the observation window in order to remove an area with *A. ligulata* heavily infected by *C. melantha* as well as a large open patch with no *Acacia* shrubs or hemiparasites (Online Resource 1). The remaining numbers of live and dead *A. ligulata* shrubs in the new observation window were 1559 and 556, respectively. The expectation of the summary statistic under random labelling in this case, therefore, was 0.26 [$\approx 556/(1559 + 556)$]. The 27 root hemiparasites all remained within the new observation window. However, the low number of root hemiparasites (i.e. <50) can create variation in the estimator of the summary statistics (Wiegand and Moloney 2014) and a cautionary approach should be taken when interpreting the results. For the trivariate random labelling analysis, the coordinates of the point patterns of live and dead *A. ligulata*, and the root hemiparasitic shrubs were adjusted to fit as grid-coordinates in a grid of 1150×750 cells. This meant that each grid cell represented a square decimetre. Confidence envelopes were created using the 5th and the 25th lowest and highest values of 999 simulations, representative of confidence levels of 0.01 and 0.05, respectively. Ring widths of both 1 and 3 metres were used to estimate the intensity normalised neighbourhood density with the bivariate pair-correlation functions [$g_{\text{rhp,dead}}(r)$ and $g_{\text{rhp,dead+live}}(r)$] over a distance r of 20 m. This distance was chosen after evaluating the study site plot of the distance function of the root hemiparasites and the dead shrub intensity plots. This analysis was conducted using the software *Programita* (Wiegand and Moloney 2004, 2014; Jacquemyn et al. 2010).

Spatial imagery and digital elevation model

Spatial imagery (CIR and RGB, 10 cm resolution) was obtained from Aerometrix (Adelaide, South Australia) and Department of Environment, Water and Natural Resources (DEWNR, South Australia). The resolution of the imagery was found to be insufficient for accurate location estimates and for estimating above-ground biomass. However, the near infrared (NIR) and red made it possible to determine the normalised

difference vegetation index, NDVI [$= (\text{NIR} - \text{red}) / (\text{NIR} + \text{red})$]. Healthy vegetation reflects back more NIR than unhealthy vegetation, and red light is absorbed by vegetation in its photosynthetic process. Vegetation with a higher level of photosynthesis therefore has a higher NDVI value. Values for the NDVI can range between -1 and $+1$, and soil has values around -0.1 to 0.2 , whereas photosynthetic vegetation commonly has values in the range of 0.5 – 0.8 (Carlson and Ripley 1997). The NDVI was created with the Imagine[®] software (ERDAS).

The elevation was recorded for many of the points within the study site using the total station. Additionally, data of contour lines and creeks were obtained from PIRSA (Primary Industries and Resources, South Australia). All these data were combined and a digital elevation model (DEM) was created in ArcGIS v10.3 (ESRI). The elevation data from the DEM were also used to produce slope and aspect. Elevation, slope and aspect were tested as covariates for the *A. ligulata* point pattern in order to test if these abiotic factors had a potential impact on either location or above-ground volume of the *A. ligulata*.

Results

General observations

In general, the heights of the *A. ligulata* and the root hemiparasites were very similar, although the *Acacia* was markedly taller than the root hemiparasites in a few cases (Online Resource 2). These tall *Acacia* shrubs were, however, not found close to the root hemiparasites. Elevation, slope or aspect as covariates could not explain the observed distribution of *A. ligulata*. The perennial species, *Sida petrophila*, was the second most frequent species, found in open patches close to *A. ligulata* shrubs growing to a height of ca. 1 m.

Density of above-ground *Acacia ligulata* biomass

The above-ground biomass density for the *A. ligulata* shrubs shows a higher density in the northwest corner of the site (Fig. 2a). The root hemiparasitic shrubs (*S. spicatum* and *E. aphyllus*) are positioned outside the high-density areas, where the *A. ligulata* density is below 0.06 shrubs per m^2 , close to the biomass

borders. They are not found in areas of very low above-ground *A. ligulata* biomass either, where the density is below 0.01 shrubs per m².

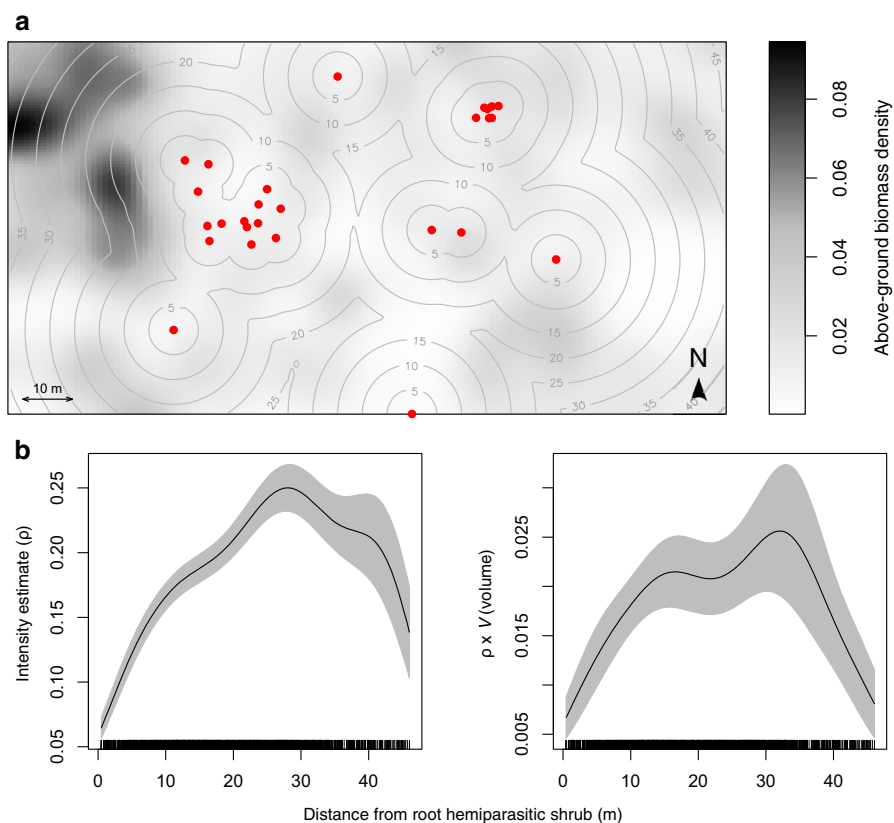
Spatial intensity estimations with root hemiparasite locations as covariate

Higher estimated intensities (i.e. $\hat{\rho}$) of *A. ligulata* shrubs are found further away from the root hemiparasites than close to the parasites (Fig. 2b, left panel), and the above-ground *A. ligulata* biomass has local ‘humps’ around 17 and 33 m away from the root hemiparasites (Fig. 2b, right panel), reflecting the above-ground biomass in the northwest corner (Fig. 2a, top left). The estimated intensities gradually increase over the distance away from the root hemiparasites with the above-ground biomass allocation of ca. 0.007 m³ per m² close to the root hemiparasites to the triple of that at 17 m and beyond.

Mortality in the vegetation

Excluding dead shrubs with *C. melantha* haustorial remnants from the dead shrub intensity plot—which is based on two covariates, namely density of *A. ligulata* and distance from root hemiparasitic shrub—points to the hemiparasitic vine as a harsh companion (Fig. 3a). This finding is likely due to the hemiparasitic vine being completely reliant on water from the host and also due to the density of its twines in the host canopy blocking the sunlight. At distances further than 20 m away from the root hemiparasitic shrubs and at an *A. ligulata* density of ca. 0.3 live shrub per m², the dead shrub intensity is ca. 0.14 shrub per m² (Fig. 3a, left panel). With this subgroup excluded (Fig. 3a, right panel), the highest dead shrub intensity is ca. 0.11 shrub per m². The distance from the root hemiparasitic shrubs is, in this case, more than 10 m, and the *A. ligulata* density is ca. 0.4 shrub per m². Intraspecific competition and the shoot parasitism are thus both

Fig. 2 Density investigations of the *A. ligulata* in relation to the root hemiparasitic shrubs. **a** Above-ground biomass densities (m³ per square metre) of *A. ligulata* shrubs within the study site. *Red discs* show locations of the root hemiparasitic shrubs and *black discs* show the locations of the *A. ligulata* shrubs. **b** The intensity estimates (*black lines*) of unmarked *A. ligulata* (left panel), and marked *A. ligulata* (right panel) using the above-ground volume of each individual shrub. Additionally, 95% confidence intervals are included (*grey bands*). (Color figure online)



likely to induce higher levels of mortality in the vegetation than the root parasitism. However, in areas where the *A. ligulata* density is near zero, the estimated intensity of mortality around root hemiparasites is approximately 0.05 dead shrubs per m² over a distance of ca. 20 m. Some level of suppression from the root hemiparasites cannot be ruled out. Following further investigations of the mortality around the root

hemiparasites with trivariate random labelling, there appear to be some distances for which the mortality is higher than expected under randomness. However, there are also distances close to the root hemiparasites where the observed mortality is well within the simulation envelopes, especially for the envelopes representative of a 0.01 confidence level (i.e. the 5th highest and lowest values from the 999 simulations).

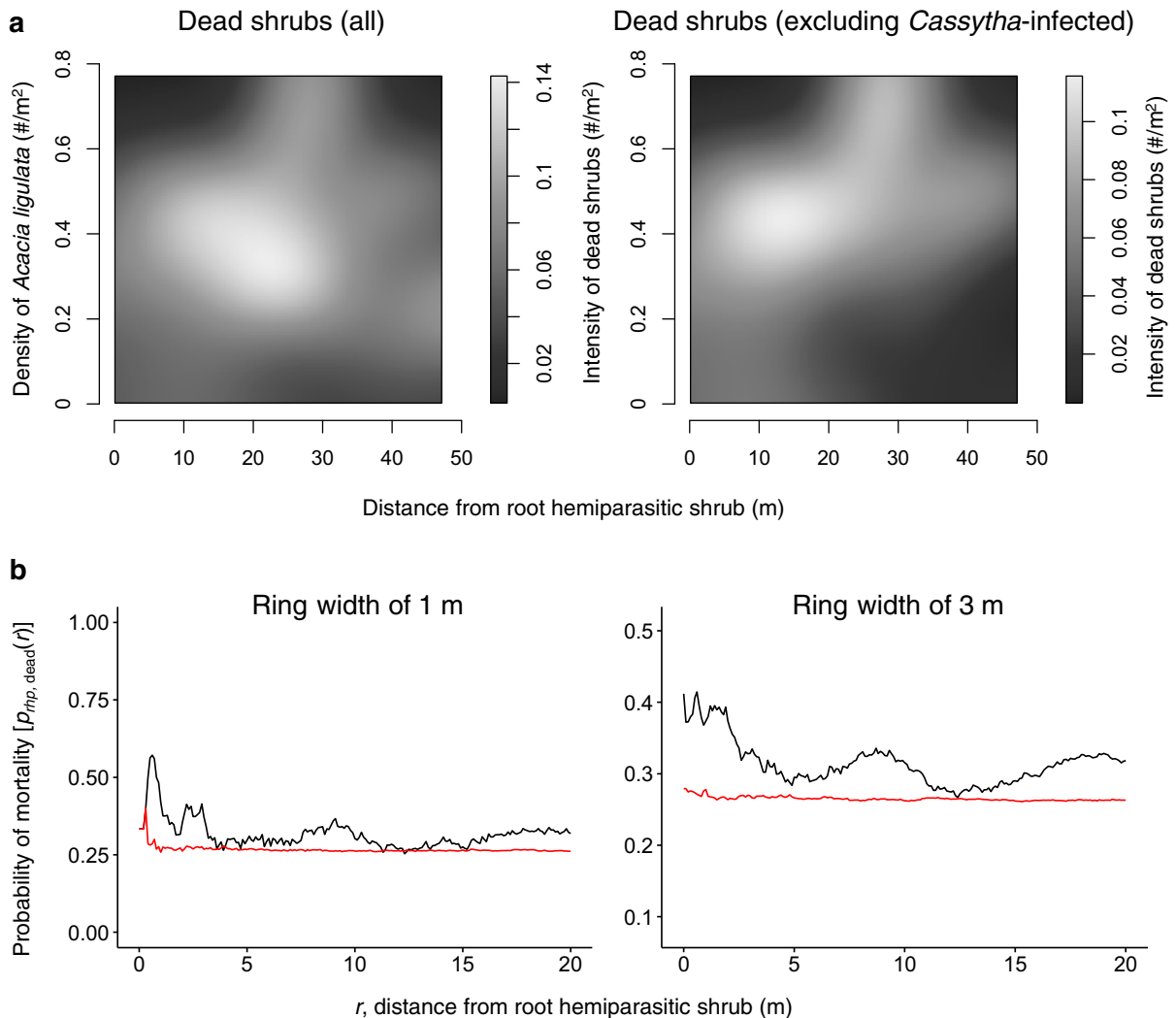


Fig. 3 Mortality investigations. **a** Estimated intensities of dead shrubs using either all shrubs (left panel) or those excluding *C. melantha* haustorial remnants (right panel) as a function of both distance from root hemiparasitic shrubs and density of *A. ligulata*. **b** Trivariate random labelling using the root hemiparasites as the antecedent focal pattern (subscript rhp) in order to investigate whether the probability of mortality of *A. ligulata* individuals (dead shrubs) within a 20-m distance from the root hemiparasites was higher than under randomness. Simulation

envelopes of random labelling were created by shuffling the qualitative marks ('dead') over the locations of dead and live *A. ligulata* shrubs (light-grey band 5th highest and lowest simulation values, dark-grey band 25th highest and lowest simulation values). The red lines are the means of the simulation results representing complete spatial randomness (i.e. $p_{rhp, dead}(r) \approx 0.26$). Two different ring widths (1 m, left panel; 3 m, right panel) were used for estimating the intensity normalised neighbourhood densities. (Color figure online)

Spatial imagery and NDVI

The resolution of the imagery was insufficient for locating dead shrubs. Animal tracks were quite visible on the RGB imagery and animals could have affected the open areas by limiting new shrubs from emerging. The NDVI of the vegetation showed some distinct bright individuals (with NDVI values of 0.6–0.7, Fig. 4) at the borders of patches even close to the root hemiparasitic shrubs. The interior of the large patch in the northeast corner (top right) has higher NDVI values (many in the range of 0.5–0.8) than other patches within the study site (many in the range of 0.4–0.6). This is likely due to the shoot hemiparasitic vines occupying many of the *A. ligulata* crowns in this part of the study site (Online Resource 1).

Discussion

The above-ground biomass allocation map (Fig. 2a) shows that the root hemiparasites in the present study grow outside high-density areas (i.e. >0.06 shrubs per m^2) with high above-ground biomass (i.e. $0.02 m^3$ per m^2). This finding is consistent with the hypothesis that the root hemiparasites are not able to compete effectively with their hosts and potential hosts for sunlight, and are restricted to areas with less above-ground productivity. Other factors than sunlight could, however, impair the establishment of the root hemiparasites within high-density areas, for instance an insufficient level of precipitation to initiate germination. The second observation is the absence of the hemiparasites from areas of very low above-ground

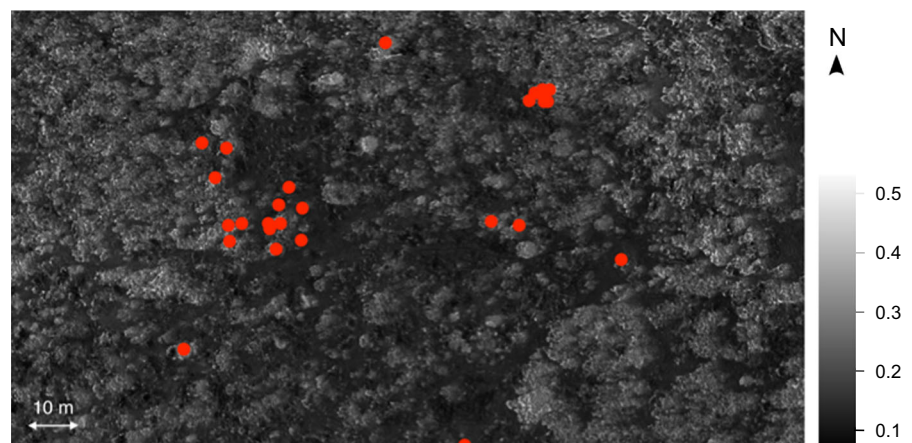
biomass. This finding suggests that suitable hosts grow too far away for the early onsets of establishment, and the soil resources may not be sufficiently high to cover the needs of the parasites. For example, in an experimental plot with seedlings of *S. spicatum* planted individually together with different host species, none of the hemiparasites survived the first 2 years with an incompatible host (i.e. *Eucalyptus loxophleba* ssp. *loxophleba*), whereas 86% survived the first 3 years with *Acacia acuminata* as the host (Brand et al. 2000). Once established, woody root hemiparasite *Santalum acuminatum* can take up much of its water from the soil (Tennakoon et al. 1997a); this may also be the case for *S. spicatum*. It should be noted that experiments of this kind have not been reported on species of *Exocarpos*.

The soil resource heterogeneity within the investigated site is not known, but there is an elevation difference of more than 15 m between the highest (148.5 m) and lowest (133.6 m) altitude (Fig. 1). This difference will likely alter the water availability and might partly explain why the above-ground biomass is higher in the northeast corner, since this area is closer to a local creek. Soil nutrient levels and water availability can potentially be primary drivers of the overall occurrence of the hemiparasites via host growth and vegetation density.

Spatial intensity estimations with root hemiparasite locations as covariate and two spatial signatures

Low estimates of intensity, both without and with weights (above-ground volume), are found close to the

Fig. 4 NDVI imagery of the study site (see text for description of NDVI). Locations of root hemiparasites are marked with red discs. The scale bar shows the matching NDVI values. (Color figure online)



root hemiparasites, gradually increasing with the distance from the root hemiparasites (Fig. 2b). Similar low-density zones are observed in natural communities in Western Australia between fully grown *S. spicatum* individuals and other shrubs in their neighbourhood (Dr Elisabeth L. Barbour, pers. comm.). Such a spatial signature, with zones of increasing host density and above-ground host biomass, may be found in other root hemiparasite–host systems. The root networks of fully grown *S. spicatum* shrubs can spread out to a distance of 30 m in natural communities (Woodall and Robinson 2003) and *Acacias* (and other plants) 10 m away, therefore, still fall within the zone for potential root parasitism. It is not known how close primary hosts can be expected to grow to *S. spicatum* and it is not known how close *S. spicatum* needs to be to a potential host in the early phase of establishment in order to create contact. It needs to be pointed out that these open zones are not necessarily, due to the hemiparasites, but could be due to other factors, biotic and/or abiotic. This cannot be determined from spatial analysis alone.

Intraspecific competition and the hemiparasitic vine seem to be the main biotic drivers of mortality, but there are numerous dead shrubs within the vicinity of the root hemiparasites where the density of *A. ligulata* is very low (Fig. 3a). Whether this observation directly relates to the parasitism (Fig. 3b) or to other factors, such as low levels of soil nutrients and water, and strong competition from other species such as *Sida petrophila* (which grows in open patches around *A. ligulata*), again cannot be determined from spatial analysis alone. However, it could be another potential spatial signature relating to root hemiparasitism and it might similarly be found in other root hemiparasite–host systems. It is advisable for future studies of root hemiparasites–host systems using the trivariate random labelling method to include a higher number of root hemiparasites (i.e. >50).

The host-quality hypothesis and Goldilocks hypothesis

Watson et al. (2007) analysed the spatial point patterns of the woody root hemiparasite, *Santalum lanceolatum* (desert quandong, Santalaceae), together with the predominant *Acacia* species, *Acacia tetragonophylla* F. Muell. (kurara, Fabaceae), within a 3.4 ha large site. They found that on average over all distances, hosts were surrounded by the same number of hosts and

parasitic plants. This finding is indicative of an upper limit of parasites-per-host, approximately one-parasite-per-host. Water accessibility has been considered to be the primary driver of this limit, since those *Acacia* appearing to serve as primary hosts grew along the ridgeline where access to water was higher. Watson et al. (2007) did not look for indications of above-ground interactions (e.g. competition for sunlight) between the root hemiparasitic shrubs and the *A. tetragonophylla* shrubs. *Acacia tetragonophylla* shrubs appear to be less intensely clustered in the study site than the *A. ligulata* shrubs in our study. This might make any potential spatial signatures of above-ground interactions less pronounced in the *A. tetragonophylla*–*S. lanceolatum* study.

The observation that the root hemiparasites within our site are not found in low-biomass areas (i.e. below 0.01 shrubs per m²) could indicate a need for appropriate hosts in their vicinity and root hemiparasites are, in this way, restrained by host-access. Further research is needed to determine which quality levels are needed of the hosts in order to enable successful establishment of the root hemiparasites, and whether any compatible host is appropriate. The ‘Goldilocks principle’ in astronomy predicts that habitable planets are most likely found within a certain zone from a star (Hart 1979). A phenomenon similar to this principle might be found for root hemiparasites with an optimal zone for growth; that is, not too close to lose in the competition for sunlight, but not too far away to lack (compatible) hosts in the early phase of establishment. This factor is only partly covered by the ‘host-quality hypothesis’, since the hypothesis does not consider above-ground density and above-ground biomass allocation as limiting for the root hemiparasite and only briefly alludes to the absence of hosts in the onset of establishment as a potentially limiting factor. The ‘host-quality hypothesis’ may thus be a better predictor for mistletoe establishment than for root hemiparasites, as mistletoes are completely reliant on a host for survival and are therefore more sensitive to host quality (Watson 2009). A ‘Goldilocks hypothesis’ which focuses on root hemiparasites should also be applicable to further investigations of herbaceous root hemiparasites, e.g. on *Rhinanthus* in grassland communities. Since both herbaceous and woody root hemiparasites are found in areas of low density [present study and ter Borg (1985)], there could be many similarities between

woody and herbaceous species of root hemiparasites and how they affect, and are affected by, other plants in natural communities. In some studies on annual herbaceous root hemiparasites, the parasites show increased growth in shade (Hwangbo and Seel 2002; Těšitel et al. 2011; Hejzman et al. 2011), which is likely a behaviour more pronounced in annual than in perennial hemiparasites, arising from greater pressure to reproduce quickly. Annual hemiparasites might be quite sensitive to shading in the early onset of establishment when they are seedlings (Těšitel et al. 2011).

Two spatial signatures are thus put forward in the present study. Firstly, density of a predominant host is low close to the root hemiparasites and increases gradually over the distance away from the parasites. Secondly, there is some level of mortality around the parasites is seemingly not linked to the competition from the predominant host. Determining whether suppression of neighbouring woody hosts by woody root hemiparasites is in fact occurring would require experimental research beyond the scope of the present study. However, the NDVI imagery indicates that *A. ligulata* shrubs growing close to the root hemiparasites can have high NDVI values (i.e. 0.6–0.7), which is indicative of a sound level of photosynthesis. Studying community dynamics require temporal data and more information on the physical connections among the different species being investigated. To determine which neighbouring shrubs serve as primary hosts, the ^{13}C or ^{14}C isotope uptake from these hosts to the root hemiparasites could be investigated. Furthermore, growth of both hemiparasite and these hosts need to be measured over a number of years. Our spatial approach provides a novel way to test the Goldilocks hypothesis and to look for host suppression in the form of increased mortality. This analysis can provide further cues about whether or not the vegetation is open because the root hemiparasite suppresses the neighbouring vegetation or the parasite is found because the vegetation was already open. It is important to stress that the two proposed explanations for the parasite–host coexistence are not mutually exclusive. The vegetation may be sufficiently open for the root hemiparasite to find a foothold and, once established, the parasite might suppress its neighbours to a level that benefits its continued residence within the community.

Conclusion

Despite the important aspects of their life strategies, we find some indications in this study that woody root hemiparasites and many herbaceous root hemiparasites potentially behave in a similar way when it comes to establishment within a natural community: they occur less frequently in high-density areas and do not grow too close to areas of high above-ground biomass, quite likely a response to shading. Studies that follow woody root hemiparasites (or perennial hemiparasites in general) from the onset to full establishment are needed to adequately test the proposed Goldilocks hypothesis, and also to investigate whether or not the woody root hemiparasites suppress their hosts to better compete for sunlight. We suggest that both the Goldilocks hypothesis and the host-quality hypothesis be tested in future studies on natural vegetation, and that the vegetation pattern of dead plants be included. Our spatial evidence, as a reflection of the development of host–parasite dynamics in a natural setting over time, supports the Goldilocks hypothesis for woody plants.

To our knowledge, this is the first study to test for potential interactions of both above- and below-ground character for root hemiparasitic shrubs and their woody hosts. Further studies with similar types of perennial root hemiparasites and hosts under different nutrient conditions, for example in moderate production sites, where the woody root hemiparasites should have more difficulty in establishing, could provide insights into the importance of abiotic conditions in the establishment and dynamics for this group of plants [see for instance the ‘resource-competition hypothesis’ in Těšitel et al. (2015)]. Spatial—and when feasible, spatiotemporal (Raventós et al. 2010)—investigations of both herbaceous and woody root hemiparasites are helpful in ascertaining their function in natural communities and what role they play in plant coexistence.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Erratum to: Spatial analysis of root hemiparasitic shrubs and their hosts: a search for spatial signatures of above- and below-ground interactions

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The original publication of the article includes an error in Figs. 2 and 3. The correct version of Figs. 2 and 3 are provided in this erratum.

The online version of the original article can be found under doi:[10.1007/s11258-016-0676-8](https://doi.org/10.1007/s11258-016-0676-8).

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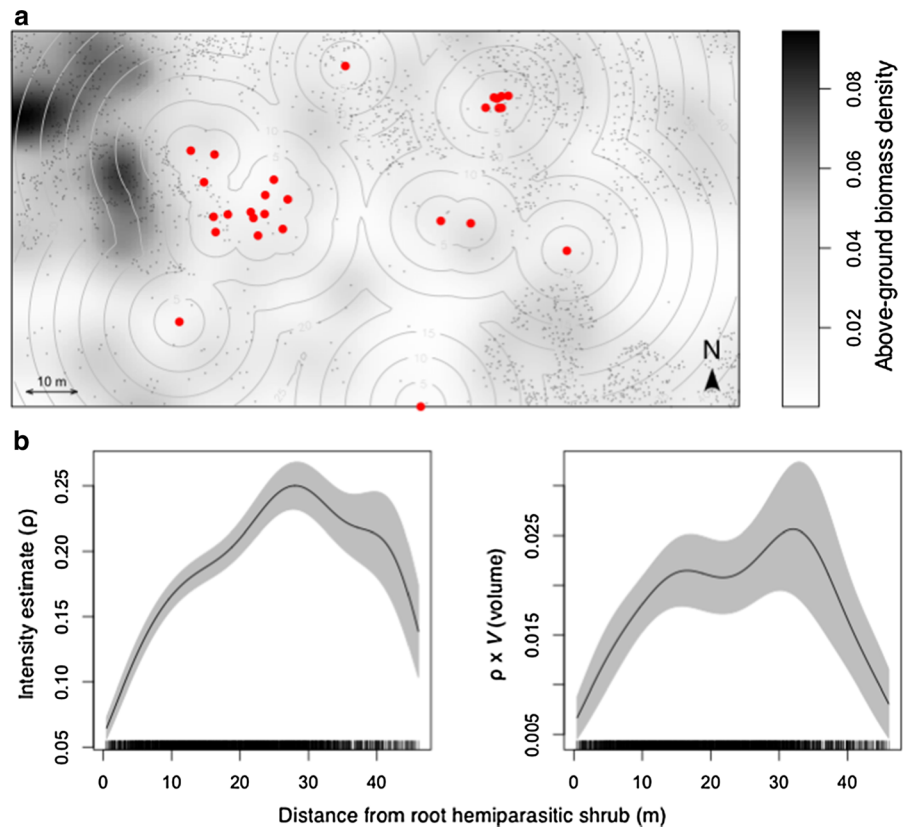
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Fig. 2 Density investigations of *A. ligulata* in relation to root hemiparasitic shrubs.

a Above-ground biomass densities (m^3 per square metre) of *A. ligulata* shrubs within the study site. *Red discs* show locations of the root hemiparasitic shrubs and *black discs* show the locations of the *A. ligulata* shrubs. **b** The intensity estimates (*black lines*) of unmarked *A. ligulata* (left panel), and marked *A. ligulata* (right panel) using the above-ground volume of each individual shrub. Additionally, 95% confidence intervals are included (*grey bands*). (Color figure online)



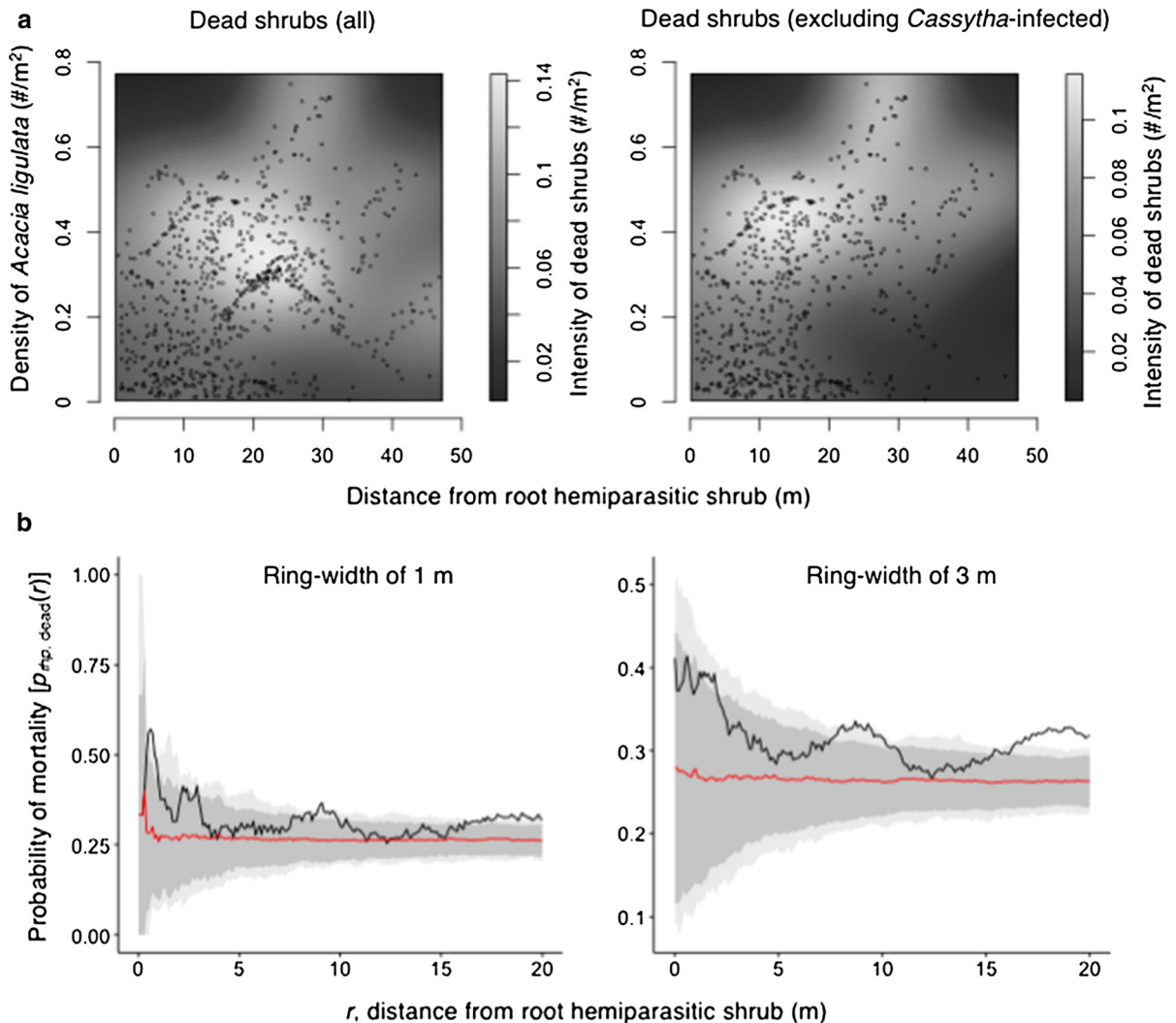


Fig. 3 Mortality investigations. **a** Estimated intensities of dead shrubs using either all shrubs (left panel) or those excluding *C. melantha* haustorial remnants (right panel) as a function of both distance from root hemiparasitic shrubs and density of *A. ligulata*. **b** Trivariate random labelling using the root hemiparasites as the antecedent focal pattern (subscript rhp) in order to investigate whether the probability of mortality of *A. ligulata* individuals (dead shrubs) within a 20-m distance from the root hemiparasites was higher than under randomness. Simulation

envelopes of random labelling were created by shuffling the qualitative marks ('dead') over the locations of dead and live *A. ligulata* shrubs (light-grey band 5th highest and lowest simulation values, dark-grey band 25th highest and lowest simulation values). The red lines are the means of the simulation results representing complete spatial randomness (i.e. $p_{\text{rhp, dead}}(r) \approx 0.26$). Two different ring widths (1 m, left panel; 3 m, right panel) were used for estimating the intensity normalised neighbourhood densities. (Color figure online)