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Article

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Title: Habitat requirements and natural history of *Tetanocera elata* (Diptera: Sciomyzidae): Case study of a dry meadow in western Ireland

Authors: Allison Bistline-East[1,2,3,4], Daniel Burke[1,2], Christopher D. Williams[5], and Michael J. Gormally[1,2]

[1] Applied Ecology Unit, National University of Ireland Galway, Galway, Ireland

[2] Ryan Institute, National University of Ireland Galway, Galway, Ireland

[3] Current affiliation: Purdue University, 901 W State St. West Lafayette, IN 47907, USA

[4] Corresponding author email: allison@bistlineeast.com

[5] School of Natural Sciences and Psychology, Liverpool John Moores University, UK

Running Title: Key habitat features for *Tetanocera elata*

Abstract

1. Terrestrial slugs are pervasive pests of agriculture throughout temperate regions and have the potential to disrupt the germination of seedlings, cause damage to fruiting bodies of crops, and vector plant pathogens.
2. *Tetanocera elata* Fabricius (Diptera: Sciomyzidae), a widely-distributed Palaearctic species, is an obligate mesoparasitoid and predator of pestiferous slugs including *Deroceras reticulatum* (Müller) (Stylommatophora: Agriolimacidae). It has the potential to be developed as a native natural enemy in a conservation biological control programme as an alternative to chemical molluscicides.
3. To better understand the ecological requirements of this species, a detailed observational study was conducted at a site in the west of Ireland possessing naturally occurring *T. elata* populations.
4. Comparison of local patches where *T. elata* were recovered revealed no association with plant community composition.
5. Taller dead vegetation was associated with *T. elata* presence throughout the site.Within the area of greatest *T. elata* aggregation, there was a significantly greater percentage cover of dead vegetation where *T. elata* occurred. Abundance of *T. elata* was also significantly correlated to hedgerow proximity. Results of this study are directly applicable for the design of a conservation biological control programme which effectively satisfies the principal habitat requirements of *T. elata* populations.

Key words: agroecology, conservation biological control, ecological engineering, hedgerow, mollusc, vegetation

Introduction

Throughout the world, terrestrial slugs (Mollusca: Gastropoda) are serious pests of tillage agriculture. One species in particular, *Deroceras reticulatum* Müller (Stylommatophora: Agriolimacidae), has spread from its native Palaearctic range (Wiktor, 2000) and established populations on all continents except Antarctica (Smith, 1989; Robinson, 1999). While large populations of *D. reticulatum* are regularly associated with agricultural land (Howlett, 2012) they can also successfully occupy a wide range of other habitats, including other frequently-disturbed habitats, such as construction sites and home gardens, as well as natural and seminatural grasslands, (South, 1992). This ability to disperse into other habitats and form aggregations outside of cropping areas makes *D. reticulatum* a particularly difficult pest to target and control. Damage incurred by *D. reticulatum* and other slug pests has been valued at £8 and £10 million (GBP) in the UK (MacDonald, 2009), primarily from feeding damage to seedlings causing crop failure (Hunter, 1968). In the EU there are currently three chemicals approved for slug control: methiocarb, metaldehyde, and ferric phosphate (European Commission, 2016a; European Commission, 2016b; European Commission, 2016c). However, methiocarb use has recently been restricted by the European Union (European Commission, 2014; European Commission, 2018) and metaldehyde will no longer be available for use in the UK beginning in 2020 (HSE, 2018), due to detrimental effects on non-target species and high potential to contaminate waterways in runoff (South, 1992; Cloyd, 2012; Howlett, 2012). There is also mounting evidence that ferric phosphate, currently approved for organic farming, is not effective at significantly reducing slug feeding damage to crops (Iglesias et al., 2001; Speiser & Kistler, 2002; Rae et al., 2009) and may have negative effects on non-target soil arthropods caused by excess iron build-up, especially when coupled with chelating substances (Langan & Shaw, 2006; Edwards et al., 2009).

Biological control of slugs offers an alternative to chemical pesticide that can be used in both conventional and organic agriculture. Currently the only widely available biocontrol agent of slugs is the parasitic nematode *Phasmarhabditis hermaphrodita* (Rhabditida: Rhabditidae) (Glen & Wilson, 1997), marketed as Nemaslug (BASF, Ludwigshafen, Germany). While *P. hermaphrodita* is useful in slug control, it is limited in its use as an inundative biological control agent. As such, *P. hermaphrodita* is prone to the same shortcomings of many such “single use” natural enemies which do not persist in the agroecosystem, including high expense, labour-intensive application multiple times per growing season, variable success rates and control levels, and short shelf life (Glen & Wilson, 1997; Speiser et al., 2001; Rae et al., 2007; Howlett, 2012), rendering them an unsustainable long-term solution (Michaud, 2018).

In an effort to both develop alternative slug control programmes and advance sustainable agriculture practices, recent research has focused on the potential use of *Tetanocera elata* (Diptera: Sciomyzidae) in a conservation biological control programme. The larval stages of *T. elata* are specifically associated with terrestrial slugs (Knutson et al., 1965). First and second instar larvae parasitise *D. reticulatum* and *Deroceras laeve* Müller as mesoparasitoids which kill the host by the end of the second instar, at which point larvae become free-living predators which feed on an expanded range of slug species (Knutson et al., 1965; Hynes et al., 2014a; D’Ahmed et al., 2019; Bistline-East et al., 2019). Predaceous larvae have the capacity to kill up to 12 prey slugs before beginning pupariation (Hynes et al., 2014a), making them potentially important natural enemies. Due to their particular biological requirements and life cycle (e.g., current challenges in mass rearing [Hynes et al., 2014b; Hynes et al., 2014c], lengthy developmental time [Knutson et al., 1965; Hynes et al., 2014c]), and the nature of cropping areas where slugs are in need of control (open cropping fields from which aerial natural enemies may disperse), *T. elata* may not be viable for use in inundative biocontrol programmes in the same way as *P. hermaphrodita*. Rather, this Palaearctic species is an excellent candidate for conservation biological control. The aim of such a programme would be to enhance agroecosystems in such a way that populations of natural enemies are self-regulating and self-sustaining, as well as maintaining essential habitat features like those promoted for biodiversity under existing agri-environment schemes, providing constant and recurring pest control (Holland et al., 2016). For *T. elata*, this would be accomplished by managing agricultural landscapes which can meet the essential requirements to complete its life cycle after initial populations are introduced or existing natural populations of *T. elata* are augmented.

In the case of conservation biological control with a single target species, the biological control output may be maximised by specifically designing habitat features to meet the biological and ecological requirements of the desired natural enemy (Van Driesche & Bellows, 2001; Ramsden et al., 2015; Holland et al., 2016). While there has been much research on the biology, physiology, and biological control potential of *T. elata* in recent years (Hynes et al., 2014a; Hynes et al., 2014b; Hynes et al., 2014c; Bistline-East et al., 2018; D'Ahmed et al., 2019; Bistline-East et al., 2019), the only habitat data for this species to date are provided by a limited number of individual collection records or species lists for the family Sciomyzidae (Chandler, 1972; Blackith et al., 1991; Williams et al., 2007; Williams et al., 2009a; Speight & Knutson, 2012). Amongst the most common habitats where *T. elata* has been collected are fens (Knutson & Berg, 1971), flood plains and callows (Maher et al., 2014), wet grassland (Carey et al., 2017), and on the margins of turloughts – temporary wetlands unique to the west of Ireland (Williams et al., 2009a, 2009b).

The current study aimed to identify specific habitat characteristics important to *T. elata* populations by undertaking an extensive examination of local habitats within a field site where *T. elata* have been regularly observed. These data may, in turn, be used to inform optimal land management strategies for supporting *T. elata* in a conservation biological control programme.

Materials & Methods

Study Site. Surveys of habitat characteristics took place within a 10.5 ha subsection of Cow Park, Clarenbridge, Co. Galway, Ireland (ITM 541725.671, 720345.825; GPS 53°13’49.1”N, -8°52’22.1”W) where *T. elata* adults had been recovered in previous years. The field site (bordered by a river and deciduous woodland on the eastern side and surrounded by hedgerows/scrub; Fig. 1) was comprised largely of a dry meadow with a patch of wet grassland to the north-east of the site (designated as GS2 and GS4 respectively after Fossitt [2000]).

Local habitat selection. The survey was comprised of a series of 0.5 m x 0.5 m plots of four categorical types placed semi-randomly throughout the study site according to category criteria. Categories of local habitats measured using these observation plots were comprised of areas that appeared visually similar (e.g., had a similar appearance in plant community and structure) to where *T. elata* adults had been collected at Cow Park in previous years (“expected”), and plots that appeared visually unsuitable for *T. elata* based on prior collections (“unexpected”). Expected plots were identified by vegetation structure and species, consisting typically of thick graminoid tussocks in tall stands, while unexpected plots possessed less densely growing vegetation (or even displayed gaps in growth) and were lower growing. Each of these categories was replicated at near (<5 m) and distant (>10 m) proximities to a hedgerow boundary, to provide four categorical types of observational plots (expected/near [E/N], unexpected/near [U/N], expected/distant [E/D], and unexpected/distant

[U/D]). Each category had 8 replicates, resulting in 32 observational plots. In addition to the above plots which were selected in May 2017 (before the *T. elata* adult flight period in Ireland [ABE, pers. obs.]), subsequent plots were included in the study as *T. elata* specimens were recovered throughout the summer (see "Ecological Measurements"), regardless of vegetation appearance or proximity to hedgerow, to comprise a fifth treatment category ("TE"). On occasions where *T. elata* collection coincided with previously designated plots, such plots were both assigned a "TE" plot number as well as maintaining their original designation. In this way, observations were made in both *T. elata*-positive and *T. elata*-negative plots. All plots were marked with a bamboo garden stake which remained in place throughout the study to ensure identical areas were observed each time. The boundaries of observational plots were marked using a 0.5 m x 0.5 m wire frame quadrat oriented using the bamboo stake and closest linear feature (e.g., hedgerow or other boundary).

Invertebrate Sampling. Sampling for *T. elata* specimens and their associated slug larval hosts (*D. reticulatum*) were conducted to determine what effect, if any, the vegetative habitat parameters being monitored had on the presence and abundance of these species. Surveys for invertebrates only took place within the active summer season (June – August 2017).

Tetanocera elata *adults.* Adult *T. elata* were collected by passing a heavy-duty sweep net (45 cm diameter, mesh size 0.1 mm) in a figure-of-eight motion through vegetation. Collections were made using short transects (approx. 2 m) in randomised directions to cover the entire study site. Transects did not run through observation plots to avoid trampling vegetation, but sweeps extended into transects to cover vegetation by reaching into plots as transects ran adjacent. Sampling was conducted every two weeks during the flight period and occurred typically between 0900 and 1200 hrs. Recovered individuals were collected in barrel-style pooters (Watkins & Doncaster, The Naturalists, Hawkhurst, Kent, UK) and returned to laboratory facilities at the National University of Ireland Galway for examination. Sciomyzidae were examined using a dissecting stereomicroscope (Olympus SZ40, X6.7 to X40 magnification) and species and sex were confirmed morphologically (Rozkošný, 1984; Rozkošný, 1987). Field locations where *T. elata* were collected were marked as a “TE” plot using a bamboo stake (as described in “Local habitat selection”) and numbered chronologically as individuals were recovered throughout the flight period. Where *T. elata* were recovered within approx. 0.5 m of a designated (*a priori*) observation plot, the existing plot was given an additional “TE” designation to indicate *T. elata* presence.

Terrestrial slugs. Pitfall traps were deployed at the end of the summer (10 August) to survey for terrestrial slug species associated with *T. elata* habitats. To minimise disturbance to study areas, traps were placed at the exterior margins of each observational plot and baited with the intention of attracting slugs from within and around observational areas. Plastic cups (180 ml) were buried with the lip placed level at topsoil and contained a bait comprised of cotton wool soaked in dark beer (Smith & Boswell, 1970). Traps were covered with a corrugated plastic square (10 cm x 10 cm) held in place by two 150 cm nails to keep out precipitation and prevent potential disturbance. Four pitfall traps were set for each plot, one along each edge. Traps were deployed overnight for approximately 18 hours, and all collections were made in a single trapping event. All slugs collected in traps were recorded, including any slugs recovered on the exterior of the cup or on the corrugated plastic cover. Slugs were recorded as either “*D. reticulatum*” or “other”. Abundance of ground beetles (Coleoptera: Carabidae), numerous species of which are known to prey on slugs, were also recorded.

Ecological Measurements.

Measurement of plant community composition consisted of both percentage cover and abundance measurements. Percentage cover of plant species was assessed first by making a visual estimation of the proportion of the plot within the quadrat frame occupied by each species visible when viewed top-down. A species list of plants was then generated for each plot by hand-searching within the delineated area, including both visible and understorey plants, and morphologically identifying present species using vegetative keys (Clark, 2015; Streeter et al., 2009; Price, 2016). The relative abundance of each species identified when hand-searching was also ranked and scored using the DAFOR scale (e.g., dominant, abundant, frequent, occasional, or rare [Sutherland, 2006]). Plant community observations were made bi-weekly during the summer flight period (June – August 2017).

Vegetation structure was assessed via measurements of the height of live and dead vegetation as well as the depth of the detritus layer in the understorey. Heights of both live and dead vegetation were taken for each plot by lowering a metre stick through vegetation until the base rested on but did not penetrate the topsoil, and then taking the maximum measurement of live (growing) vegetation and dead vegetation *in situ* height at that point. Points were taken near each corner of the quadrat and at a random location within the frame and measurements were subsequently averaged to yield a mean live and mean dead vegetation height per plot. The detritus layer was measured similarly using a tapered garden stake (to better penetrate detritus to reach topsoil without compressing the layer) marked with corresponding measurements (cm). These measurements were completed in five random locations throughout the plot and pooled to give a mean detritus depth per plot. Unlike plant community analysis, structural features were measured only at the start and end of the adult flight season to track the seasonal growth of plants in survey plots.

Finally, vegetation “openness” (i.e., thickness or thinness of plant coverage) at each plot was measured at the beginning (16 June) and end (10 August) of the sampling period using the golf-ball method for rangeland assessment described by Schultz *et al.* (2017) to compare changes in plant structure over the peak growing period. Ten golf balls (fluorescent orange for easier visual detection [Links Choice, VA, USA]) were dropped perpendicularly into each plot from a height of approximately 2 m and each was assigned a score based on visibility of the golf balls. Lower scores (e.g., fewer golf balls visible) correspond to a “closed” vegetation structure suggesting more dense growth, while plots with high scores (e.g., higher visibility of golf balls) indicate a more “open” structure. The exception to this was where vegetation had such a closed structure that the balls could not penetrate; in these cases, golf balls were assigned a score of 0 associated with extremely dense vegetation (Schultz et al., 2017).

After the end of the peak summer growth season and *T. elata* flight period (September 2017), observations continued for percentage cover and height of live and dead vegetation every 6 to 8 weeks, dependent on weather conditions. The 2017 winter season experienced numerous storms in western Ireland, and observations were occasionally delayed when weather conditions were considered to be hazardous or when vegetation was not accessible (e.g., under snow). Observations continued until May 2018, to complete a 12 month survey period of primary parameters.

Indirect parameter assessment. In addition to direct measurements, other ecological parameters were calculated and examined for their potential influence on *T. elata* presence and abundance: light penetration (L), soil moisture (F), reaction/pH (R), and nitrogen content (N). These criteria were generated using Ellenberg index values for vegetation (Equation 1), adapted by Hill *et al.* (1999) for use in the UK. A weighted average for each plot was produced using flight period measurements, as adapted by Diekmann and Grerup (1998) where x = the median percentage cover for a species of plant in that plot over the duration of the study, y = the Ellenberg index value for the plant. Ellenberg values were calculated using measurements taken during *T. elata* flight period.

$$WA = \frac{(x_1 \times y_1) + (x_2 \times y_2) + \cdots + (x_n \times y_n)}{(x_1 + x_2 + \cdots + x_n)} \qquad \textbf{Eq 1}$$

2.4. Statistical Analyses. Analysis of categorical environmental factors (i.e., distance category from hedgerow and *T. elata* presence/absence) were completed using a Chi-square test. Comparisons of invertebrate collections in pitfall traps were conducted using Wilcoxon rank-sum or t-tests, as appropriate based on normality of data sets. Similarity of plant community (e.g., percent cover) and structure (e.g., vegetation height, depth of detritus, density) were compared between treatment types using individual measurements over the 12-month period using Kruskal-Wallis tests, with *post-hoc* Dunn tests with Bonferroni adjustment for multiple comparisons where Kruskal-Wallis were significant. Comparison was also made between plots pooled by *T. elata* presence or absence in a subset of plots along the east/southeast field margin near the hedgerow boundary (“E/SE subset”) (Fig. 1). This subset was isolated because plots along the eastern site margin accounted for nearly all *T. elata* presence, and restricting the analysis to these plots limited potential complicating variables, namely aspect. Additionally, data were restricted to “near” plots due to a significant correlation ($\chi^2_1 = 4.7055$, $P = 0.03$) between distance category and *T. elata* presence (as concluded by Chi-square analysis). These comparisons were performed using Wilcoxon rank-sum tests with continuity correction and approximate P-values to account for rank ties.

Principle components analysis (PCA) plotting environmental variables against *T. elata* presence/absence was carried out using PC-ORD v.6 (McCune & Mefford, 2011). The primary matrix was comprised of direct and indirect quantitative environmental variables, including: percentage cover of the five most abundant plant species (*Dactylis glomerata* L.

[Poales: Poaceae], *Festuca pratensis* Huds. [Poales: Poaceae], *Poa pratensis* L. [Poales: Poaceae], *Centaurea nigra* L. [Asterales: Asteraceae], and *Plantago lanceolata* L. [Lamiales: Plantaginaceae]), percentage cover of dead vegetation, mean height of live and dead vegetation, vegetation thickness, depth of detritus layer, and Ellenberg calculated values (light, moisture, reaction [pH], nitrogen). Measurements were entered as the mean value per plot over the 12 month trial period. The categorical variable of *T. elata* absence (0) or presence (1) comprised the second matrix and was used as a grouping factor. A preliminary PCA was conducted at a site level including all plots, and secondary PCAs were run subsequently using data from the E/SE subset for environmental variables recorded during the flight period and for the 12 month trial. All PCA analyses used a variance/covariance centred matrix with scores calculated based on distance biplot.

Following PCA analysis, environmental variables were examined for their influence on *T. elata* abundance in the E/SE subset with a multiple regression analysis, using values of Primary Components 1 and 2 as the independent variables and *T. elata* abundance as the dependent variable. Analyses (with the exception of PCA) were conducted using R (R version 3.2.5, R Core Team 2013, The R Foundation for Statistical Computing, Vienna, Austria) in R Studio.

Results

Invertebrate Sampling

During the summer flight period, a total of 32 individual *T. elata* were collected from 13 discrete plots within the field site (Table 1). Of the 13 plots where *T. elata* were recovered, seven plots were unique (54%) and six (46%) coincided with both expected and unexpected pre-designated survey plots (Table 1). Only two TE plots occurred distant from the hedgerow, with 85% of TE plots occurring at "near" proximity. Four individuals (12.5%) were recovered at plots designated as having a superficially dissimilar physical appearance ("unexpected") to where *T. elata* had been previously recovered, however 96% were collected near the hedgerow (Table 1), indicating the importance of this feature. Overall, there were significantly greater numbers of *T. elata* captured in "near" proximity to the hedgerow ($\chi^2_1 = 4.7055$, $P = 0.03$), and the majority of captures (87.5%) occurred near the hedgerow comprising the east/southeast margin of the site (Fig. 1). Based on these collection numbers, environmental factors were examined both at site level and for this E/SE subset specifically.

Pitfall trapping returned 31 slugs, including one *D. reticulatum*, in addition to 93 carabid specimens (Fig. S1). The only *D. reticulatum* recovered was found near the hedgerow. Within the E/SE subset, presence of *T. elata* was not associated with variability in slug density ($t = -0.48617$, $P = 0.9572$), however there were significantly fewer carabids recovered in plots where *T. elata* were present than in other plots ($t = -3.4378$, $P = 0.002$), potentially indicating a negative association.

Characterisation of Vegetation

Plant community. At site level, a total of 35 plant species/groups were identified across the plots during the 12 month period (Table 2). Grasses occurred at the highest frequency across all plots, the most frequent being *P. pratensis* (100%), *D. glomerata* (97%), and *F. pratensis* (72%). The most frequently occurring forb species throughout the site were *Centaurea nigra* (54%) and *P. lanceolata* (36%) (Table S1). Significant differences were observed between categories for each of these most frequently occurring species (Table S2), however *post-hoc* pairwise comparisons between plot types showed no consistent trends either across species or with respect to *T. elata* presence (Table S3). *Dactylis glomerata* cover was the most variable, while *F. pratensis* showed the least variability across plots (Table S3) The plant community composition described using the DAFOR scale was highly variable between plots (Table S1), and the species present where *T. elata* was recovered varied considerably between plots. Graminoids and forbs comprised similar proportions in all plot categories at site level, while scrub (*Rubus fruticosus*) and other vegetation types (e.g., *Pteridium aquilinum*, lichens and mosses) were present only in those categories of plots occurring near a hedgerow (Fig. 2A).

Vegetation in the E/SE subset demonstrated similar patterns to site-wide frequency and percentage cover. The E/SE subset of observational plots demonstrated similar relative frequencies of these dominant species (100%, 100%, 81%, 38%, and 38% respectively), and dead vegetation was again observed in all plots, with a mean percentage cover of 40.9 ± 3.0 SE. These dominant species provided similar coverage across plots pooled according to *T. elata* presence/absence (Table 2). As observed at site scale, graminoid and forb vegetation types were represented at similar levels in E/SE subset plots when pooled according to *T. elata* presence/absence (Fig. 2B). When pooled in this manner, plots where *T. elata* were present had significantly higher percentage cover of dead vegetation and *P. lanceolata* (W = 2268, $P = 0.0172$ and W = 2743.5, $P < 0.001$, respectively); no significant differences were observed in the remaining dominant species (Table 2).

Local structure. The majority of observational plots (62%), representing plots from every treatment category, received the maximum possible vegetation closeness score (0). The remaining plots were distributed in incrementally increasing categorical scores, corresponding to increasing vegetation openness (Table 3). In plots where *T. elata* specimens were recorded, the median vegetation closeness score was 0 and ranged from 0 to 3.5. A significant difference was observed in median vegetation openness between plot types (χ^2_4 =

10.692, $P = 0.0303$) with unexpected/distant plots having more open structure than any other plot type (Table 3), but not when pooled by *T. elata* presence/absence in the E/SE subset (W = 68, $P = 0.7855$).

At site level, maximum live vegetation height ranged from 1 cm to 150 cm, with a site-wide mean height of 46.8 cm ± 1.8 SE. In the plots where *T. elata* were recorded, live vegetation height ranged from 3 cm (overwinter) to 139 cm (peak summer). Maximum height was highly variable across plots and treatment types, with a mean live vegetation heights of 53.56 cm ± 11.4 SE (expected/near), 40.21 cm ± 9.5 SE (unexpected/near), 55.00 cm ± 12.0 SE (expected/distant), 44.84 cm ± 9.4 SE (unexpected/distant), and 42.18 cm ± 8.0 SE (TE) (Table 3). Live vegetation height differed between plot categories ($\chi^2_4 = 12.62$, $P = 0.0133$), but the high variance of heights within and between plot categories rendered pairwise comparisons nonsignificant when adjusted (Bonferroni) for multiple comparisons.

Maximum dead vegetation height at site-level ranged from 1 cm to 184 cm, with a site mean height of 33.24 cm ± 1.8 SE (Table 3). In plots where *T. elata* specimens were recovered the average dead vegetation height was 34.01 cm ± 8.9, with a range from 2 cm to 184 cm, representing the second shortest and tallest dead vegetation measurements at the site. The mean height of dead vegetation was greater in areas where *T. elata* were collected during the flight period than in most other plots (Table 3). Dead vegetation height varied significantly between plot categories ($\chi^2_4 = 14.607$, $P = 0.0056$), with significant pairwise differences observed between expected and unexpected/near plots (Z = 3.466, $P_{adj} = 0.0053$) as well as expected/near and unexpected/distant (Z = 2.996, $P_{adj} = 0.0274$). When plots were examined based on *T. elata* presence in the E/SE subset, mean dead vegetation height was greater and live vegetation was shorter on average in plots where *T. elata* was recovered (Fig. 3), though neither difference was statistically significant (W = 695, $P = 0.2621$ and W = 778, $P = 0.3573$, respectively).

Detritus depth had a site-wide mean of 5.7 cm ± 0.4 SE. In the plots where *T. elata* were recorded, the average depth was 6.00 cm ± 1.0. Measurements of detritus depth varied less than measurements of vegetation height, however there was still enough variability within plots of the same category to render comparisons between categories non-significant ($\chi^2_4 = 6.6312$, $P = 0.1567$) (Table 3). In the E/SE subset, there was no difference in detritus depth between plots pooled by *T. elata* presence/absence ($W = 83.5$, $P = 0.7855$) (Fig. 3).

Indirect parameters. Ellenberg values showed small variations between plots due to differences in light, moisture, pH, and nitrogen, however when means were calculated for each treatment there was little variation evident (Table 3). No significant differences existed for indirect parameters between plot types.

Effects of environmental factors on *T. elata* populations

At the site level, significantly greater abundance ($\chi^2_1 = 4.7055$, $P = 0.03$) of *T. elata* was recorded close to the hedgerow in comparison to distant plots. Results of site-level PCA produced two axes which accounted for over 97% of observed variation (83.5% and 13.8% on PC1 and PC2, respectively) in environmental factors, with near complete overlap between plots when grouped by *T. elata* presence/absence (Fig. 4A). When considering data from only the E/SE subset, there was a much clearer separation of groups based on *T. elata* presence/absence. During the flight period, PCA ordination accounted for over 99% of variation, with 82.9% attributed to PC1 and 16.3% explained by PC2 (Fig. 4B). Similarly, ordination of mean data over 12 months explained over 98% of variation; 86.2% represented on PC1 and 11.9% on PC2 (Fig. 4C). Environmental factors with R^2 values > 0.2 were overlaid as biplots on all PCA graphs, however only those related to structure (live and dead vegetation height, detritus depth, and density) resolved, and oriented on PC2 in all cases, indicating the presence of *T. elata* may be positively correlated with the height of dead vegetation and negatively correlated to live vegetation height. A multiple linear regression using the results of the E/SE subset PCA with 12-month data indicated significant differences in *T. elata* abundance with PC2 ($t = 2.512$, $P = 0.02733$), however the non-significant global values for the model ($F_{2,12} = 3.22$, $P = 0.07594$) suggest a lack of power to this relationship.

Discussion

The primary finding of the current study is that hedgerow proximity is significantly associated with *T. elata* populations. Similar effects may be observed for smaller patches of scrub and treelines within agroecosystems, as they likely provide valuable refugia, however isolated trees have not been observed to convey any benefit for *T. elata* (ABE, pers. obs.). The authors have observed anecdotally that hedgerows may be important features in habitats when collecting *T. elata*, and data presented here comprise the first instance which quantitatively supports this assertion. These results support growing evidence that presence and proximity of hedgerows have significant positive effects on the abundance of natural enemies, with a higher abundance of beneficial species closer to the hedgerow (Morandin et al., 2014; Holland et al., 2016; Garratt et al., 2017). A majority of *T. elata* specimens recovered in the study were collected near the south-eastern hedgerow border, in a grouping comprising the E/SE subset (Fig. 1). There are several possible explanations for this including hedgerow quality, a lack of connectivity between hedgerow sections (e.g., gaps in hedgerows for human or livestock movement or thin growth of hedgerow species), or hedgerow orientation relative to wind patterns and sun exposure. Although specific hedgerow characteristics were not quantified, the hedgerow bordering areas where most *T. elata* were recovered was characterised by a mixture of tall tree species (*Fraxinus* spp., *Acer* *pseudoplataus*, and *Fagus* spp.) commonly found in woodland habitats and smaller hedgerow species (*Crataegus monogyna*), compared to the other hedgerows in this study which were dominated by a single smaller species (*C. monogyna*). Hedgerow quality has been shown to influence invertebrate communities, with richness and abundance of beneficial invertebrate species (e.g., natural enemies and pollinators) increasing with increasing hedgerow quality. I Increased diversity of woody species and trees, hedges laid to prevent gapping, and the maintenance of a healthy understory (through reduced mowing and herbicide/pesticide application) are all known to contribute to increased arthropod biodiversity (Garratt et al., 2017). Localisation of *T. elata* around the southeast hedgerow could also be attributed to a lack of connectivity between hedgerows. Several gaps were observed in the hedgerow at the study site, primarily caused by a footpath leading from the grassland into adjacent woodland on the distal SE margin, and a large gap in the NE corner of the site used for livestock passage to adjacent fields. Patchy or uneven growth was also noted along the northern margin. Due to the sedentary behaviour of adult Sciomyzidae (Williams et al., 2009a; Williams et al., 2009b), the dispersal of *T. elata* to other hedgerows across the site may have been hampered by the lack of a continuous hedgerow, as has been observed for other invertebrates with limited dispersal capacity (Holland et al., 2016).

The study also revealed the positive association between *T. elata* presence and dead vegetation height, and an inverse relationship with live vegetation height. This contrasts somewhat with previous research, which while also finding vegetation structure to be an important factor influencing marsh fly communities (Williams et al., 2009a; Williams et al., 2009b), the structure discussed in literature refers to the height of living vegetation. In the current study, while plots in the E/SE subset did not significantly differ from one another in composition/structure based on *T. elata* presence, there was a significantly greater coverage of dead vegetation in plots where *T. elata* were recovered, potentially indicating a build-up of dead vegetation over an extended period of time. This observation coincides with records of *T. elata* being collected from ungrazed or abandoned agricultural land and grasslands (Knutson et al., 1965; Speight, 2004a; Speight & Knutson, 2012). When considering these findings in a three-dimensional scale, the combination of high cover and height suggests a greater overall volume of dead vegetation, again potentially indicative of grazing which is low-intensity or absent. This may be important for a number of reasons, such as providing a more sheltering canopy allowing for development of a mesocosm within, which is more buffered against changes in temperature, humidity, or light penetration (Gontijo, 2019). The larger amounts of decaying vegetation may also influence soil and invertebrate communities and provide desirable shelter and alternative food sources for slugs (Godan, 1983), including *D. reticulatum*. It would, therefore, benefit *T. elata* larvae greatly to also inhabit a similar spatial niche. Adult *T. elata* are known for having high patch fidelity and low dispersal rates (Speight & Knutson, 2012), which suggest if these areas do provide ideal juvenile habitats, the adult life stage will likely remain closely associated. There was no impact detected from detritus levels or vegetation openness as influencing *T. elata* presence, however it should be noted that the majority of plots throughout the study site were dominated by *D. glomerata*, a species that forms dense tussocks over several growing seasons. Tscharntke and Greiler (1995) have suggested that tussock-forming grasses are important for providing shelter for ground-dwelling arthropods, especially as they build up and decompose in regular cycles. Terrestrial slugs, such as *D. reticulatum*, are also known to associate with tussock-forming grasses for the shelter they provide (South, 1965). This tussock structure, combined with high volumes of dead vegetation, could provide valuable refuges for developing *T. elata* larvae. Carey *et al.* (2017) also identified an association of *T. elata* with wet grasslands dominated by *Juncus* spp. While these plants can also form dense tussocks, they do not possess the same amounts of dead vegetation build-up. This association, instead, may be considered similar to that with hedgerows and the shelter and shade supplied by these providing a different type of refugia.

While some significant differences were identified between plot categories in the coverage of the most abundant plant species, plant community composition did not show any consistent trends with relation to where *T. elata* were present throughout the study site. Collected individuals were distributed across nearly all *a priori* treatment types (all except unexpected/distant) possessing variable habitat parameters. The clustering of the E/SE subset may be explained in part by the site being bordered to the east by a river (Fig. 1), which likely created a physical boundary for distribution. Conversely, the north border of the site was adjacent to additional grass and pasture fields separated by gappy hedges, which may have allowed for more distribution if *T. elata* populations were present in that area.

Plant community composition in wet and dry grasslands can be confidently excluded as an important indicator of the presence and abundance of *T. elata* populations. This result was not unexpected as *T. elata* have been recorded in a variety of habitats (Knutson et al., 1965; Speight, 2001; Williams et al., 2007), which in itself suggests that *T. elata* are able to survive in a range of habitats and do not depend on particular host or shelter plants. This lack of association between *T. elata* and plant species may also be attributed to the distribution and feeding habits of its larval host/prey species (*D. reticulatum*) which is a generalist herbivore (Cook et al., 2000). It is also one of the most widely distributed terrestrial slug species, occupying a range of habitats from frequently disturbed tillage fields to intensively managed agricultural land to abandoned fields (Hunter, 1966; South, 1992). This association is widened still further as *T. elata* larvae mature to predaceous third instars, at which point they are capable of predating several other slug species (Knutson et al., 1965; Knutson & Vala, 2011; Giordani et al., 2014; Bistline-East et al., 2019), none of which have a specialist diet (Hunter, 1968; South, 1992). In addition to the larvae feeding on generalist molluscs, adult *T. elata*, which rely on a largely carbohydrate-based diet, are not known to associate with specific nectar-producing plants and have not been observed feeding on floral or extrafloral resources. Recent research has demonstrated that adult Sciomyzidae including *T. elata* may associate opportunistically with specialist and generalist insect herbivores (Hemiptera) to fulfil part or all of their dietary requirements by consuming honeydew (Bistline-East et al., 2018). Such herbivores may be expected to a distribution within a single site ranging from uniform to patchy, depending on the level of homogeneity of the site. However, even when a site may have a patchier distribution of Hemiptera, such as the one in which the current study was conducted, the range of dietary plasticity observed for T. elata means it is unlikely that adult flies were restricted in their distribution based solely on this trophic association.

When the Ellenberg index values for secondary habitat parameters were compared based on *T. elata* presence/absence, adult *T. elata* adults did not appear to be influenced by light penetration, soil moisture, soil pH, or nitrogen content throughout the site. However, as these values were calculated indirectly based on plant community, there may be some difference in actual environmental conditions within the understorey in locations where *T. elata* occurred compared to the wider site. Future research should aim to measure such factors directly (e.g., through the use of environmental data loggers).

The findings of this study (e.g., little to no association with particular plant communities) may in fact be promising for the potential for *T. elata* to be established as a self-sustaining natural enemy in a conservation biological control scheme because it means that the vegetation composition of arable field margins will not likely have to be heavily manipulated to provide a suitable habitat. The correlation of *T. elata* presence to hedgerow proximity is both promising and challenging for its potential future use in biological control. The findings of this study further validate the importance of maintaining hedgerows in field margins, in this case for the benefit of *T. elata* populations, but hedgerows are also widely acknowledged for their importance for other natural enemies, pollinators, and biodiversity within agroecosystems (Thomas & Marshall, 1999; Holland et al., 2016; Garratt et al., 2017; Van Vooran et al., 2017). In addition, hedgerows have been also shown to provide beneficial habitats for birds, mammals, and woodland plants (Garratt et al., 2017; Heath et al., 2017; Brien et al., 2016; Wehling & Diekmann, 2009). As a result, providing a habitat for *T. elata* can be multifunctional by also increasing biodiversity at the agroecosystem level. Within agroecosystems lacking hedgerows, it can now be recommended with confidence that establishment of a hedgerow is likely essential to support populations of this natural enemy. Although the planting of hedgerows is profitable over time, initial investment is high and could prove prohibitive for growers. It also takes time to establish high-quality hedgerows, which may result in introduced *T. elata* populations not initially being self-sustaining. This should also be considered as a deterrent for hedgerow removal. Aside from the general loss of biodiversity, the decision to reinstall hedgerows for the purposes of biological control can expected to be very costly and labour-intensive. Alternatively, *T. elata* population establishment may be more likely to succeed when introduced into sites which already benefit from well maintained, mature hedgerows. The current study recovered only two individuals in the central field of the study site, which indicates *T. elata* adults may not be inclined to disperse away from the hedgerow with which they are associated. In a biological control context, this could result in high levels of pest suppression around the edges of a crop field (e.g., the margin(s) nearest a hedgerow) but insufficient control of pests within the field itself. This could potentially be counteracted by establishing low hedgerows within tillage fields, similar to what is done with intercropped beetle banks, however this adds a degree of logistical difficulty with regard to the continued tillage and harvest of the field.

When considering the implication of vegetation structure for the use of *T. elata* as a self-sustaining biological control agent of slugs, it is important to note that the vegetation structure in the study site, which had not been mown or grazed for at least three years (E. O'Riordan, *pers. comm.*), differs from what would be found in and around tillage fields in agroecosystems. Specifically, the importance of land being undisturbed for extended periods should not be underestimated. Plots where *T. elata* adults were recovered were all characterised by tall, thick dead vegetation, which can only occur if grasses have been allowed to grow and die back over several cycles. If *T. elata* populations are to be established, the landscape requires areas of abandonment (e.g., unmanaged field margins or fallow portions of tillage fields), which may prove difficult or undesirable for some growers. Under the current Green Low-carbon Agri-environmental Scheme (GLAS) in Ireland, farmers are required to graze, mulch, or mow such areas at least once per year to be eligible to receive payment (DAFM, 2015); additionally, the Basic Payment Scheme (BPS) requires farmers to mow or graze grass margins annually (DAFM, 2017). Ultimately, habitat features of importance for *T. elata* populations and other arthropod biodiversity (e.g., ground beetles) should be easily applied to existing agroecological landscapes, especially those which already have some areas of semi-natural habitat, but some accommodations will likely need to be made with regard to the criteria of agri-environmental support schemes.

The identification of these features is the first step to developing a viable conservation biological control scheme (Holland et al., 2016) and lays the groundwork for future conservation biological control development. However, while this is a valuable first step, the authors acknowledge the small scale of the study. It should, therefore, be viewed as a preliminary case study and proof of concept and be used to conduct further wider scale studies in future. While a mild negative correlation was observed in the current study, between carabids and *T. elata*, this was the result of only a single night of sampling. For any true association to be made, a more robust survey of carabid populations is required, preferably across the entire flight period. Further research is also needed to examine what impact slug community composition, density, and distribution have on *T. elata*. It was beyond the scope of this study to directly survey the honeydew producers in the site. It has previously been shown that the chemical composition of honeydew can vary between species of producers (Douglas, 2006). Consequently, honeydew with a different chemical composition could impact the fitness of adult *T. elata*. The presence of a hedgerow rather than a grassy verge at field margins has previously been shown to increase densities of the honeydew producers such as aphids (Hemiptera: Aphidoidea) (Van Vooran et al., 2017) and should be further explored. Hedgerow characteristics were not examined in this study although this could now (based on the results of this project) be an important factor for the success of *T. elata* as a biological control agent.

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Author contributions

ABE conceived the overall scope for the studies presented here. ABE and DB designed the vegetation study and conducted field observations. Analysis of vegetation study was examined by DB (summer months) with further analysis by ABE (overall trends), with advice provided by CDW. The manuscript was prepared by ABE with contributions from DB. All research was overseen by MJG.

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Table 1. Plot classification and *T. elata* collection locations in Cow Park during the trial period (June – August 2017). Specimens that were recovered in the absence of designated plots were used to establish "unique" plots; others which were recovered within approx. 0.5 m of an *a priori* selected plot were associated with that plot as well as being given a TE designation. For these co-occurring plots, the associated plot is listed.

TE plot	No. *T. elata* collected	Hedgerow proximity	Unique plot?	*a priori* plot type
TE 1	3	Near	Y	-
TE 2	2	Near	Y	-
TE 3	9	Near	Y	-
TE 4	3	Near	N	U/N
TE 5	2	Near	N	E/N
TE 6	1	Distant	N	E/D
TE7	3	Near	N	E/N
TE 8	3	Near	Y	-
TE 9	1	Near	Y	-
TE 10	1	Distant	Y	-
TE 11	1	Near	N	U/N
TE 12	2	Near	Y	-
TE 13	1	Near	N	E/N
Site total	32			

Plot category abbreviations: E/N = expected/near; U/N = unexpected/near; E/D = expected/distant; U/D = unexpected/distant; TE = plot where *T. elata* was recovered

Table 2. Mean percentage cover of the five most abundant plant species and dead vegetation in E/SE subset, pooled based on *T. elata* presence or absence. Statistical comparisons are given per plant species between *T. elata* present and absent plots based on two-sample Wilcoxon tests, and indicated as significant (* P < 0.05) and highly significant (** P < 0.001).

	Mean Cover (%) ± SE			**P-value**	**Test statistic (W)**
	Subset total	***T. elata* present**	***T. elata* absent**		
Dead vegetation	40.9 ± 2.6	44.6 ± 4.0	34.0 ± 2.9	0.0173 *	2268
Dactylis glomerata	29.2 ± 2.0	28.6 ± 3.3	28.2 ± 3.3	0.6260	1250.5
Poa pratensis	12.1 ± 1.7	12.7 ± 2.5	12.0 ± 3.4	0.9960	1941.5
Festuca pratensis	11.6 ± 1.7	9.5 ± 1.5	13.7 ± 5.0	0.5013	2140
Centaurea nigra	1.7 ± 0.8	2.2 ± 1.4	1.0 ± 0.8	0.6940	2085.5
Plantago lanceolata	1.3 ± 0.5	1.6 ± 0.7	0 ± 0	< 0.0001 **	2743.5

Table 3. Summary of vegetation structure by plot category, including mean live and dead vegetation height (12 month and flight period means; min/max), mean depth of detritus layer, median vegetation thickness score (Schultz et al. 2017), and mean calculated Ellenberg values (Hill et al. 1999). Statistically significant differences between plot categories per variable are indicated by the same superscript letter. Pairwise differences are the result of *post-hoc* Dunn tests with Bonferroni adjustment for multiple comparisons following significant Kruskal-Wallis tests for each variable.

Plot category	Mean height (cm) ± SE (min – max)				Mean detritus depth (cm) ± SE	Median structure score	Mean Ellenberg values			
	Live vegetation		Dead vegetation							
	12 mo.	Flight Period	12 mo.	Flight Period			Light (L)	Soil moisture (F)	pH (R)	Nitrogen (N)
E/N	53.56 ± 11.4 (8 – 150)	90.97 ± 9.1 (8 – 150)	43.15^{A,B} ± 12.2 (3 – 184)	59.75 ± 14.4 (8 – 184)	5.65 ± 1.0	0	7.03 ± 0.2	5.10 ± 0.1	6.52 ± 0.2	5.38 ± 0.2
U/N	40.21 ± 9.5 (1 – 125)	69.70 ± 8.0 (2 – 125)	26.75^{A} ± 9.9 (1 – 121)	34.27 ± 12.0 (1 – 121)	5.39 ± 1.6	1.3	7.03 ± 0.1	5.22 ± 0.1	6.25 ± 0.1	5.23 ± 0.2
E/D	55.00 ± 12.0 (3 – 140)	91.86 ± 9.6 (5 – 140)	36.62 ± 11.5 (1 – 136)	52.09 ± 13.5 (1 – 136)	6.79 ± 1.6	0	7.16 ± 0.1	5.21 ± 0.1	6.71 ± 0.1	5.62 ± 0.1
U/D	44.84 ± 9.4 (7 – 110)	71.66 ± 6.4 (9 – 110)	27.09^{B} ± 8.2 (1.5 – 128)	34.94 ± 9.8 (1.5 – 128)	5.11 ± 1.6	0	7.06 ± 0	5.60 ± 0.2	5.96 ± 0.2	5.02 ± 0.1

TE	42.18 ± 8.0 (3 – 139)	78.35 ± 7.3 (8 – 139)	34.01 ± 8.9 (2 – 184)	56.34 ± 10.9 (4.5 – 184)	6.00 ± 1.0	0	7.17 ± 0.1	5.25 ± 0.1	6.61 ± 0.1	5.58 ± 0.2
Site	46.80 ± 1.8	80.48 ± 2.25	33.24 ± 1.8	47.01 ± 3.76	5.97 ± 0.4	0	7.07 ± 0.1	5.27 ± 0.1	6.40 ± 0.1	5.39 ± 0.1

Plot category abbreviations: E/N = expected/near; U/N = unexpected/near; E/D = expected/distant; U/D = unexpected/distant; TE = plot where *T. elata* was recovered

[A] Z = 3.466, $P = 0.0053$

[B] Z = 1.437, $P = 0.0274$

Figure 1. Habitat map of vegetation study site, Cow Park, Clarenbridge, Co. Galway.

Figure 2. Mean proportion of graminoids, forbs, and other growth (*Pteridium aquilinum*, *Rubus fruticosus*) per plot category over 12 months (**A**) at site level (E/N = expected/close; U/N = not expected/close; E/D = expected/distant; U/D = not expected/distant; TE + = *T. elata* present in plot) and (**B**) in the E/SE subset (TE + = *T. elata* present in plot; TE - = *T. elata* absent from plot).

Figure 3. Mean and range of vegetation heights (live and dead) and detritus depth over 12 months in plots from the E/SE subset. Plots are pooled by presence or absence of *Tetanocera elata* (TE).

Figure 4. Graphical representations of PCA ordinations, overlaid with environmental variables which resolved with an R^2 value greater than 0.2. (**A**) Site-level over 12 months; (**B**) E/SE subset in the flight period and (**C**) over 12 months.


Legend
Habitat map & features
Hedgerow/scrub (WL1/WS1)
Dry meadow (GS2)
Wet grassland (GS4)
Footpath
River
Site boundary
Plot categories
Expected/Near (E/N)
Unexpected/Near (U/N)
Expected/Distant (E/D)
Unexpected/Distant (U/D)
Tetanocera elata recovered (TE)
No. TE collected 1 2 3 9
0 50 m

Figure 1

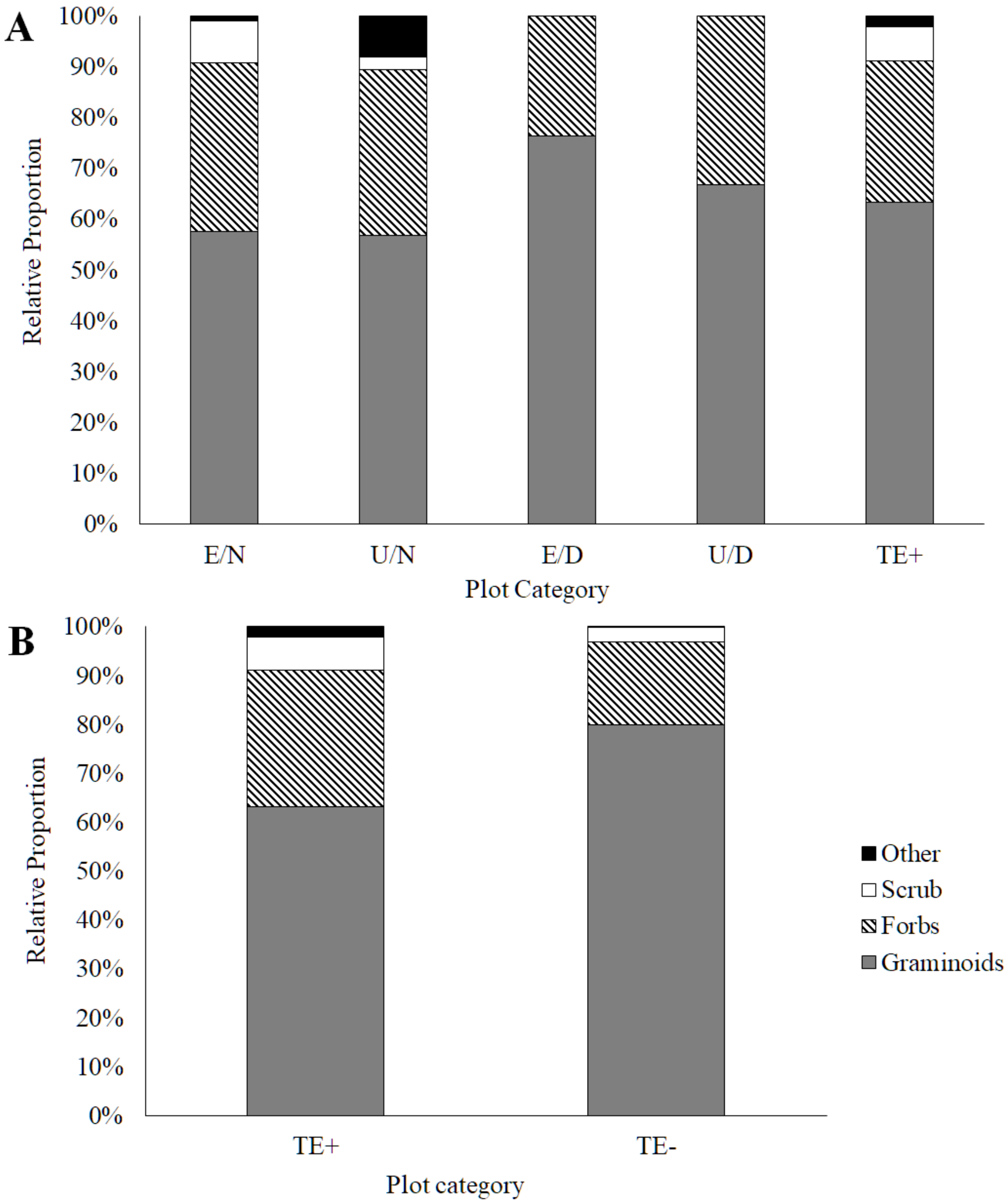

A
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Relative Proportion
E/N
U/N
E/D
U/D
TE+
Plot Category
B
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Relative Proportion
TE+
TE-
Plot category
■ Other
□ Scrub
▨ Forbs
■ Graminoids

Figure 2

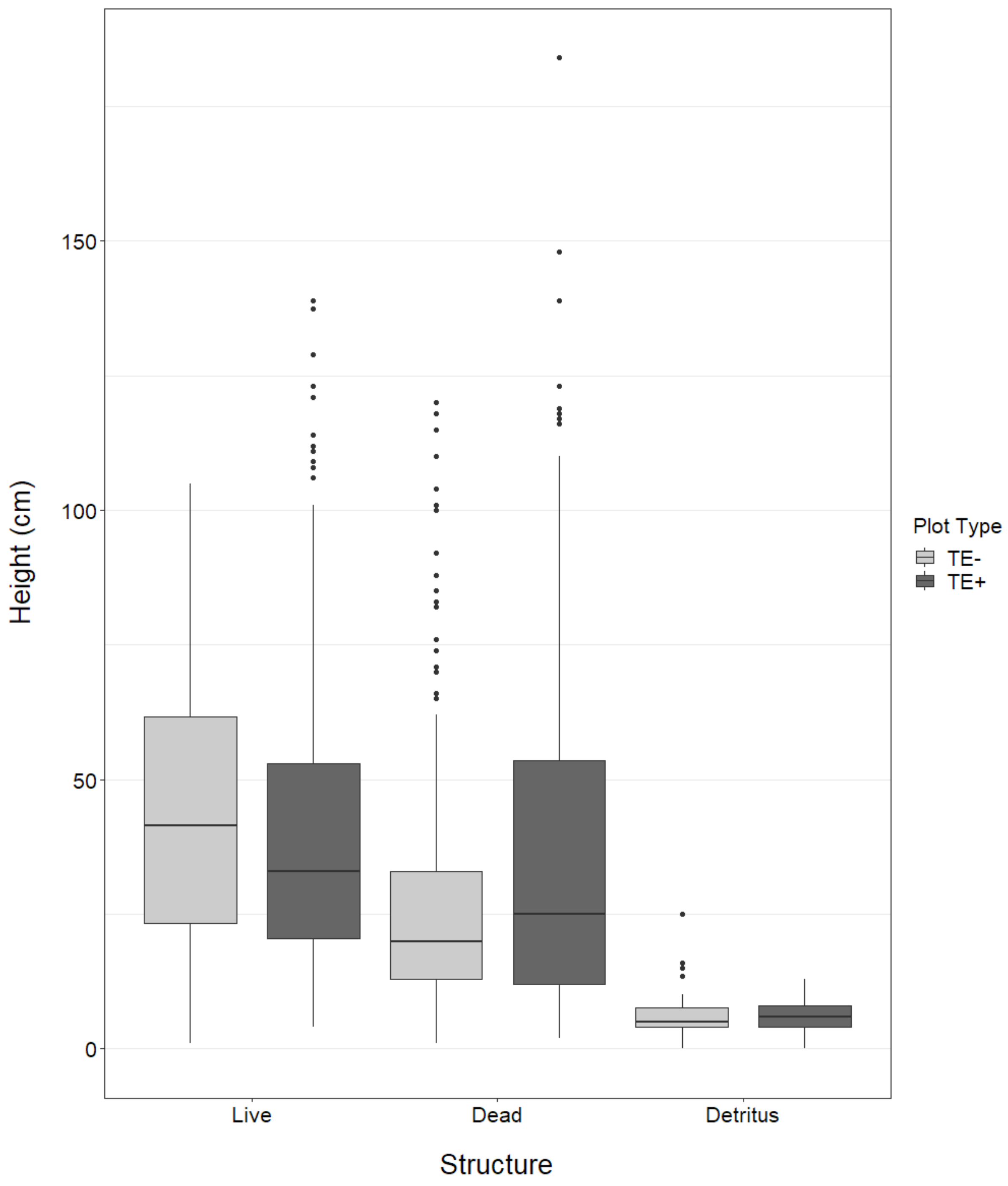
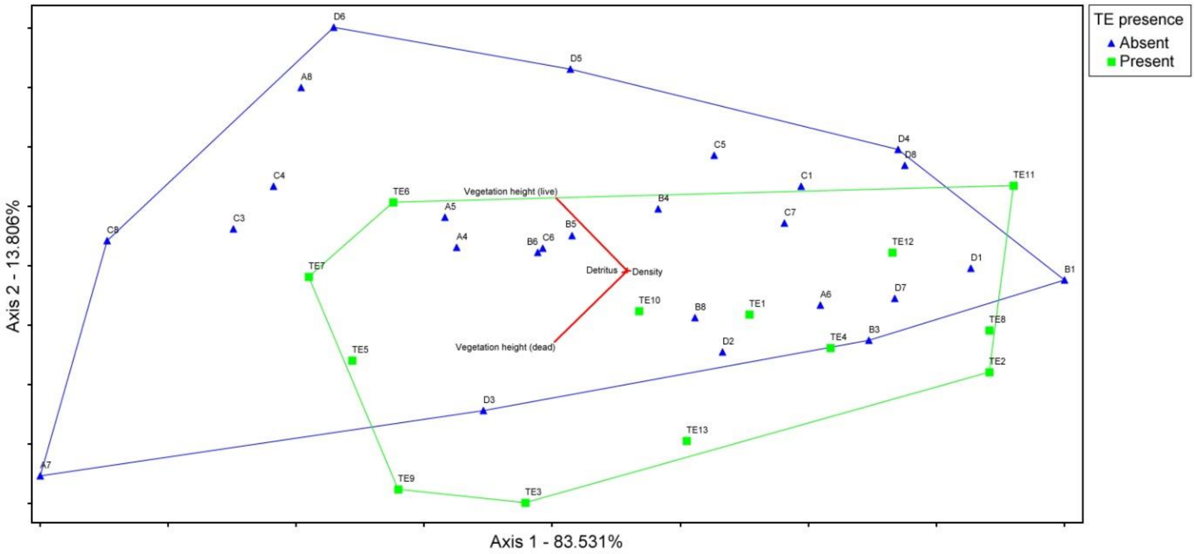
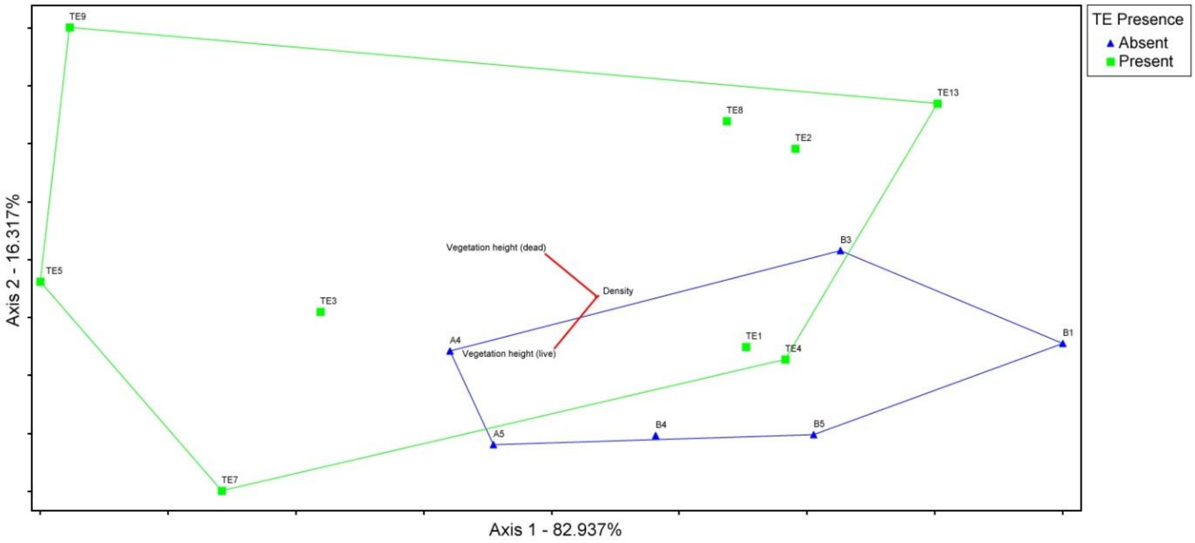

Height (cm)
150
100
50
0
Live
Dead
Detritus
Structure
Plot Type
TE-
TE+

Figure 3


TE presence
Absent
Present
Axis 2 - 13.806%
Axis 1 - 83.531%
D6
D5
A8
D4
D8
C5
C4
C1
TE11
TE6
Vegetation height (live)
B4
A5
C8
C3
C7
A4
B6
C6
B5
TE12
D1
TE7
Detritus
Density
B1
A6
D7
TE10
B8
TE1
TE8
Vegetation height (dead)
TE5
D2
TE4
B3
TE2
D3
TE13
A7
TE9
TE3


TE Presence
Absent
Present
Axis 2 - 16.317%
Axis 1 - 82.937%
TE9
TE13
TE8
TE2
Vegetation height (dead)
B3
TE5
Density
TE3
B1
A4
TE1
Vegetation height (live)
TE4
A5
B4
B5
TE7

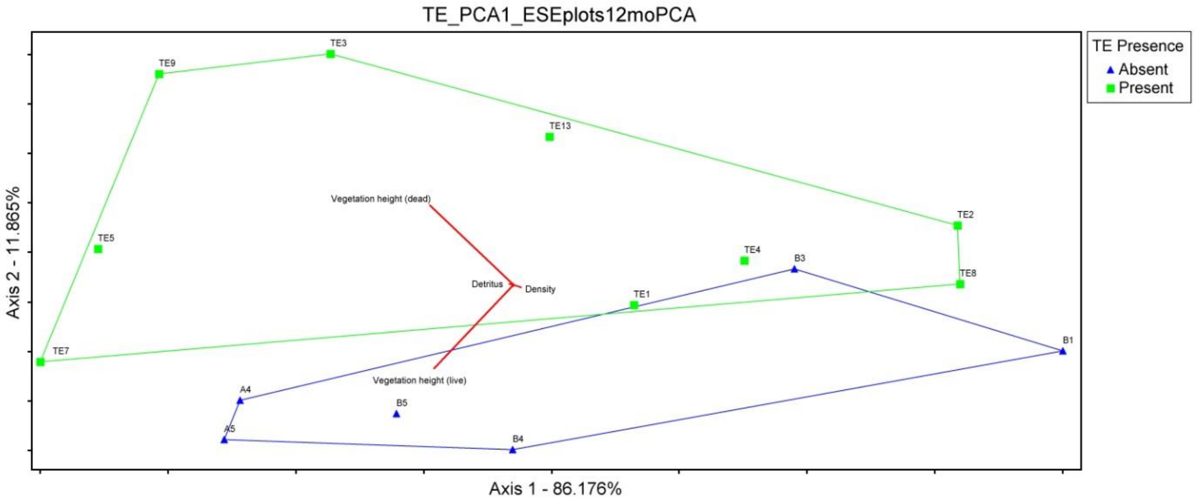

TE_PCA1_ESEplots12moPCA
TE Presence
Absent
Present
Axis 2 - 11.865%
Axis 1 - 86.176%
TE3
TE9
TE13
Vegetation height (dead)
TE2
TE5
TE4
B3
TE8
Detritus
Density
TE1
TE7
B1
Vegetation height (live)
A4
B5
A5
B4

Figure 4