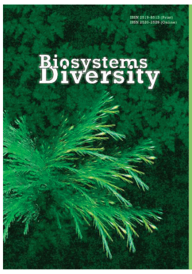

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# Traits and land transformation change the fortunes of grasshopper generalists vs. specialists in a biodiversity hotspot

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Understanding the link between species traits and how they use various elements in a heterogeneous agro-natural landscape is essential for conservation planning. Land-use and season affect the availability of resources for herbivorous insects such as grasshoppers. Also, the level at which these herbivores utilise these resources on the landscape depend on their traits. We focus here on the Cape Floristic Region biodiversity hotspot, which is rich in both endemic plants and narrow-range grasshoppers. We assessed dispersion patterns and abundance of the grasshopper species across the agro-natural mosaic, while specifically focusing on species traits and how they change over two seasons (spring and summer). We found that land-use and species traits played major roles in grasshopper spatial dispersion across the landscape, with season a highly significant variable. Not surprisingly, highly mobile, generalist feeders were abundant and widely dispersed across the landscape. Importantly however, this was especially the case in late season, when they could take advantage of high plant productivity in the vineyards. In contrast, low mobility, specialist feeders were limited to occupying only natural fynbos vegetation in both seasons. Generally, the highly mobile generalists benefitted in two ways: occupation of transformed areas, and receiving a population boost late season. This was not the case for the low-mobility specialists, which were doubly disadvantaged: not able to move far, and lacking their specific host plants in the transformed areas. From a conservation perspective, our results indicate the importance of improving functional connectivity using natural fynbos for conservation of the endemic specialists, while the generalists can largely look after themselves across this agro-natural mosaic.

*Keywords*: species traits; seasonality; grasshoppers; mobility; fynbos; vineyards.

## Introduction

Linking landscape patterns and species traits to ecological processes is important in landscape ecology (Chen et al., 2008; Smith et al., 2015). Animal dispersal, which is dictated by inherited traits, is vital for understanding how organisms effectively use different resources and features located in different patches across the landscape (Griebeler & Gottschalk, 2000; Ewers & Didham, 2006). For species that require heterogeneous habitats for persistence on the landscape, proximity of different patches containing the various habitats and the required resources are key (Taylor et al., 1993; Brooker et al., 1999; Schirmel et al., 2010; Mandelik et al., 2012). In the case of insects, this is often because different life stages require different resources or microhabitats for their development (Gardner et al., 1995; Jeanneret et al., 2003).

For instance, in the USA, wild bees use both agricultural and old fallow fields in different seasons while occasionally visiting natural fields (Mandelik et al., 2012). Similarly, in Sweden, semi-natural pastures act as population sources for the dispersal of butterflies to agricultural fields (Öckinger & Smith, 2007). This illustrates the importance of agriculture and other habitat patches (e.g. natural habitats) in maintaining populations of some arthropod species, especially out of the production season. In Germany, grasshoppers require a mixture of dwarf shrubs and sand dunes for their persistence (Schirmel et al., 2010). Others require wetlands or grassy areas (Van der Plas et al., 2012; Keller et al., 2013) emphasizing the importance of heterogeneous landscapes for some terrestrial insects. These studies help us to understand how to improve insect conservation, especially threatened species (Hansen, 2011), and emphasize that appropriate management is necessary to maintain population levels of highly impacted animals (Sayer et al., 2013). Biodiversity studies in agro-natural landscapes are important, because of the need to improve production without compromising species diversity (Hutton, 2010).

The Cape Floristic Region (CFR) biodiversity hotspot has an exceptional number of endemic species under threat (Myers et al., 2000), especially as the area is also used for intensive agricultural production (Mittermeier et al., 2004; Rutherford et al., 2006). Across such an important conservation area, identification of the relative importance of the various landscape elements that have particular conservation value is important when integrating production and conservation planning (Morris & Brown, 1992). A total of 19% of the total land cover of the CFR has been transformed for agricultural production (Maree & Govender, 2013), especially viticulture, while 78% is still covered by natural, sclerophyllous vegetation, mostly fynbos (Maree & Govender, 2013).

These differences in vegetation type and land-use directly and indirectly affect grasshopper population dynamics in the CFR (Adu-Acheampong et al., 2016). It has been known for some time that differences in vegetation type and land-use, as well as seasonal variations of temperature and other abiotic factors, influence grasshopper population dynamics directly (Uvarov, 1966), while resource availability can affect them indirectly (Smith & Capinera, 2005). For instance, sprouting of leaves in vineyards is ephemeral because it is a deciduous fruit, leading to the loss of faunal habitats in the winter season (Mullins et al., 1992), affecting grasshopper diversity indirectly through lack of food and microhabitats for life support. This resource loss can be off-set by intercrops between the vine rows. In contrast, fynbos vegetation is evergreen (Rutherford et al., 2006; Allsopp et al., 2014).

In a favourable habitat under optimal environmental conditions such as optimum temperature, rainfall and enough sunlight or insolation (Uvarov, 1966), grasshoppers have high quality resources necessary for effective development and maintenance of high population levels, which are not possible in adjacent and relatively poor habitats (Adu-Acheampong et al., 2016) i.e. conditions outside those mentioned earlier on. These population responses are regulated by traits such as their level of mobility, food preferences, as well as local dispersion patterns of their preferred habitat, all contributing to how and where they use various patches within agro-natural mosaics. Species with high mobility have a higher chance of locating and occupying optimal patches (Hansson & Åkesson, 2014). In contrast, species with low mobility are more confined to specific optimal habitats on the landscape, yet in the CFR, they are highly adapted to natural disturbances such as fire (Schlettwein & Giliomee, 1987). In addition, these patches must have adequate food requirements, which become critical for those species that are not only weakly mobile but also very particular in their food requirements, resulting in not all potential habitat patches being occupied. In contrast, polyphagous and highly mobile species can use many host plant species and move freely between patches in search of food (Wahlberg et al., 2002).

Being a food specialist with low mobility, yet highly adapted to local environmental events, compares strongly with being a food generalist with high mobility which can readily move to lessen the impacts of local events such as agricultural production. Differences in these two trait groups also determines how we approach the conservation of the two groups. Furthermore, food type and availability, as well as environmental conditions, change over time as well as space. So here, we investigate how two such grasshopper groups (high mobility food generalist vs. low mobility food specialists) respond in terms of abundance to patches in a CFR agro-natural landscape mosaic across two seasons: spring vs. summer. We relate occupation of patches to the grasshopper species traits (i.e. mobility and feeding types) according to availability of optimal conditions during the year. Specifically, we investigate how two habitat patches are used by the two grasshopper trait groups over two seasons, spring and summer.

Grasshoppers were selected for this study because they are known to be good indicators of change in the environment, especially in a landscape consisting of different vegetation patches (Hao et al., 2015; Adu-Acheampong et al., 2016, 2017). While it would not be surprising that highly-mobile, food-generalist species will be of lesser conservation concern than those of low-mobility and a more restricted diet, we hypothesize that the two trait groups will be moved further apart as a result of landscape transformation. In other words, vineyards, which have attractive cover crops will actually increase the abundance, and hence population viability of the high mobility/food generalist group, while disfavouring the low-mobility/food specialist group, and this widening of the gap between the two will be enhanced by greater food availability not just in terms of space, but also time of year. If this is true, there will be higher abundance of highly mobile/food generalists during the summer season, when plant production is optimal in the inter-rows of vineyards, but change little in natural fynbos. Furthermore, we hypothesise that there will be less change in grasshopper abundance across seasons in the fynbos, as the native plants are evergreen, as opposed to seasonal planting of cover crops in the vineyards, where abundance will track plant productivity. This characteristic fluctuation in grasshopper abundance can be linked to habitat occupancy where species occupy the best possible habitats dictated by vegetation conditions and species traits. We then make recommendations for grasshopper conservation in this CFR agro-natural landscape.

## Materials and methods

*Geographical areas and sampling seasons.* Two land-use types, natural fynbos vegetation and vineyards, were sampled at 32 sites within four geographic areas in two sampling seasons. The elevation of sampling sites ranged from 90 to 592 m a.s.l. The selected geographical areas within the CFR were Stellenbosch (33°55'56" S, 18°51'37" E), Somerset West (34°04'33" S, 18°50'36" E), Paardeberg (34°27'00" S, 19°36'00" E) and Grabouw (34°09'08" S, 19°00'13" E). Within these areas, we selected these farms: Vergelegen at Somerset West, Delvera and Delheim at Stellenbosch, Slent and Vondeling at Paardeberg and Paul Cluver at Grabouw. All fynbos sites were in protected areas: Hottentots Holland at Grabouw, Jonkershoek at Stellenbosch, Helderberg at Somerset West and Limietberg provincial nature reserves at Paardeberg. The four areas constituted four independent landscape mosaics because they were distant from each other (23–35 km to the nearest site), and largely separated by mountains. These distances, while seemingly short for northern-hemisphere temperate regions, are biogeographically highly signifycantly different for the CFR (Vrdoljak & Samways, 2014) (Fig. 1).

The two sampling seasons in which the study was conducted were, an early one (late spring to mid-summer) called 'spring' throughout and spanning November to February. The other season was the late season (late summer to early autumn) called 'summer' throughout and spanning February to April.

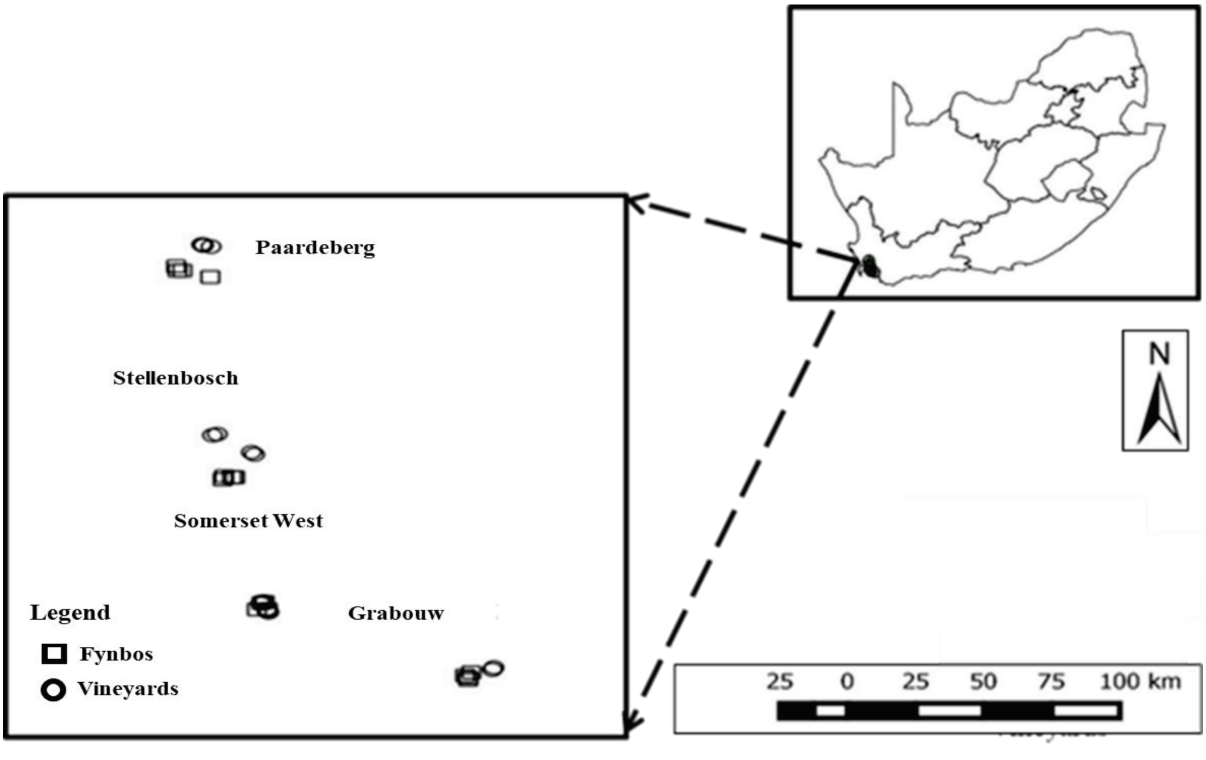

**Fig. 1.** The study area in the Cape Floristic Region, South Africa: thirty-two sites were sampled at four locations and in two land-use types; the map shows how the thirty-two sites are distributed across the four study areas

*Sampling grasshoppers.* Sampling was conducted on clear sunny days with low wind speed by two collectors on four occasions (two per season) between 09:00 and 17:00. A 50 x 50 m quadrat was delineated at the centre of each site >30 m from the edges, to avoid edge effects (Bieringer et al., 2013). The choice of quadrat size was based on successful use elsewhere in South Africa (Bazelet & Samways, 2012). Grasshoppers were initially flushed out of the swards, with individuals seen hopping, walking or flying caught with an insect net (Larson et al., 1999; Bazelet & Samways, 2012). The timed quadrat count method is appropriate for scrubland vegetation (fynbos) and vineyards (Gardiner et al., 2005; Bazelet & Samways, 2012). Captured grasshoppers were frozen and later identified in the laboratory using Dirsh (1965), Jago (1984), Johnsen (1984, 1991), Spearman (2013) and Cigliano et al. (2016). Cape Nature granted a permit for collection of specimens, which are retained in the Entomology Museum, Department of Conservation Ecology and Entomology, Stellenbosch University.

Two traits, feeding preference and degree of mobility, were chosen to characterise species (Grunshaw, 1986; Bazelet & Samways, 2012). Traits of individual species were identified according to Dirsh (1965), Jago (1984), Johnsen (1984, 1991), Grunshaw (1986), Bazelet & Samways (2012) and Cigliano et al. (2016). For 10 out of the 37 species, traits were inferred from their closest relatives (mostly in the same genera) as no other information was available. The extrapolation was mainly done at the genus level. Grasshoppers were grouped into either 1) medium/high mobility ('high') and highly polyphagous, graminivorous to mixed feeders ('generalist feeders') (HMG), or 2) low mobility and plant species-restricted feeders ('specialist feeders') (feed on certain grasses, Restionaceae and forbs, LMG). Grasshoppers belonging to subfamilies Acridinae, Oedipodinae and Eyprepocnemidinae were placed in the HMG group (Ritchie, 1981; Bazelet & Samways, 2012) while, mostly apterous to brachypterous, low mobility species in the Hemiacridinae subfamily and the Lentulidae familiy were placed in the LMG group. These two main groups were demarcated for easy analysis and interpretation of our study results. Fluctuations of grasshopper abundances within the different habitats were used as proxy measures for habitat occupancy in this study.

All selected vineyard sites used Integrated Production of Wines guidelines (IPW, www.ipw.co.za), and between vine rows were interrows of several green leafy cover crops in summer (Fig. 2a) but no or minimal dry cover crops in spring (Fig. 2b). The most important cover crops were *Raphanus raphanistrum*, legumes (*Vicia* spp.), *Hypochoeris radicata*, rye grasses (*Lolium* spp.), *Bidens pilosa*, *Erodium moschatum*, and oats (*Avena fatua*).

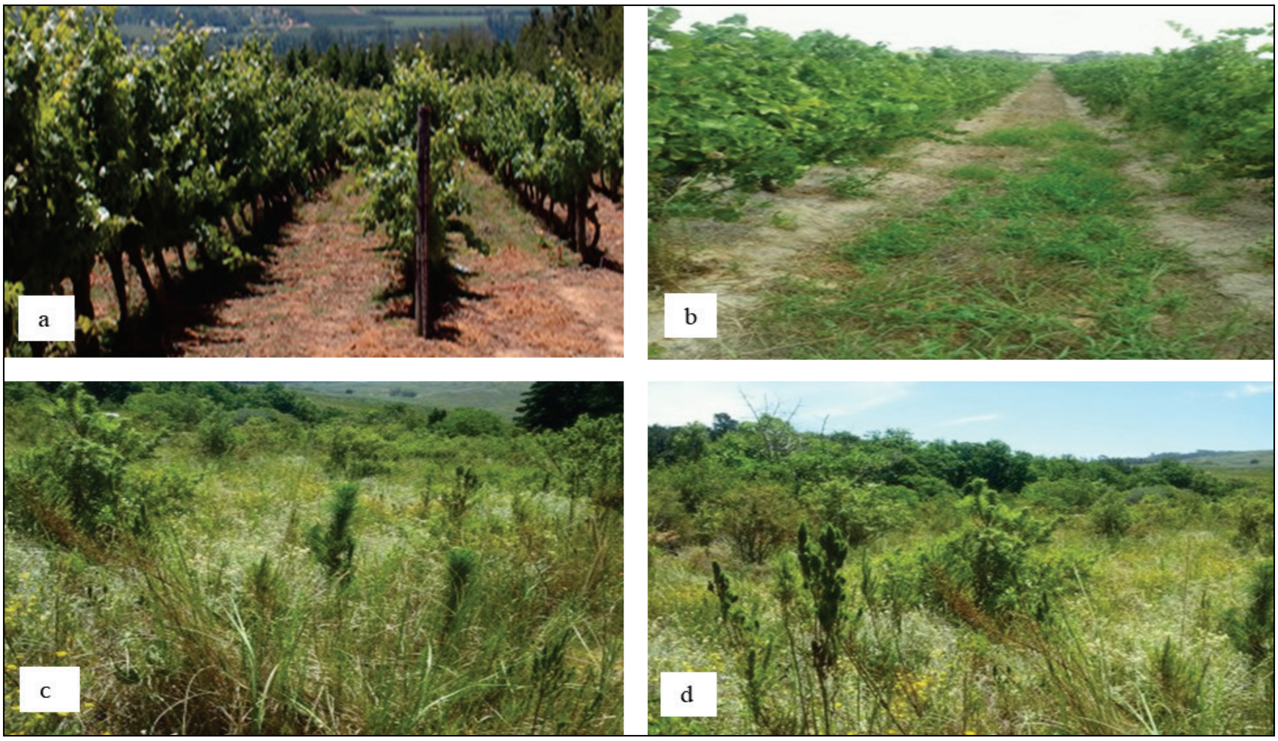

**Fig. 2.** Interspersed cover crops in between rows of vines in spring (*a*) and summer (*b*), and in natural fynbos vegetation in spring (*c*) and summer (*d*)

Pure natural fynbos, defined as a scrubland dominated by Restionaceae, Ericaceae and Proteaceae, and high in endemic plant species (Rutherford et al., 2006), was the reference natural vegetation used. Fynbos plant phenology does not differ significantly between the two seasons because there are different flowering times for different plant species in fynbos especially for Restionaceae (Cowling et al., 2003; Rouget et al., 2003). Because of these alternating flowering times for different species the fynbos biome constantly has flowers and vegetative parts throughout hence no differences in the phenology could be observed at any time of the year. The unchanging phenology of the fynbos impacts on the abundance of different grasshopper species at different times throughout the year with some species populations peaking in spring while others peak in summer.

*Statistical analyses.* Generalized linear mixed model (GLMM) fit by maximum likelihood (Laplace Approximation) were constructed in Statistica 13.0 and used to compare grasshopper abundance of each of the above-mentioned groups based on seasonality and land-use. Poisson distribution was used because the response variable was discrete count data and GLMM was also used to account for the underlying spatial structure in the experimental design. For analysis, abundance of grasshoppers was categorised into spring (early season) vineyards (ESV), spring fynbos (ESN), summer (late season) vineyards (LSV), and summer fynbos (LSN).

We specifically compared grasshopper abundance (dependent variable) of each of the two groups (HMG and LMG) based on land-use type (vineyards/fynbos) in different seasons (spring vs. summer) as independent variables. In other words, we assumed that the abundance of each of the two trait groups depended on land-use type and season. Spearman's correlation analysis was constructed in Statistica version 13.2 to relate group dispersion patterns to different seasonal dispersion patterns to ascertain any relationships.

## Results

We recorded a total of 37 species, most of which (24 species) were in the HMG (high mobility/generalist) trait group. A total of 1916 individuals were in the HMG group, and 198 individuals in the naturally very rare, CFR endemic LMG (low mobility/food specialist) group.

**Table 1**
Abundance of grasshopper species in the two trait groups based on two land-uses and two seasons in the Cape Floristic Region

| Species | Species traits | ESN | ESV | LSN | LSV |
|---|---|---|---|---|---|
| *Acanthacris ruficornis ruficornis* (Uvarov, 1924) | HMG | 2 | 4 | 2 | 35 |
| *Acrida* sp1. | HMG | 16 | 2 | 20 | 24 |
| *Acrotylus bilobatus* (Miller, 1932) | HMG | 2 | 0 | 3 | 1 |
| *A. deustus* (Thunberg, 1815) | HMG | 2 | 6 | 2 | 19 |
| *A. apricarius* (Stål, 1873) | HMG | 2 | 0 | 3 | 10 |
| *Aiolopus thalassinus thalassinus* (Fabricius, 1781) | HMG | 6 | 29 | 7 | 81 |
| *Anaeolopus dorsalis* (Thunberg, 1815) | HMG | 22 | 150 | 30 | 400 |
| *Calliptamicus semiroseus* (Serville, 1838) | HMG | 75 | 20 | 58 | 66 |
| *Cyrtacanthacris aeruginosa* (Stoll, 1813) | HMG | 3 | 0 | 8 | 6 |
| *Eyprepocnemis calceata* (Serville, 1838) | HMG | 50 | 60 | 50 | 134 |
| *Gastrimargus crasicollis* (Saussure, 1888) | HMG | 5 | 2 | 5 | 7 |
| *G. determinatus vitripennis* (Walker, 1871) | HMG | 3 | 0 | 4 | 0 |
| *Gymnobothrus carinatus* (Uvarov, 1941) | HMG | 8 | 1 | 20 | 4 |
| *G. linea-alba* (Bolívar, 1889) | HMG | 3 | 0 | 6 | 0 |
| *Heteropternis couloniana* (Saussure, 1884) | HMG | 40 | 5 | 49 | 32 |
| *H. pudica* (Serville, 1838) | HMG | 10 | 0 | 15 | 3 |
| *Keya capicola* (Uvarov, 1941) | HMG | 3 | 0 | 6 | 1 |
| *Oedaleus nigrofasciatus* (De Geer, 1773) | HMG | 10 | 7 | 17 | 33 |
| *Paracinema tricolor tricolor* (Thunberg, 1815) | HMG | 0 | 0 | 2 | 2 |
| *Paragymnobothrus rufipes* (Uvarov, 1925) | HMG | 10 | 0 | 11 | 0 |
| *Plegmapterus sinuosus* (Martínez y Fernández-Castillo, 1898) | HMG | 6 | 2 | 5 | 10 |
| *Sphingonotus nigripennis* (Serville, 1838) | HMG | 1 | 7 | 2 | 17 |
| *Thyridota nasuta* (Johnsen, 1991) | HMG | 0 | 0 | 2 | 2 |
| *Vitticatantops humeralis* (Thunberg, 1815) | HMG | 7 | 30 | 16 | 75 |
| *Devylderia bothai* (Dirsh, 1956) | LMG | 3 | 0 | 4 | 0 |
| *D. coryphistoides* (Sjöstedt, 1923) | LMG | 1 | 0 | 1 | 0 |
| *Dictyophorus spumans* (Thunberg, 1787) | LMG | 1 | 2 | 2 | 2 |
| *Euloryma cederbergensis* (Spearman, 2013) | LMG | 0 | 2 | 0 | 0 |
| *Eu. lapollai* (Spearman, 2013) | LMG | 6 | 0 | 10 | 0 |
| *Eu. lasernorum* (Spearman, 2013) | LMG | 12 | 0 | 9 | 0 |
| *Eu. ottei* (Spearman, 2013) | LMG | 15 | 16 | 47 | 10 |
| *Eu.* sp. 1 | LMG | 1 | 0 | 1 | 0 |
| *Eu. umoja* (Spearman, 2013) | LMG | 10 | 3 | 12 | 6 |
| *Gymnidium cuneatum* (Rehn, 1944) | LMG | 2 | 0 | 4 | 1 |
| *G.* sp. 1 | LMG | 0 | 0 | 1 | 0 |
| *Lentula minuta* (Dirsh, 1956) | LMG | 7 | 0 | 7 | 0 |

*Notes*: ESV – early season in vineyards, ESN – early season in fynbos, LSV – late season in vineyards, LSN – late season in fynbos, HMG – medium to high mobility and graminivorous to mixed feeders, LMG – low mobility and forb to mixed feeders.

The result of the GLMM indicated a statistically significant difference between the abundance of the LMG group according to land-use type (vineyard vs. fynbos) (Z = 6.83, P < 0.01, Fig. 3a, b). However, there were no significant differences in abundance between seasons for each land-use separately (Z = 0.23, P = 0.82). Furthermore, GLMM results for different seasons for the HMG group showed significant differences (Z = –2.70, P < 0.05, Fig. 3c, d). This was because the late season samples in the HMG group showed significantly higher abundance than the rest (i.e. spring in vineyards and fynbos, Fig. 3b, d, Table 2).

**Table 2**
Results of Wilcoxon's matched-pairs test of abundance of two groups of grasshoppers based on species traits and land-use two seasons in vineyards and fynbos

| Grasshopper groups | Paired land-uses and seasons | GLMM by maximum likelihood |
|---|---|---|
| LMG | vineyard vs. fynbos | Z = 6.83 P < 0.01** |
| | early vs. late | Z = 0.23, P = 0.82* |
| HMG | vineyard vs. fynbos | Z = 7.16, P < 0.01** |
| | early vs. late | Z = –2.70, P < 0.05** |

*Note*: HMG – medium/high mobility and highly polyphagous, graminivorous to mixed feeders ('generalist feeders'), LMG – low mobility and plant species-restricted feeders ('specialist feeders') (feed on certain grasses, Resionaceae and forbs; ** – significantly different, * – no significant differences.

Spearman's correlation analysis between group dispersion patterns per land-use in spring vs. summer in vineyards showed a strong positive correlation between the HMG and summer dispersion patterns ($r_s = 0.87$, $P < 0.05$). The LMG group on the other hand, showed a very weak positive correlation between summer dispersion patterns in vineyards ($r_s = 0.07$, $P > 0.05$). Summer abundance was used as the basis for comparison because it was near to three times that of spring. The LMG group showed no significant difference in abundance between the two land-uses within each of the two seasons. In contrast, the HMG group showed a significant difference between summer samples in vineyards compared to the rest. Higher grasshopper abundance in both land-uses and seasons corresponds to using more patches for the HMG and the reverse is the case for the LMG groups. The summary of findings of this study showing the relationship between grasshopper mobility, trophic level and land-use is presented in Figure 4.

## Discussion

Land-use had a major effect on site abundance (measure of habitat occupancy), and varied according to both grasshopper species traits, and importantly, also season. Highest abundance was in vineyards in summer for most species in the HMG group (high mobility/generalist feeders), which also use many patches on the landscape. In contrast, there were no clear differences in abundance within the LMG group (low mobility/specialist feeders) between the two seasons and the two land-use types. Furthermore, they used less patches than the HMG species. In effect, they were rare on both land-use types investigated in the study.

The seasonal abundance response must also be seen against changes in vegetation structure, which were far less in fynbos compared to vineyards (Fig. 2c, d vs. 2a, b). Summer coincides with peak plant production in the vineyard inter-rows. Species abundance of the most dominant species, e.g. *A. dorsalis*, *H. couloniana*, *E. calceata* and *C. semiroseus* (all in the HMG group) were likely influenced by an increase in palatable cover crops in the inter-rows, as found elsewhere (Pyke et al., 1977; Kruess & Tscharntke, 2002). Yet in vineyards in spring, there were no significant differences in abundance between fynbos and vineyards. However, when more productive vineyard vegetation conditions developed in summer, there was a great increase in abundance of HMG vineyard grasshoppers compared to those in natural fynbos.

The characteristic spatio-temporal distribution pattern of the HMG species group, coupled with their high mobility traits, and their ability to take advantage of high plant productivity in late summer, suggest that although occupation of patches is mainly based on suitability of habitat, it is nonetheless achievable because the grasshoppers can also easily move across the landscape. Also, being highly generalist feeders, means that HMG species can survive in both fynbos and vineyards where a wide range of palatable plants are present in both land-use types, but particularly in summer vineyards. In contrast, the LMG species traits in combination with seasonal abundance in both fynbos and vineyards, meant that these species did not use vineyards to any great extent at any time. Besides their adverse response to agricultural land transformation production in general (Adu-Acheampong et al., 2016), they characteristically have low mobility, which disadvantages them in moving between optimal habitat patches. Fynbos leafy vegetation changes little across seasons (although the flowers change greatly) (Cowling et al., 2003; Rouget et al., 2003), and so historically under natural conditions, it has not been necessary for LMG species to expend a great deal of energy in their search of readily-available host plants at any time of year. However, the continuity within their natural habitat is broken for these LMG species by the presence of vineyards. Furthermore, the absence of their host plants means also that there are no possible attractive feeding sites in vineyards. This contrasts greatly with the HMG species, which are provided with great occupation opportunities by the vineyards, especially late season.

A further consideration is the dynamics of the landscape, which change over time, with, for example German grasshopper diversity strongly associated with community succession of alluvial pine woodland and steppe grasslands (Fartmann et al., 2012; Helbing et al., 2014). The passing of time also leads to changes in spatial differences in vegetation and soil, including in the agro-natural landscape of the CFR (Adu-Acheampong et al., 2016, 2017). Such spatio-temporal and habitat quality differences have an effect on grasshopper life stages, which require different resources at different development times e.g. early instar nymphs prefer a different type and food structure compared to later ones (Uvarov, 1966; Jeanneret et al., 2003; Gardiner et al., 2005). These various life history requirements define 'the habitat' of any one species, and which can be affected even by subtle anthropogenic impacts, which may not all be negative, as with our HMG in summer vineyards. German bush-crickets (Orthoptera: Tettigoniidae) have a higher rate of persistence under optimal habitats surrounded by sub-optimal ones than optimal habitats only (Griebeler & Gottschalk, 2000). Indeed, human impacts appear to variously impact different grasshopper species at different times (Matenaar et al., 2015). The vineyards and fynbos here provide such heterogeneous environments for these life history traits, especially the HMG species, with seasonality of the CFR being an important factor in this.

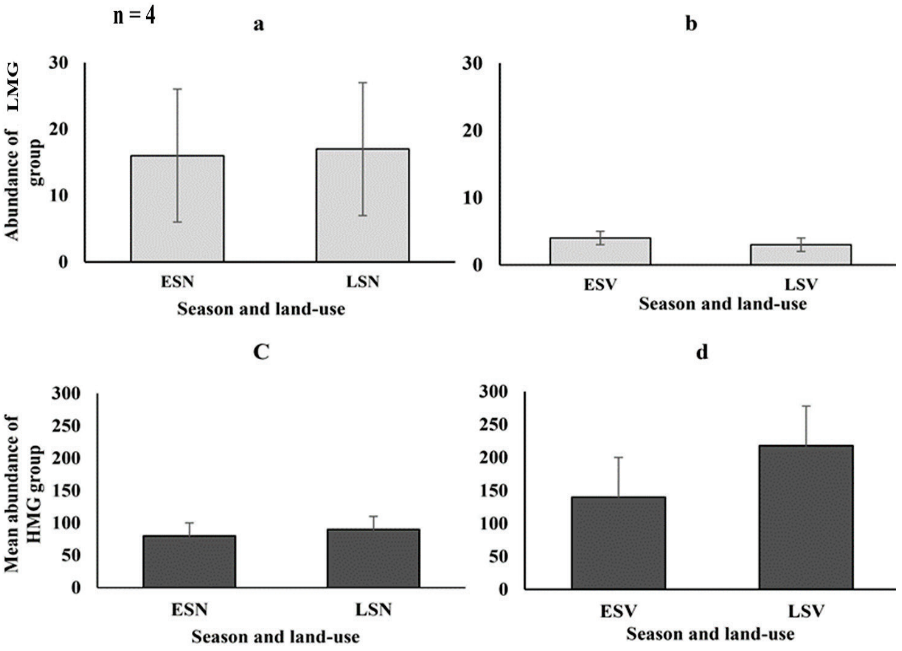

**Fig. 3.** Mean ± SE seasonal abundance of two trait groups of grasshoppers LMG and HMG: LMG – low mobility, specialist feeders, HMG – high mobility, generalist feeders, ESN – spring in fynbos, ESV – spring in vineyards, LSN – summer in fynbos, LSV – summer in vineyards; the study was conducted at 32 sites on 4 occasions (n = 4, N = 128)

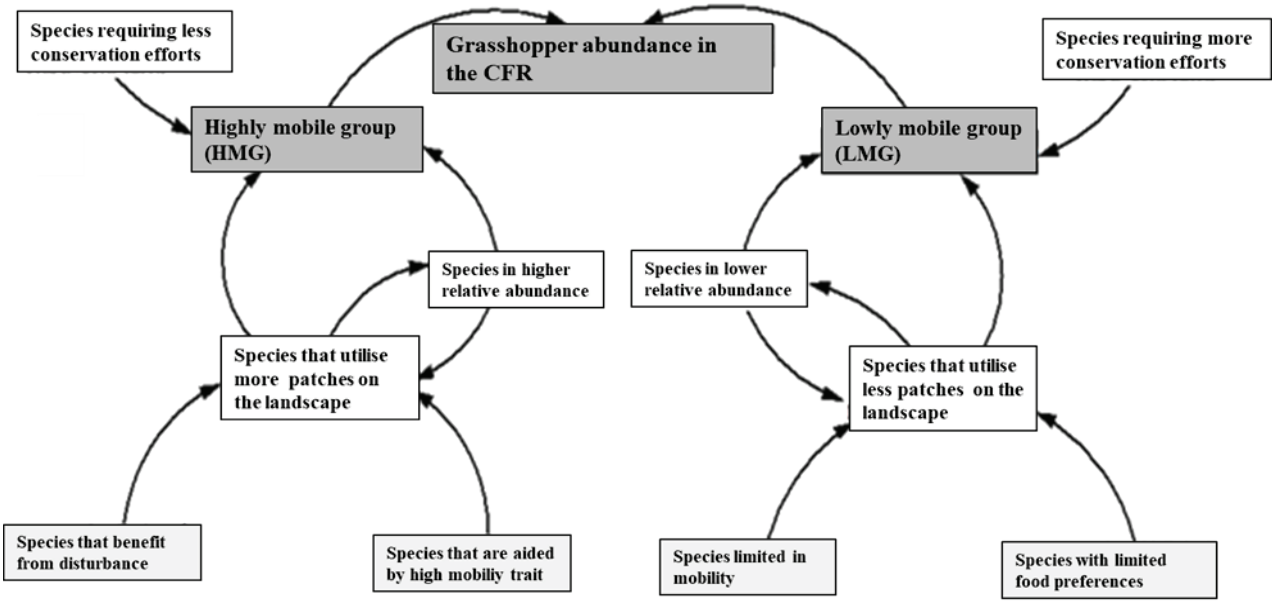

**Fig. 4.** Summary of findings of grasshopper use of different patches in the agro-natural landscape of Cape Floristic Region (CFR): arrows in the graph point towards inclusion; HMG – high mobility, generalist feeders, LMG – low mobility, specialist feeders

Most Lentulidae, Hemiacridinae, Eyprepocnemidinae, Pyrgomorphidae and some Oediponidae (mostly apterous to brachypterous, localised/endemic, forb to mixed feeders with limited to medium mobility) species use only one or few habitat patches in heterogeneous landscapes. This is because most species in these groups, especially Hemiacrididae (Spearman, 2013) and Lentulidae species (except for a few, such as *E. ottei*), are only associated with fynbos with slight changes in densities throughout the seasons (Matenaar et al., 2014, 2018). Under optimum environmental conditions these species will locate the best possible habitats in the fynbos or any other patch on the landscape within a particular period of the year (Loreau et al., 2013).

## Conclusions

Grasshopper species that are highly mobile and generalist feeders occupy more patches across the landscape than do the low mobility specialist feeders, which only use those with high natural value that are continuously available. This means from a conservation point of view that the highly mobile generalist feeders are more than being simply maintained across the agro-natural mosaic, for they are actually benefitting from the transformed areas. Importantly, this is particularly the case in the lush summer vineyards with an abundance of cover crops. The conservation perspective on the rare, endemic, low mobility specialists is completely different. They are strongly disadvantaged by the transformed vineyard patches. This means that to conserve these species, there needs to be good functional connectivity in the form of conservation corridors linking high quality remnants across the CFR landscape, summarized in Figure 4.

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