Soil Invertebrates in Different Agricultural Ecosystems in Greece

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Κεφάλαιο 1

Περίληψη στα Ελληνικά

1.1 Εισαγωγή

Οι άνθρωποι χρησιμοποιούν περισσότερο από το ένα τρίτο της παγκόσμιας φυσικής παραγωγής επι της ξηράς. Περίπου 52 εκατομμύρια τετραγωνικά χιλιόμετρα χρησιμοποιήθηκαν το 2004 για αγροτική παραγωγή σε όλο τον κόσμο. Αυτή η κατάσταση έχει προκαλέσει πολλά προβλήματα στο περιβάλλον. Όμως, αν στο μέλλον σκοπεύουμε να θρέψουμε ικανοποιητικά τον ανθρώπινο πληθυσμό του πλανήτη μας, 1,2 εκατομμύρια τετραγωνικά χιλιόμετρα γης θα πρέπει να μετατραπούν σε νέες καλλιεργήσιμες εκτάσεις έως το 2030. Αυτό σημαίνει ότι καθώς οι φυσικοί βιότοποι ¨πιέζονται¨ περισσότερο, η προστασία της άγριας φύσης στα αγροτικά οικοσυστήματα μπορεί να αποκτήσει μεγαλύτερη σημασία.

Οι αγροτικές περιοχές με υψηλό επίπεδο ετερογένειας έχουν βοηθήσει στην προστασία της άγριας φύσης. Οι περιοχές αυτές δημιουργούν τις κατάλληλες συνθήκες για την ύπαρξη ομάδων ασπόνδυλων όπως, π.χ., Carabidae, Araneae και Lepidoptera.

Πολλές αγροτικές περιοχές στην Ελλάδα έχουν υψηλό ποσοστό ποικιλότητας καλλιεργιών. Αυτό σημαίνει ότι οι περιοχές αυτές είναι ετερογενείς και κατετμημένες σε διαφορετικά είδη χρήσεως. Οι εν λόγω περιοχές αποτελούν το κατάλληλο πεδίο για τη διερεύνηση των επιδράσεων της ετερογένειας στην άγρια φύση.

Σκοπός της μελέτης αυτής, είναι η σύγκριση ανάμεσα σε ετερογενείς και ομοιογενείς αγροτικές περιοχές, με γνώμονα τις διαφορετικές πτυχές της ετερογένειας τους. Για τη σύγκριση των ετερογενών και ομοιογενών αγροτικών περιοχών χρησιμοποιήθηκαν τα αποτελέσματα που προέκυψαν από την τοπογραφική ανάλυση. Επιπρόσθετα, η μελέτη επεδίωκε τη σύγκριση των ετερογενών και ομοιογενών περιοχών βάση των ταξινομικών βαθμίδων των ασπόνδυλων, τη σύγκριση των οικογενειών των Coleoptera, των ειδών των Carabidae και τα μορφοείδη των φυτών. Τέλος, η κανονικοποιημένη ανάλυση αντιστοίχισης χρησιμοποιήθηκε για να προσδιοριστούν ποιες πτυχές της ετερογένειας των περιοχών έχουν την μεγαλύτερη επιρροή στις βιοκοινότητες των Carabidae.

1.2 Μέθοδοι

Η περιοχή μελέτης που επιλέχτηκε ήταν η κοιλάδα του ποταμού Σπερχειού, στον νομό Φθιώτιδας. Οι συντεταγμένες της περιοχής έρευνας είναι οι ακόλουθες, $38^\circ 53' 52.32''$N, $22^\circ 15' 49.58''$E (Σχήμα 3.1). Η κοιλάδα του Σπερχειού διαθέτει καλλιέργειες, λιβάδια, δάση, χέρσες περιοχές και τμήματα γης που βρίσκονται σε καθεστώς αγρανάπαυσης.

Επιλέχτηκαν τρεις μικρότερες περιοχές, οι οποίες περιείχαν μια (α) ετερογενή περιοχή και μια (β) ομοιογενή περιοχή. Οι ετερογενείς περιοχές αντιστοιχήθηκαν με τις ομοιογενείς περιοχές και βρίσκονταν σε παρόμοιο υψόμετρο, παρόμοιες αποστάσεις από τους κύριους δρόμους, τους ποταμούς, από τις μεγάλες δασικές εκτάσεις και από τις μεγάλες χέρσες περιοχές.

Από τις 3 ετερογενείς και 3 ομοιογενείς περιοχές, επιλέχτηκαν τέσσερα ζεύγη χωραφιών. Ένα μέλος κάθε ζεύγους χωραφιών επιλέχτηκε στην ετερογενή περιοχή και το άλλο στην ομοιογενή περιοχή. Τα ζεύγη χωραφιών αντιστοιχήθηκαν με βάση τον τύπο καλλιέργειας, τον προηγούμενο τύπο καλλιέργειας, την ηλικία της καλλιέργειας, το χρόνο της συγκομιδής, τα φυτοφάρμακα, τα λιπάσματα που χρησιμοποιήθηκαν καθώς και το εάν οι καλλιεργήσιμες εκτάσεις αρδεύονται ή όχι. Οι τύποι καλλιέργειας στα ζεύγη των χωραφιών ήταν, καλαμπόκι, ελαιόδενδρα, σιτάρι και βαμβάκι.

Για κάθε περιοχή μελέτης δημιουργήθηκε ένας χάρτης με τη χρήση δορυφορικών φωτογραφιών. Τα όρια των χωραφιών επισημάνθηκαν στους χάρτες, ενώ προσδιορίστηκε η χρήση για κάθε κομμάτι γης (Σχήματα 1, 2 και 3). Λόγω του μεγάλου μεγέθους της περιοχής 3, δημιουργήθηκαν δύο χάρτες. Ο χάρτης της περιοχής 3bi παρουσιάζει την περιοχή γύρω από το χωράφι με το σιτάρι, ενώ η περιοχή 3bii παρουσιάζει την περιοχή γύρω από το χωράφι με το βαμβάκι.

Πλέγματα αποτελούμενα από τετράγωνα των 25 τετρ. μέτρων έκαστο, τοποθετήθηκαν πάνω από τους προαναφερθέντες χάρτες. Οι τύποι χρήσης γης σε κάθε τετράγωνο καταχωρήθηκαν ως ακέραιοι αριθμοί, δημιουργώντας πίνακες στοιχείων, οι οποίοι εισήχθησαν στο πρόγραμμα FRAGSTATS. Το πρόγραμμα χρησιμοποιήθηκε για την τοπογραφική ανάλυση (landscape analysis) των περιοχών μελέτης, η οποία πραγματοποιήθηκε σε τρία επίπεδα. Οι μετρήσεις πραγματοποιήθηκαν στο επίπεδο των χωραφιών, στο επίπεδο του είδους χρήσης των χωραφιών και στο επίπεδο της περιοχής. Για κάθε περιοχή δημιουργήθηκαν δύο διαφορετικοί πίνακες στοιχείων, με το πρώτο πλέγμα να καλύπτει έκταση 10 εκταρίων και το δεύτερο μία έκταση 50 εκταρίων. Αυτό οφείλεται στις διαφορές του μεγέθους μεταξύ των υποπεριοχών και αυτό διότι ένας πίνακας που είχε το κατάλληλο μέγεθος για τις ετερογενείς περιοχές, εάν είχε χρησιμοποιηθεί σε μία ομοιογενή περιοχή θα προκαλούσε την απώλεια πολλών στοιχείων από την συγκεκριμένη περιοχή. Από την άλλη πλευρά, όταν τα πλέγματα των 50 εκταρίων χρησιμοποιήθηκαν στις μικρές ετερογενείς περιοχές, προέκυψε αρκετός κενός χώρος. Έτσι για να συγκρίνουμε τις μετρήσεις, οι οποίες μεταβάλλονται ανάλογα με το μέγεθος της υπό εξέταση περιοχής, χρησιμοποιήθηκαν για ένα μικρό αριθμό μετρήσεων, τα πλέγματα των 10 εκταρίων. Όλες οι άλλες μετρήσεις πραγματοποιήθηκαν με τη χρήση των πλεγμάτων των 50 εκταρίων. Συνολικά πραγματοποιήθηκαν 19 είδη διαφορετικών μετρήσεων, οι οποίες κάλυψαν πολλές πτυχές της ετερογένειας των υπο μελέτη περιοχών (Σελίδα 33).

Η λήψη δειγμάτων για τα ασπόνδυλα πραγματοποιήθηκε μεταξύ Μαΐου-Οκτωβρίου, με τη χρήση παγίδων παρεμβολής. Δέκα παγίδες τέθηκαν σε κάθε χωράφι, σε απόσταση 10 μέτρων η μία από την άλλη. Οι παγίδες τοποθετήθηκαν σε ίση απόσταση από τα όρια των χωραφιών και περισυλλέγονταν κάθε 15 ημέρες. Η πρόσβαση στα χωράφια εξαρτήθηκε από τις εργασίες που έκαναν οι αγρότες σε αυτά, με αποτέλεσμα να μην εξεταστούν όλα τα ζεύγη χωραφιών κατά την διάρκεια της κάθε περιόδου δειγματολειψίας.

Τα ασπόνδυλα ταξινομήθηκαν σε ανώτερα τάξα. Τα Coleoptera αναγνωρίστηκαν ως προς την οικογένεια και τα Carabidae ως προς τα είδη ή τα υποείδη που ανήκουν. Τα χωράφια στα οποία πραγματοποιήθηκε η έρευνα συγκρίθηκαν με βάση τη σχετική αφθονία των τριών ομάδων που αναφέρθηκαν νωρίτερα, δηλαδή των ταξινομικών βαθμίδων των ασπονδύλων, των οικογενειών των Coleoptera, και των ειδών των Carabidae

Τα δεδομένα που χρησιμοποιήθηκαν για την πραγματοποίηση της εν λόγω σύγκρισης, προήλθαν από 40 αξιοποιήσιμες παγίδες, οι οποίες είχαν τοποθετηθεί σε κάθε χωράφι. Με βάση τα δεδομένα που προέκυψαν από αυτές τις παγίδες, υπολογίστηκε και ο αριθμός των ειδών για κάθε χωράφι. Ακολούθως υπολογίστηκαν οι δείκτες ποικιλότητας (δείκτης Simpson, Whittaker, Shannon και Margalef) και ο δείκτης ομαλότητας (δείκτης Shannon) με βάση τα δεδομένα που αντλήθηκαν από τις 40 αξιοποιήσιμες παγίδες. Αξιοποιώντας τα αποτελέσματα του δείκτη Shannon και όλες τις μετρήσεις που υπολογίστηκαν κατά τη διάρκεια της τοπογραφικής ανάλυσης, πραγματοποιήθηκαν εν συνεχεία οι δοκιμές συσχέτισης. Κατά αυτό τον τρόπο, προσδιορίστηκαν οι μετρήσεις που σχετίζονταν στενότερα με την ποικιλότητα Carabidae και των φυτών.

Επιπλέον πραγματοποιήθηκαν συγκρίσεις μεταξύ των διαφορετικών ειδών καλλιεργειών. Στις συγκρίσεις αυτές αξιοποιήθηκαν όλα τα δεδομένα των ασπόνδυλων που προέκυψαν από τις 80 παγίδες που τοποθετήθηκαν σε κάθε καλλιέργεια.

Έξι διαφορετικές μέθοδοι χρησιμοποιήθηκαν για να εκτιμηθεί ο συνολικός αριθμός των ειδών Carabidae (species richness estimates) σε κάθε χωράφι μελέτης, ενώ για τα μορφοειδή φυτά χρησιμοποιήθηκαν πέντε μέθοδοι.

Τελικά, η σχετική αφθονία (relative abundance) για κάθε οικογένεια Coleoptera και για κάθε τάξα ασπόνδυλων, υπολογίστηκε ανά παγίδα σε κάθε ένα από τα χωράφια μελέτης. Και στην περίπτωση αυτή χρησιμοποιήθηκε η δοκιμή Mann-Whitney U για να εξεταστεί η στατιστική σημασία των πληροφοριών που συγκεντρώθηκαν.

Για τη διεξοδικότερη μελέτη της σχετικής αφθονίας των ασπόνδυλων, χρησιμοποιήθηκε η μέθοδος ανάλυσης ομάδων (cluster analysis). Η παραπάνω μέθοδος χρησιμοποιήθηκε σε δείγματα Carabidae, σε δείγματα των οικογενειών των Coleoptera και στα στοιχεία που σχετίζονται με την αφθονία των ανώτερων τάξα. Για την ανάλυση των ομάδων χρησιμοποιήθηκε ο αλγόριθμος UPWGA και το μέτρο διαφορετικότητας Bray-Curtis.

Από τις περιοχές δειγματοληψίας λήφθηκαν επίσης περιβαλλοντικά δείγματαήτα καθώς και δείγματα φυτών. Τα περιβαλλοντικά δείγματα που συγκεντρώθηκαν ήταν, υγρασία εδάφους, θερμοκρασία εδάφους, pH εδάφους, ένταση φωτός, η σύσταση της οργανικής ύλης και τέλος το είδος του εδάφους. Το ποσοστό κάλυψης του κάθε μορφοείδους φυτών καταγράφηκε και ένα δείγμα από κάθε μορφοείδος φυτών συγκεντρώθηκε και συντηρήθηκε. Τα δεδομένα τα οποία χρησιμοποιήθηκαν για την ανάλυση προήλθαν από το σύνολο των 50 δειγμάτων που συλλέχθηκαν σε κάθε χωράφι μελέτης.

Τα φυτά αναγνωρίστηκαν με βάση το μορφοείδος, ώστε ένα είδος να μπορεί να διακριθεί από τον άλλο. Επιπλέον υπολογίστηκε το σύνολο των δεικτών ποικιλότητας των δεδομένων που προήλθαν από την μελέτη των φυτών. Οι διαφορές στην ποικιλότητα μεταξύ των ετερογενών και των ομοιογενών περιοχών εξετάστηκαν και ακολούθως οι διαφορές στην ποικιλότητα μεταξύ των διαφορετικών καλλιεργειών εξετάστηκαν. Τέλος πραγματοποιήθηκαν δοκιμές συσχέτισης αξιοποιώντας τα στοιχεία του δείκτη Shannon και όλες τις μετρήσεις.

Τα περιβαλλοντικά στοιχεία που συλλέχθηκαν περιελάμβαναν, την μέτρηση της εδαφικής υγρασίας, της εδαφικής θερμοκρασίας, του εδαφικού pH, της εδαφικής οργανικής ουσίας, του μεγέθους των εδαφικών μορίων και το επίπεδο του φωτός.

Για την μελέτη της σύνθεσης των ειδών των Carabidae χρησιμοποιήθηκε η ανάλυσης αντιστοίχισης (Correspondence Analysis - CA). Τα στοιχεία που χρησιμοποιήθηκαν για την ανάλυση προήλθαν από τις 40 αξιοποιήσιμες παγίδες από το κάθε χωράφι της μελέτης. Στα στοιχεία αυτά έγινε λογαριθμισμός πριν από την ανάλυση. Το επόμενο βήμα ήταν η διερεύνηση των επιρροών των περιβαλλοντικών μεταβλητών στα Carabidae χρησιμοποιώντας την κανονικοποιημένη ανάλυση αντιστοίχισης (Canonical Correspondence Analysis - CCA).

Χρησιμοποιήθηκε η CCA για την ανεύρεση των περιβαλλοντικών μεταβλητών που είχαν την μεγαλύτερη επιρροή στα Carabidae. Στην δεύτερη φάση της ανάλυσης, αυτά τα περιβαλλοντικά δεδομένα χρησιμοποιήθηκαν ως συμμεταβλητές. Η διαδικασία αυτή απέκλεισε την επιρροή των περιβαλλοντικών μεταβλητών από την ανάλυση. Επίσης μία νέα ομάδα ανεξάρτητων μεταβλητών, η οποία δημιουργήθηκε από τις μετρήσεις που έγιναν κατά την διάρκεια της τοπογραφικής ανάλυσης, χρησιμοποιήθηκε στη CCA. Εντούτοις, πολλά από τα αποτελέσματα των μετρήσεων της τοπογραφικής ανάλυσης συσχετίστηκαν έντονα. Για αυτό το λόγο, πολλές από τις μετρήσεις αφαιρέθηκαν πριν από την ανάλυση. Η στατιστική δοκιμή τύπου Monte Carlo permutation πραγματοποιήθηκε και για δεύτερη φορά. Από την δοκιμή αυτή βρέθηκαν οι πτυχές της ετερογένειας που επηρεάζουν περισσότερο τα Carabidae.

1.3 Αποτελέσματα

1.3.1 Τοπογραφική Ανάλυση

Επίπεδο των Χωραφιών—Οι ετερογενείς περιοχές είχαν γενικά: μικρά χωράφια μελέτης, χωράφια μελέτης που βρίσκονταν μακριά από τα χωράφια του ίδιου τύπου καλλιεργειών και χωράφια μελέτης που βρίσκονταν μακριά από τα χωράφια παρόμοιου τύπου χρήσης γης (Σελίδα 42).

Επίπεδο του Είδους Χρήσης—Οι ετερογενείς περιοχές είχαν γενικά: λιγότερες καλλιέργειες, μεγαλύτερες εκτάσεις με δάσος, φυσική περίφραξη από θάμνους και κομματιών γης που δεν καλλιεργούνταν. Επιπλέον, οι ετερογενείς περιοχές περιελάμβαναν τις μεγαλύτερες περιοχές του ημι-φυσικού βιότοπου, τις περιοχές με τη χαμηλότερη ομοιότητα των καλλιεργειών. Τα κομμάτια γης του ημι-φυσικού βιότοπου στις ετερογενείς περιοχές, ήταν ανάμεικτα με άλλου είδους καλλιεργειών. Τα τμήματα γης των καλλιεργειών ήταν διεσπαρμένα και αναμεμειγμένα. Τα κομμάτια του δάσους και της φυσικής περίφραξης από θάμνους, ήταν περισσότερο συγκεντρωμένα. Εντούτοις τα κομμάτια του δάσους και της φυσικής περίφραξης από θάμνους ήταν λιγότερο καλά συνδεδεμένα. Τέλος τα χέρσα τμήματα γης ήταν καλύτερα συνδεδεμένα (Σελίδα 44).

Επίπεδο των Περιοχών—Οι ετερογενείς περιοχές είχαν γενικά: μεγαλύτερο αριθμό κομματιών διαφορετικής χρήσης της γης, μικρότερα κομμάτια γης, χαμηλότερη εγγύτητα των διαφορετικών τύπων χρήσης γης και χαμηλότερη ομοιότητα των τύπων χρήσης γης.

Είχαν επίσης τη χαμηλότερη συνόρευση τύπων χρήσης γης και τη χαμηλότερη συνάθροιση των τύπων χρήσης γης. Οι τύποι χρήσης γης ήταν καλύτερα αναμεμειγμένοι στις ετερογενείς περιοχές. Επιπλέον στις ετερογενείς περιοχές υπήρχε μεγαλύτερος αριθμός διαφορετικών τύπων χρήσης γης και ποικιλότητας (Σελίδα 55).

Ασυνήθιστα Αποτελέσματα για την Περιοχή 3—Κατά τη διάρκεια της έρευνας στην περιοχή 3 αρκετές μετρήσεις κατέληξαν σε διαφορετικά αποτελέσματα από τις περιοχές 1 και 2 (Πίνακα 4.42). Όπως φαίνεται η διαφορά μεταξύ των ετερογενών και των ομοιογενών περιοχών στην περιοχή μελέτης 3 δεν ήταν τόσο ξεκάθαρη όσο στις περιοχές μελέτης 1 και 2. Για αυτούς τους λόγους η ταξινόμηση των περιοχών a και b θα μπορούσε να έχει αντιστραφεί, αλλά επειδή αυτό δεν ίσχυε για όλες τις μετρήσεις, η ταξινόμηση των υπο-περιοχών της περιοχής 3 παρέμεινε όπως αρχικά είχε προσδιοριστεί.

1.3.2 Ασπόνδυλα

Η συνολική αφθονία των ασπόνδυλων ήταν πάντα υψηλότερη στα χωράφια μεγάλου μεγέθους που μελετήθηκαν. Αυτό υποδεικνύει ότι τα μεγάλα χωράφια παρέχουν χώρο για την ύπαρξη μεγάλου αριθμού ασπόνδυλων. Το επίπεδο ετερογένειας όπως προσδιορίστηκε από την τοπογραφική ανάλυση των περιοχών μελέτης, δεν φαίνεται να έχει σημαντική επιρροή.

Τα χωράφια με το σιτάρι διέθεταν τους μεγαλύτερους πληθυσμούς ασπόνδυλων. Τα Diptera, Hemiptera, Hymenoptera, Isopoda, Chilopoda και Orthoptera καταγράφηκαν με σημαντικά μεγαλύτερη αφθονία μόνο σε ετερογενείς περιοχές. Τα Acari και τα Diplura είχαν μεγαλύτερη αφθονία μόνο στις ομοιογενείς περιοχές. Η μέθοδος ανάλυσης ομάδων των στοιχείων αφθονίας των ανώτερων τάξα έδειξε ότι υπάρχει κάποια επιρροή της ετερογένειας, παρά το γεγονός ότι το είδος της καλλιέργειας είχε υψηλότερο επίπεδο επιρροής.

Η ετερογένεια δεν φαίνεται να έχει σημαντική επιρροή στη σχετική αφθονία των οικογενειών των Coleoptera. Για αυτά τα δεδομένα η μέθοδος ανάλυσης ομάδας έδειξε ότι τα είδη καλλιέργειας είχαν ελαφρά μεγαλύτερη επιρροή παρά ετερογένεια. Παρόλα αυτά τα Staphylinidae, Carabidae και Elateridae είχαν σημαντικά υψηλότερη αφθονία μόνο στις ετερογενείς περιοχές, ενώ τα Tenebrionidae είχαν σημαντικά υψηλότερη αφθονία μόνο στις ομοιογενείς περιοχές.

Σύμφωνα με την τοπογραφική ανάλυση των περιοχών μελέτης τα είδη *Pterostichus (Platysma) niger*, *Poecilus cupreus*, *Microlestes luctuosus* και *Tapinopterus taborskyi* εντοπίστηκαν στις περιοχές όπου υπήρχε μεγαλύτερη ετερογένεια. Η ανάλυση ομάδας των στοιχείων των ειδών έδειξε ότι η ετερογένεια είχε ορισμένη επιρροή. Ωστόσο το είδος των καλλιεργειών είχε μεγαλύτερη επιρροή από το επίπεδο της ετερογένειας και της χρονικής περιόδου συλλογής των δειγμάτων.

Ο συνολικός αριθμός των ειδών των Carabidae σε κάθε χωράφι υπολογίστηκε ότι είναι υψηλότερος στις ετερογενείς περιοχές εκτός από τους ελαιώνες, όπου υπολογίστηκε ότι υπάρχει μεγαλύτερος αριθμός των Carabidae στην ομοιογενή περιοχή. Ωστόσο, η διαφορά μεταξύ των δύο περιοχών ήταν μικρή.

Το επίπεδο ετερογένειας δεν φάνηκε να επηρεάζει την ποικιλότητα ή το δείκτη ομαλότητας των Carabidae. Μεγαλύτερη επιρροή είχε το είδος της καλλιέργειας, με τα υψηλότερα είπεδα ποικιλότητας να εντοπίζονται στους ελαιώνες. Ωστόσο, υπήρχαν σημαντικοί συσχετισμοί μεταξύ της ποικιλότητας των Carabidae και του ποσοστού των περιοχών που είναι σε αγρανάπαυση και είναι χέρσα γη.

Η Επιρροή των Περιβαλλοντικών Μεταβλητών—Οι πιο σημαντικές περιβαλλοντικές μεταβλητές σχετικά με τη σύνθεση των Carabidae είναι, το είδος της καλλιέργειας, το είδος του εδάφους, η θερμοκρασία του εδάφους και η υγρασία του εδάφους.

Η Επιρροή των Διαφορετικών Πτυχών της Ετερογένειας—Η επιρροή των περιβαλλοντικών μεταβλητών αφαιρέθηκε με τη χρήση της CCA. Οι ακόλουθες πτυχές της ετερογένειας είχαν τη μέγιστη επιρροή στις βιοκοινότητες των Carabidae (Τμήμα 4.2.14). Παρατίθενται κατά σειρά με βάση το επίπεδο επιρροής τους:

- **1o) Το ποσοστό της χέρσας γής και των χωραφιών σε αγρανάπαυση στην περιοχή**—Όπου τα επίπεδα ήταν από μέτρια προς υψηλά, πολλά είδη ευρέθησαν σε μεγάλη αφθονία.

- **2o) Επίπεδο συνάθροισης στην περιοχή μελέτης**—Όπου τα επίπεδα συνάθροισης ήταν από μέτρια προς υψηλά, πολλά είδη ευρέθησαν σε μεγάλη αφθονία.

- **και 2o) Το ποσοστό αγρανάπαυσης**—Όπου τα επίπεδα ήταν από μέτρια προς υψηλά, πολλά είδη ευρέθησαν σε μεγάλη αφθονία.

- **3o) Η διασπορά των χωραφιών σε αγρανάπαυση**—Όπου τα επίπεδα ήταν από χαμηλά προς μέτρια, πολλά είδη ευρέθησαν σε μεγάλη αφθονία.

- **και 3o) Μέγεθος χωραφιών**—Όπου τα χωράφια ήταν μεσαίου μεγέθους προς μικρό (περίπου μισό εκτάριο), πολλά είδη ευρέθησαν σε μεγάλη αφθονία.

1.3.3 Φυτά

Αναφορικά με την μελέτη των καλλιεργειών με ελαιόδενδρα στην ετερογενή περιοχή, υπήρξαν σημαντικά μεγαλύτερα επίπεδα κάλυψης φυτών. Το χωράφι με το βαμβάκι που είχε τη μεγαλύτερη ομοιογένεια σύμφωνα με την τοπογραφική ανάλυση, είχε επίσης σημαντικά επίπεδα κάλυψης φυτών Τμήμα 4.3.1).

Η ποικιλότητα των φυτών επηρεάστηκε περισσότερο από το είδος των καλλιεργειών παρά από το επίπεδο της ετερογένειας. Τα υψηλότερα επίπεδα ποικιλότητας εντοπίστηκαν στους ελαιώνες. Ωστόσο, η ποικιλότητα των φυτών συσχετίστηκε αρνητικά με τον αριθμό των χωραφιών όπου καλλιεργείται βαμβάκι υποδηλώνοντας ότι όταν σε μία περιοχή υπάρχουν πολλά χωράφια όπου καλλιεργείται βαμβάκι, η ποικιλότητα των φυτών είναι χαμηλή (Τμήμα 4.3.2).

Στο σύνολο των συγκρίσεων που έγιναν, με εξαίρεση αυτών που πραγματοποιήθηκαν στα ελαιόδενδρα, η πληθώρα των μορφοειδών για τα φυτά ήταν υψηλότερη στις ετερογενείς περιοχές (Τμήμα 4.3.3).

Ο συνολικός αριθμός των μορφοειδών φυτών εκτιμήθηκε ότι ήταν υψηλότερος σε περιοχές που είχαν υψηλότερη ετερογένεια σύμφωνα με την τοπογραφική ανάλυση. Αυτό ίσχυε σε όλες τις συγκρίσεις με εξαίρεση τη σύγκριση που πραγματοποιήθηκε στα δύο χωράφια με καλαμπόκι όπου τα επίπεδα υγρασίας ήταν πολύ υψηλά στις ομοιογενείς περιοχές.

1.4 Συμπεράσματα

Η μελέτη αυτή έδειξε ότι ορισμένες διαφορές στις κοινότητες των ασπόνδυλων σχετίζονται με το επίπεδο της ετερογένειας στις καλλιέργειες. Υψηλά επίπεδα σχετικής αφθονίας και μεγάλοι αριθμοί συγκεκριμένων ταξα βρέθηκαν σε καλλιέργειες με υψηλά επίπεδα ετερογένειας. Η επιρροή της ετερογένειας ήταν παρόλα αυτά σχετικά μικρή και δευτερεύουσας σημασίας σε σχέση με την επιρροή που είχαν το είδος των καλλιεργειών και ορισμένοι περιβαλλοντικοί παράγοντες.

Η μελέτη αυτή προσδιόρισε ποιές από τις διαφορετικές πτυχές της ετερογένειας άσκησαν τη μεγαλύτερη επιροή στα Carabidae. Οι πτυχές της ετερογένειας με την μεγαλύτερη επιρροή ακολουθούν με βάση τη σημασία τους

- Το ποσοστό των περιοχών που βρίσκονται σε αγρανάπαυση και είναι χέρσα γη,
- Το επίπεδο συνάθροισης στην περιοχή μελέτης και επίσης το ποσοστό των περιοχών που βρίσκονται σε αγρανάπαυση,
- Η διασπορά των περιοχών που βρίσκονται σε αγρανάπαυση και επίσης το μέγεθος των χωραφιών.

Τα υψηλά ποσοστά εκτάσεων που βρίσκονται σε αγρανάπαυση και είναι χέρσα γη, καθώς και τα υψηλά ποσοστά των καλλιεργειών δένδρων σχετίζονται με τα υψηλά ποσοστά ποικιλότητας των Carabidae. Αυτό πιθανόν συνέβη επειδή οι συγκεκριμένες χρήσης γης έχουν περισσότερα κοινά χαρακτηριστικά με το φυσικό περιβάλλον που ζούσαν τα Carabidae.

Περισσότερη έρευνα θα απαιτηθεί για βρεθεί η φύση των σχέσεων που ανακαλύφτηκαν σε αυτή τη μελέτη, όμως παρόλα αυτά είναι χρήσιμο να έχουμε μία εικόνα για το ποιες πτυχές της ετερογένειας είναι οι πιο επωφελείς για τις βιοκοινότητες των Carabidae. Η μικρής κλίμακας εκμετάλλευση της γης, δεν είναι μία επικερδής μορφή καλλιέργειας. Επομένως, εντοπίζοντας ποιες πτυχές της ετερογένειας είναι οι πιο σημαντικές για την άγρια ζωή, μπορεί να μετατρέψει την διατήρηση της βιοποικιλότητας πιο αποτελεσματική οικονομικά για τον αγρότη.

Σύμφωνα με την έρευνα που πραγματοποιήθηκε, φαίνεται ότι τα κάτωθι αποτελούν με σειρά σημασίας, τον καλύτερο τρόπο για την ωφέλεια των ασπόνδωλών που ζουν στις καλλιέργειες:

- Η δημιουργία διασυνδεδεμένων χέρσων εκτάσεων και περιοχών που βρίσκονται σε αγρανάπαυση,
- Η αποφυγή καλλιεργειών του ιδίου είδους, σε γειτονικά χωράφια, την ίδια χρονική περίοδο,
- Η επιλογή μικρών χωραφιών για καλλιέργειες, έκτασης περίπου μισού εκταρίου (5 στρέμματα) και η αύξηση του ποσοστού της γης που χρησιμοποιείται για την καλλιέργεια δένδρων όπως, ελιές, καρυδιές, αμυγδαλιές, κλπ.

Chapter 2

Introduction

2.1 The Importance of Agricultural Ecosystems

In one way or another, humans consume over a third of the planet's terrestrial production (Tilman *et al.*, 2001 [170]). This has a dramatic effect on the environment, most noticeably through the conversion of natural habitat to agricultural land (Matson *et al.*, 1997 [122]).

In Europe, agriculture is the dominant land use, with natural areas being left as islands within a sea of agricultural land (Duelli & Obrist, 2003 [50]). The European Union of 2010 was using an average of around 40 % of its land area for agriculture. In Hungary, Holland, Luxembourg, Poland and Romania; however, agriculture accounted for over 50 % of land use. In Denmark and Ireland the figures were over 60 %, while in the United Kingdom over 70 % of land had been converted to agriculture (EUROSTAT, 2012 [61]).

Worldwide, about 37 % of the earth's land surface is used for agriculture (FAOSTAT 2012 [67]). Despite this; however, out of a global population of 7 billion, an estimated 850 million people go without sufficient nourishment (FAO, 2012 [66]).

Paradoxically, the number of undernourished people is expected to halve by the year 2015, in spite of a predicted increase in population (FAO, 2012 [66]). This inevitably means that agricultural production will have to increase still further in order to provide enough food for the growing population (Trewavas, 2001 [175]).

Around 70 % of the predicted increase in agricultural production is expected to come from higher yields on existing farmland. However, if the forecast population is to be adequately nourished, an extra 1.2 million square kilometers of natural habitat will need to be converted to farmland by 2030 (FAO, 2002 [65]) and perhaps even 10 million square kilometers by the year 2050, something which may rival climate change in the level of impact it will have on biodiversity (Tilman *et al.*, 2001 [170]).

In northern Europe, where there has already been widespread land conversion to agriculture and subsequent agricultural intensification, the effect on biodiversity has been enormous (Donald *et al.*, 2001 [46]; Krebs *et al.*, 1999 [100]; Flowerdew, 1997 [72]; Sotherton & Self, 2000 [162]) and the need has been recognized to find a more appropriate balance between agricultural production and biodiversity conservation (Firbank, 2005 [71]).

So, in future years, if yet more land is to be converted to agriculture and the extent of natural areas is to diminish still further, effective biodiversity conservation in agroecosystems will become increasingly important.

2.2 Agricultural Intensification in Europe

In recent decades, the level of agricultural intensification in most EU countries has been high. One reason for this has been the past policies of the Common Agricultural Policy (CAP), which until recently, encouraged intensification by rewarding intensive farming practices, at the expense of extensive ones (Donald *et al.*, 2002 [47]).

The CAP was introduced with the establishment of the EEC under "The Treaty of Rome" in 1957. Its aims were to provide self-sufficiency in food production for member states, to stabilize the prices of agricultural products, and to create wealth and employment in the agricultural sector. These aims were achieved successfully through market price support and the provision of subsidies for agricultural commodities (Scottish Executive, 2004 [153]).

If the market price of an agricultural product fell below a set intervention price, the EU would buy up that product at a fixed price, so insuring stability. Additionally, EU producers were protected against foreign imports by import duties, while exports were encouraged by the payment of export subsidies, which bridged the gap between world and EU prices. This meant that EU products could be traded competitively on the foreign markets (Scottish Executive, 2004 [153]).

Such high levels of protection allowed European farmers to expand and intensify production, while another CAP policy, the payment of capital grants, gave farmers the opportunity to invest in new farm machinery, resulting in increased mechanization of farming practices (Donald *et al.*, 2002 [47]).

At the same time, there was a period of rapid technological development, which facilitated widespread agricultural intensification. This period saw the development of high-yielding crop varieties and the increased use of industrial pesticides and fertilizers (Firbank, 2005 [71]).

Most importantly; however, the CAP provided direct subsidy payments to farmers, which were directly linked to food production levels. This created the incentive for farmers to dramatically increase their yields of many agricultural products (Scottish Executive, 2004 [153]).

2.2.1 The Problems Caused by Agricultural Intensification

During the early years of the CAP, increased yields were much needed and welcomed, but the intensification process did not stop there. It continued throughout the 1970s and 80s, eventually causing massive overproduction. By the 1980s this had led to the creation of huge food surpluses, which proved to be wasteful and very costly for the EU (Scottish Executive, 2004 [153]).

However, the cost of overproduction was not only economic. It soon became clear that the decades of intensification and increased yields had taken a great toll on the environment.

2.2.1.1 Increased Agrochemical Use

To start with, intensification resulted in the increased use of agrochemicals. This caused serious pollution of the agricultural environment, through agrochemical drift, runoff and the leaching of nutrients. It is known, for instance, that between 30 % and 80 % of the nitrogen applied in fertilizers, as well as a significant percentage of the pesticides, enter the air, water and agricultural products (Pretty, 1998 [144]).

In the 1960s, Rachel Carson drew attention to the detrimental effects of organochlorine insecticides. These accumulated in the bodies of organisms, causing more severe effects as they were passed up the food chain (Carson, 1963 [24]).

Although these products were banned, problems were later found with other groups of pesticides, which were seen to affect species such as *Apodemus sylvaticus* (Shore *et al.*, 1997 [156]), *Mustela putorius* (Shore *et al.*, 2003 [155]) and *Tyto alba* (Newton *et al.*, 1990 [127]).

The general effects of agrochemical use on farmland were well illustrated when De Snoo *et al.* (1999 [45]) described the benefits to birds, insects and wild plants of not spraying field margins with pesticides and fertilizers. This meant that it was not only pesticides that had a direct impact on biodiversity, but fertilizers too. In fact Kleijn *et al.* (2009 [99]) showed that, on many different farms throughout Europe, high inputs of nitrogen were associated with low levels of wild plant diversity.

2.2.1.2 The Loss of Natural and Semi-Natural Habitat

The drive to increase yields also meant that farmers were encouraged to remove many natural and semi-natural features from their land. This meant that woodlands, scrublands, trees and hedges were removed, in order to make room for the operation of large farm machinery (Macdonald & Johnson, 2000 [119]; Barr *et al.*, 1991 [8]; Pollard *et al.*, 1974 [141]).

This had a number of detrimental consequences. As well as destroying important habitats for wildlife, the removal of such areas caused agricultural problems. Areas devoid of hedges, woods and scrub were more prone to soil erosion and to the leaching of nutrients. This meant that fields in such areas decreased in fertility, requiring yet more fertilizer inputs, which exacerbated the problem of agrochemical pollution (Forman, 1995 [73]).

Loss of hedgerows and other natural and semi-natural habitat may also be blamed for increased numbers of agricultural pests in an area. This is because such habitats are known to sustain large populations of natural enemies, which can invade the surrounding agricultural land and help to control pest outbreaks (El Titi, 1991 [57]).

2.2.1.3 Agricultural Specialization

Once large amounts of natural and semi-natural habitat had been removed from farmland, and large farm machinery had come into widespread use, it proved more cost-effective for farmers to specialize in the production of just a few agricultural products. Consequently there was a reduction in the number of crop and animal species being farmed. Specialization increased and the widespread development of monocultures was seen (Matson *et al.*, 1997 [122]).

Monocultures; however, are known to encourage pest outbreaks, meaning that still more chemical pesticides are required. Polycultures, on the other hand, experience fewer problems with pests, because a high diversity of crop types within an area sustains a high diversity of insect natural enemies. These species, often Coleoptera, feed on crop pests and so keep them under control (Andow, 1991 [5]; Russell, 1989 [147]).

2.2.1.4 The Loss of Biodiversity

The combined result of these three aspects of intensification has been an all round loss of biodiversity from agroecosystems.

Biodiversity losses were first noticed when farmland birds, which are good indicators of the impact of intensification, started to show population declines (Donald *et al.*, 2001 [46]; Krebs *et al.*, 1999 [100]). Since the 1970s, declines have been seen across Europe, in many different species (Siriwardena *et al.*, 1998 [159]; Schifferli, 2000 [149]; Donald *et al.*, 2001 [46]), something which was almost certainly due to the intensification of agriculture (Matson *et al.*, 1997 [122]; Chamberlain *et al.*, 2000 [25]; Aebischer *et al.*, 2000 [1]).

In the UK, where intensification has been particularly severe, 10 species of farmland birds lost 10 million breeding individuals between the late 1970s and the late 90s (Krebs *et al.*, 1999 [100]), while out of 13 species of farmland birds monitored, 11 suffered serious reductions in the size of their populations between 1968 and 1995 (Siriwardena *et al.*, 1998 [159]).

In fact, Donald *et al.* (2001 [46]) found that across Europe, where intensification had increased, the amount of available food and suitable habitat for birds had decreased. In subsequent research Donald *et al.* (2002 [47]) identified a number of factors as being probable causes of the observed declines. These factors were:

- The loss of hedgerows and non-cropped habitat.
- Increased pesticide use, leading to reduced food levels.
- The loss of winter wheat stubbles, due to changes in sowing and harvesting times.
- The increased use of silage, rather than hay.
- The conversion of low-input grassland and cereal farming to high input arable systems.
- Increased stocking densities and agrochemical input levels on pastures.
- Reduced habitat diversity.
- Increased field size and mechanization.
- The abandonment of extensive agricultural areas, which generally have greater biodiversity.

Birds; however, were not the only group of species declining due to intensification. Birds were suffering because the species they relied on for food and shelter were also suffering. In fact, once one group of species was affected by intensification, there were knock-on effects impacting many other groups of species. For example, the loss of wild plant species was shown to reduce farmland butterfly diversity (Smart *et al.*, 2000 [160]) and farming practices that reduced insect populations, in turn, reduced bird populations (Benton *et al.*, 2002 [10]). Soon, it became clear that no group of species was immune to the effects of intensification, which were also blamed for declines in farmland mammals (Flowerdew, 1997 [72]), wild plants and invertebrates (Sotherton & Self, 2000 [162]).

2.2.2 Addressing the Problems

2.2.2.1 Reform of the CAP

In the early 1990s, it became obvious that agricultural production levels were unsustainable and the need for CAP reform was recognized. The MacSharry reforms aimed to combat the problem of food surpluses by reducing the level of protection and intervention in the markets (Scottish Executive, 2003 [152]). They also introduced the first agri-environmental schemes, in the form of the UK's Countryside Stewardship Schemes. These provided incentives for farmers to manage their land in ways that were beneficial for wildlife (Wilson *et al.*, 2009 [189]).

Further reforms of the CAP were made at the Berlin summit in 1999, under Agenda 2000. Here the intervention prices of cereals and milk were further reduced, in order to increase market orientation. The money gained from these cuts was then put into a programme for the environment and rural development. Agri-environmental schemes had their funding increased and were made compulsory across all EU member states, with the payment of subsidies to farmers being linked to their compliance with such schemes (European Commission, 1999 [59]; Wilson *et al.*, 2009 [189]).

Then, in 2003, still greater reforms were introduced, with subsidies being completely decoupled from production, thereby removing the incentive to overproduce. The CAP moved to a system of Single Farm Payments based on the area of land farmed, and farmers were encouraged to respond to market forces, by producing the products they could get the best prices for (European Commission, 2003 [60]).

In 2005, cross-compliance was introduced, meaning that in order to qualify for the basic Single Farm Payment, farmers had to comply with basic environmental standards. In the UK, the Countryside Stewardships Schemes were replaced by Environmental Stewardship Schemes. These had two levels. Entry-level schemes involved easy and low-cost measures, which allowed the participation of all farmers. Higher-level schemes allowed farmers to earn additional money by performing more complicated and expensive management tasks (Wilson *et al.*, 2009 [189]).

The 2014 CAP reforms increased the budget for the environment by 5 %. The new Greening Measures aim to raise the percentage of permanent grassland to 5 % in all member states. So any farm with less than 5 % permanent grassland will have to reinstate it. The measures also aim to increase crop diversity on large and medium sized farms, using the new the 3 Crop Rule. Farmers with over 10 ha of land will be required to plant a minimum of 2 different crop types, while farmers with over 30 ha of land will have to plant at least 3 different crop types, with the most common crop not occupying more than 75 % of the land. Finally, Ecological Focus Areas will be required on farms with over 15 ha of arable land. These will cover 5 % of what was once arable land and will include measures such as planting wildflower strips, trees, nitrogen fixing crops, catch crops or cover crops, improving ditches, hedgerows and leaving areas of land fallow (DEFRA, 2014 [39]).

While the latest CAP reforms appear to be moving in the right general direction, as far as the environment is concerned, there are still worries regarding their overall level of implementation, and concerning the efficacy of particular measures.

Due to the high number of exemptions and the possibility of farmers opting out, it is thought that only about 50 % of EU land will benefit from the new Greening Measures. More specifically and in spite of the CAP's goal of halting declines in permeant grassland, it appears that under the new rules, areas of grassland may still be converted to arable, as long as the 5 % minimum is maintained on each farm. This may actually result in a net decrease in permanent grassland across the EU. Also, as there are no specific management requirements for these areas of grassland, low-input pastureland may end up being converted to high-input pasture, which is much less ecologically valuable. Finally, it is believed that while the 3 Crop Rule may benefit biodiversity on the largest, most homogeneous farms, overall the measure may result in diversity levels lower than the current EU average (Pe'er *et al.*, 2014 [135]).

2.2.2.2 Successful Agri-Environmental Schemes

In their review of the results of European agri-environmental schemes, Wilson *et al.* (2009 [189]) listed the management practices that produced the most positive outcomes for wildlife. These were:

- Encouraging hedgerows, allowing them to grow higher and thicker.—This was seen to improve conditions for wild plants, invertebrates, small mammals and birds. In fact, replacing hedgerows that had previously been removed was found to be the best method of increasing carabid numbers in agricultural areas (Fournier & Loreau, 1999 [74]).

- Improving the management of ditches, their aquatic plants and adjacent vegetation.—This created improved habitats for amphibians, aquatic invertebrates, soil invertebrates and the birds that fed on them.

- Leaving un-cropped strips or wildflower strips next to field margins.—This created valuable habitat for invertebrates and small mammals. It also provided foraging and nesting sites for birds, while protecting non-agricultural habitats from agrochemical drift. Wild flower strips, for example, were seen to increase carabid numbers by providing food and overwintering sites (Frank, 1997 [76]; Lys & Nentwig, 1994 [118]).

- Planting wildflower mixtures.—This was seen to increase the number of nectar and pollen-feeding insects in agricultural areas.

- Planting bird-seed mixtures.—This increased feeding opportunities for farmland birds.

- Leaving stubble un-ploughed over winter.—Also provided birds with more food.

- Creating beetle banks.—This increased the numbers of predatory arthropods, not only beetles, which could then feed on agricultural pests and provide food for birds. Beetle banks are now often put into agricultural land to encourage the overwintering of carabids. They are raised banks, planted with a low layer of herbage, usually tussock-forming grass, which creates a dry microclimate (Holland & Luff, 2000 [90]).

- Converting pastures to low-input systems and encouraging a diverse sward structure through mixed stocking.—Such practices favoured invertebrates and birds respectively.

2.3 Agricultural Ecosystems in Greece

2.3.1 Greek Agriculture

In 2010, Greece produced just over 4 million tonnes of cereals and over 1.4 million tonnes of fruit and vegetables. The agricultural sector employed 1.1 million people and had an output of 6.3 billion Euros (EUROSTAT, 2012 [61]).

Agriculture in Greece is more extensive and small-scale than in many European countries, with only a few areas of intensive cultivation occurring on the flatter and more fertile land. Overall only 28 % of land is currently being used for agriculture, a much lower figure than the EU average of 40 % (EUROSTAT, 2012 [61]).

Like the Mediterranean region as a whole, Greece has many agricultural difficulties, which result in increased production costs. The climate can be very unpredictable, many areas have poor soils and annual rainfall is low, leading to seasonal and more permanent periods of drought (Caraveli, 2000 [22]).

In many areas, the land is best suited to the production of specialized Mediterranean products. These; however, due to the fact that they cannot be produced in Northern and Central Europe, have not been well protected by the CAP. This has meant that farming incomes in such areas have been low and there has been little incentive to intensify production (Mergos & Donatos, 1996 [125]; Potter, 1997 [143]).

For this reason, farm sizes in Greece are generally small. The average utilized agricultural area per farm, which reflects the degree to which farming practices can be mechanized, is much lower than the EU average (EUROSTAT, 2012 [61]). Another reason for such small farm sizes is that in Greece farming is still a family based activity, with the majority of farm workers coming from the families of the land owners (Caraveli, 2000 [22]; EUROSTAT, 2012 [61]).

2.3.2 Agricultural and Environmental Problems

While the extensive and small-scale nature of Greek farming has spared many areas of the country the environmental problems associated with agricultural intensification, it is not very lucrative.

To start with, CAP subsidies are paid according to the area of land farmed, so small-scale farms received less money than large farms. Although this in itself is reasonable, small farms such as those seen in Greece, tend to have proportionally higher production costs, which put them at a competitive disadvantage. Land is often fragmented, with fields belonging to a single land owner being widely spaced, making the operation of farm machinery more difficult and expensive (Kasimis *et al.*, 2003 [96]).

Other difficulties are that the products of small-scale farmers are generally under-marketed. Co-operatives were rare in the country and farmers have suffered from a highly bureaucratic public administration system, which has made the dissemination of appropriate information difficult. For these reasons Greek farmers have long found it hard to compete on the foreign markets (Kasimis *et al.*, 2003 [96]).

Recently though, the situation has deteriorated further. Despite predictions that the Single Farm Payment Scheme would have a positive impact on the kind of small-scale farming seen in Greece (Vrolijk *et al.*, 2010 [185]), so far this has not been apparent. Between 2005 and 2011, subsidies payed to Greek farmers have fallen by 333 million Euros, while total farming incomes have fallen by around 31 % (EUROSTAT, 2012 [61]).

2.3.3 The Future of Small-Scale Farming

Due to CAP reform and the EU's decision to open markets to foreign imports, the country's small-scale, extensive farmers are now likely to become even less competitive. The combined pressures of high production costs, cheap foreign imports, reduced subsidies and lowered farming incomes, may threaten the future of small-scale farming in Greece.

This means that farmers may be faced with a choice between abandoning their land, or intensifying their production, in order to be more competitive on the open market. Already though, these two processes, land abandonment and intensification, where they have occurred in Greece, have had severe effects on the environment.

2.3.3.1 Land Abandonment

Land abandonment has been occurring over a long period in the Mediterranean, where extensively farmed land is vacated for economic reasons (Caraveli, 2000 [22]). Although returning land to its natural state may at first sight seem good for biodiversity, in many cases the reverse is true. Extensive agricultural systems, like those in the Mediterranean, have a long history and are high in biodiversity. In fact, it is the presence of people within them, working the land and grazing their stock, which maintains their heterogeneity and provides important habitats for wildlife (Farina, 2006 [68]; Blondel & Aronson, 1999 [12]).

In Greece, for years, there has been a trend towards land abandonment, especially in mountainous areas, which have lost large proportions of their rural populations because of political and socioeconomic factors (Kasimis & Papadopoulos, 2001 [95]). This happened most widely in the 1960s and 70s, but has continued to a lesser extent to this day. Since the early 1990s, in fact, the agricultural population dropped from 30 % of the overall population to around 10 %. This has happened despite EU socio-structural policies aimed at increasing the number of young people taking over farms (Kasimis *et al.*, 2003 [96]; EUROSTAT, 2012 [61]).

2.3.3.2 Intensification

The other alternative open to farmers, intensification, although still relatively rare in Greece, has nevertheless caused problems in parts of the country. A significant period of intensification occurred in the 1980s because of production linked CAP subsidies and the national agricultural policy. It resulted in increased levels of irrigation, the expansion of irrigation onto previously unirrigated land, an increase in the use of agrochemicals and the replacement of permanent pasture with crops (Louloudis & Maraveyas, 1997 [111]).

Between the 1960s and 90s the amount of land under irrigation in flat areas increased from 17 % to 45 %, while in semi-mountainous areas the increase was from 11 % to 24 %. This caused the depletion of water resources, soil erosion, and the leaching of nutrients from soils, which led to the increased use of fertilizers in the production of subsidized crops such as cotton, maize, sugar beet and tobacco. This, in turn, led to increased pollution of water courses (Caraveli, 2000 [22]).

In some cases, the process of intensification can lead indirectly to land abandonment. During the 1990s, for example, some traditional olive groves and vineyards were removed, because their cultivation could not be mechanized easily and produced low economic returns. In fact, CAP subsidies actively encouraged the removal of traditional terrace fields, in favour of olive monocultures. In some places; however, the removal of terraces caused serious erosion, meaning that people could not continue production and so had to abandon the land (Caraveli, 2000 [22]).

Another case like this was seen with tobacco farming. Traditional varieties of the plant had long been farmed successfully in certain areas of the country. However, when farmers were encouraged to grow the more productive Virginia tobacco instead, traditional tobacco farming land was abandoned in favour of areas where the process could be more easily intensified (Caraveli, 1998a [20], b [21]).

Obviously, both situations, land abandonment and intensification, need to be avoided if the extensive farming common to Greece is to be maintained. The CAP is now paying huge amounts to recreate a more extensive form of agriculture in Northern Europe. However, extensive farmers in the South of Europe have seen large cuts in their incomes, leaving them with only two choices, to intensify, or to give up farming. It would be unfortunate if, while Northern Europe tries to enhance extensivity through agri-environmental schemes, Southern Europe were to loose its extensive agriculture, due to reduced subsidies and market pressures.

2.4 The Importance of Heterogeneity in Agricultural Ecosystems

Extensive farming systems, such as those seen in many places in Greece, maintain a high level of heterogeneity, which is thought to benefit biodiversity. In their 2003 review paper, Benton *et al.* [11] described the biodiversity benefits of heterogeneity in the agricultural environment, arguing that its loss was what had caused widespread reductions in biodiversity. They described the ways in which heterogeneity had been lost from agricultural areas and suggested that enhancing farmland heterogeneity would help to reverse biodiversity declines.

2.4.1 The Biodiversity Benefits of Heterogeneity

Under extensive, small-scale farming, the mosaic of different habitats created is one of the most important aspects of heterogeneity for biodiversity. Where such mosaics occur, benefits have been seen for many groups of species. These include the Coleoptera (Ostman *et al.*, 2001 [130]), the Aranea (Sunderland & Samu, 2000 [164]), the Lepidoptera (Weibull *et al.*, 2000 [187]), as well as many species of farmland birds (Galbraith, 1988 [78]; Freemark & Kirk, 2001 [77]).

When it comes to increasing biodiversity, the presence of non-cropped habitat is another important aspect of farmland heterogeneity. Non-cropped habitat may take the form of grassy or scrubby field margins, hedgerows, woodland, scrubland, ponds, streams, ditches and areas of fallow. Many of the studies reviewed by Benton *et al.* (2003 [11]) showed the presence of non-cropped habitat to be highly beneficial for a range of different species. In fact, once one group of species is encouraged, this will in turn encourage other groups. For example, high wild plant diversity will often lead to a greater diversity of herbivorous insects, which may in turn encourage their predators.

Field margins are thought to be a particularly beneficial type of non-cropped habitat. This is because they provide food, cover for foraging and dispersal corridors for many different species (Holland & Fahrig, 2000 [89]; Hinsley & Bellemy, 2000 [87]). Coleoptera have been shown to be positively influenced by the presence of hedgerows (Holland & Fahrig, 2000 [89]) and Lepidoptera by the presence of green lanes between fields (Dover & Sparks, 2000 [48]). Also, as previously mentioned, arable field margins, which were not treated with pesticides, have been shown to benefit wild plant diversity and abundance (De Snoo, 1999 [45]).

2.4.2 The Loss of Heterogeneity from Agricultural Ecosystems

Many of the aspects of agricultural intensification mentioned in previous sections, amount to a reduction in farmland heterogeneity. Benton *et al.* (2003 [11]) listed those aspects, which have resulted in the greatest losses of heterogeneity from agroecosystems. These were:

- Landscapes being dominated by just one type of agriculture, either cultivation or pasture.
- Increased farm sizes.—This meant that larger areas of land were brought under similar management regimes.
- A reduction in the number of crop varieties being used per farm.
- Crops being planted more homogeneously within farms.
- The loss of hedgerows, to aid the use of larger farm machinery.
- The loss of other types of semi-natural habitat, such as ponds and scrubland, in order to create more space for cultivation.
- Increased mechanization.—This led to greater uniformity in planting, fertilizer application, irrigation and drainage, which created more homogeneous swards.
- The improvement of crop varieties.—This meant that crops out-competed weed species, leading to within-field monocultures.

2.4.3 Quantifying Heterogeneity

2.4.3.1 Landscape Analysis

Heterogeneity in landscapes can be described, quantified and compared using landscape analysis.

A landscape is an area of land that is spatially heterogeneous in at least one factor of interest. It is composed of different habitat patches, corridors and in some cases, a background matrix. The term landscape is not specific to any one spatial scale, so can therefore be applied at many different scales (Forman, 1995 [73]).

The spatial patterns within landscapes have long been known to influence their ecology (Turner, 1989 [179]), meaning that numerous methods of quantifying landscape patterns have been developed, leading to the creation of hundreds of different of landscape metrics (McGarigal *et al.*, 2002 [123]). Turner *et al.* (2001 [180]) grouped these landscape metrics into the following categories:

- Metrics of Patch Size.—These calculate the size or area of habitat patches.
- Metrics of Patch Shape.—These describe the shape of habitat patches.
- Metrics of Patch Configuration.—These include measures of patch perimeter, connectivity between patches, and the proximity of patches to one another.
- Metrics of Spatial Configuration.—These quantify the probability of adjacency and contagion between different habitat classes.
- Metrics of Landscape Composition.—These measure the proportion of the landscape occupied by particular habitats, the relative richness of the habitat classes present, the diversity of the different habitat classes, the dominance of the specific habitat classes, and the connectivity of the specific habitat classes.

The program FRAGSTATS is a spatial analysis program for use on categorical maps. It quantifies the extent and spatial configuration of habitat patches within a landscape, by calculating metrics at the patch, class and landscape levels. Categorical maps are converted into numerical data sheets and then input into the program (McGarigal *et al.*, 2002 [123]).

Once such metrics have been calculated, those associated with particular patterns of species composition may be identified, and ultimately used as predictors of species richness and diversity (Schindler *et al.*, 2008 [150]).

2.5 The Carabidae

2.5.1 The Carabidae in Agricultural Ecosystems

The Carabidae are an important group when it comes to studying agro-ecosystems. It has long been known that the changes in farming techniques accompanying agricultural intensification have an impact on carabid assemblages. In 1937, Gersdorf [80] noted that extensively farmed areas with many weeds contained more carabid species than intensively farmed areas. Then in the 1950s and 60s, other studies found similar results (Heydemann, 1953 [85]; Tischler, 1958 [171]; Kirchner, 1960 [98]; Rivard, 1964 [146]).

Usually, the carabid species found in agricultural habitats are not of much conservation value, but in extensive areas, rarer species can often be found (Kromp, 1999 [102]). Assemblages in agroecosystems are thought to resemble those of early successional habitats, due to the high level of disturbance they are subjected to (Tonhasca, 1993 [172]). However, some species in agricultural areas are believed to originate from areas of natural woodland or grassland. When these areas were converted to agriculture, some carabid species remained where they were (Thiele, 1977 [167]) and evolved life history traits that allowed them to survive on agricultural land (Holland & Luff, 2000 [90]). Where very high levels of intensification have occurred; however, the original forest or grassland species are usually replaced with those adapted to living in frequently disturbed environments (Burel *et al.*, 1998 [18]).

Generally, carabid species found in agricultural areas prefer drier conditions, whereas species found in woodland prefer darker and damper conditions (Kromp, 1999 [102]). Locally; however, soil moisture and soil type will have an impact on carabid distributions (Meissner, 1984 [124]; Heydemann, 1953 [85]).

The most common carabid species found in cultivated areas in Central and Eastern Europe are listed in Table 2.1 (Thiele, 1977 [167]).

Table 2.1: The most common carabid species found in cultivated areas in Europe.

Central Europe	**Eastern Europe**
Pterostichus melanarius	*Dolichus halensis*
Poecilus cupreus	*Amara consularis*
Harpalus rufipes	*Calosoma auropunctatum*
Harpalus aeneus	*Harpalus griseus*
Platynus dorsalis	*Brachinus explodens*
Agonum mülleri	*Zabrus tenebrioides*
Bembidion lampros	*Calathus ambiguus*
Trechus quadristriatus	*Harpalus distinguendus*
	Carabus scheidleri

2.5.1.1 Natural History

The family Carabidae contains the greatest number of species of all adephagan beetle families. More than 40,000 species have so far been described world wide, with around 2,700 in Europe (Lövei & Sunderland, 1996 [112]).

They are relatively fast moving, most often active on the ground, but some species may also be active in vegetation. Macropterous species possess fully developed hind wings and can disperse by flying. This means that they can inhabit agricultural areas where disturbance is frequent, so are classed as eurytopic. Brachypterous species, on the other hand, only have vestigial wings and are unable to fly. These species are classed as stenotopic, meaning that they cannot disperse easily. They tend to live in undisturbed habitats so are usually only present in woodland (Kromp, 1999 [102]).

In Europe, reproduction usually only occurs once per generation. However, in some species, adults may live through the following winter and breed again the next year (Kromp, 1999 [102]). Species can generally be divided into two reproductive groups. The first of these produce larvae that are present in the summer and whose adults hibernate in winter, while the second produces larvae that hibernate in winter (Lindroth, 1992 [110]).

The adults lay their eggs in dead leaves, soil or decaying wood. Carabids have three larval stages that live in the soil. There also, the pupa forms its pupal chamber, then the adults hatch out, sclerotinize and gain their adult colour. Although the majority of carabid species are dark in colour and nocturnal, some species with metallic colouring may be active during the day (Kromp, 1999 [102]).

2.5.1.2 Nutrition

Most carabids are polyphagous. Some species prey on agricultural pests, of which they can consume their own body weight in a day. The genera *Amara, Harpalus* and *Zabrus* are thought to eat mainly plant food. The genera *Agonum, Bembidion, Calathus, Carabus, Cychrus, Dyschirius, Elaphrus, Notiophilus* and *Pterostichus,* on the other hand, are scavengers of animal material, while the genera *Cylindera* and *Calosoma* are thought to be predators of insects (Lindroth, 1992 [110]).

Carabid species are believed to have an impact on a number of different agricultural pests. For a start, they are known to reduce aphid populations, by feeding on individuals that have fallen to the ground from crop plants. They are also thought to feed on Gastropoda and Lepidoptera pest species. Additionally, carabids are believed to decrease the numbers of other Coleoptera pest species, as they feed on their larvae, while some species may also help to control agricultural weeds, by consuming their seeds (Kromp, 1999 [102]).

2.5.1.3 The Impact of Agricultural Intensification on Carabids

The first indication that agricultural intensification was affecting carabids came from samples taken in Germany between the 1950s and 70s. During this period, one of large scale intensification, Heydemann & Meyer (1983 [86]) saw reductions in carabid species richness of between 48 % and 85 %. Then, in the 1970s and 80s, species such as *Pterostichus melanarius*, *Platynus dorsalis* and *Carabus auratus* were seen to be declining, due to the increased use of insecticides in winter wheat. Also, an 81 % decrease was seen in the number of individuals trapped between the early 70s and early 80s (Basedow, 1987 [9]).

In the 1980s and 90s, long term declines in carabids were blamed on the loss of field margins, combined with other aspects of agricultural intensification, such as agrochemical use (Basedow, 1987;

Duffield & Aebischer, 1994 [52]; Heydemann & Meyer, 1983 [86]). Then, in the early 1990s, loss of unforested, semi-natural habitat was found to be the cause of reductions in carabid diversity. Where this had occurred, common species were seen to become more common, and rare species to become rarer (Desender & Turin, 1989 [44]). Later still, Büchs *et al.* (1997 [15]) found that increasing farming intensity resulted in lower levels of carabid species richness. Similarly, a reduction in carabid diversity, linked to agricultural intensification, was also seen in the UK during this period (Holland *et al.*, 1998 [88]).

2.5.1.4 Habitat Preferences

In recent years, carabids have become widely used as bioindicators, to compare the impacts of different farming practices. For example, carabids are known to be negatively affected by intensive farming practices, such as deep ploughing, but positively affected by extensive practices, like organic fertilization and green manuring (Kromp, 1990 [101]).

Different habitats can often be characterized by the species of carabids found there. This is because carabids are very sensitive in their choice of habitat. The larvae are the most vulnerable life stage, so the ability of carabids to persist in a given habitat will depend on the survival of their larvae within it. The larvae are not very mobile, meaning that their survival will depend on local food abundance and the presence of competitors. Also the larvae lack a high level of chitin, so cannot cope with local extremes in humidity and temperature (Lövei & Sunderland, 1996 [112]).

While carabid assemblages differ depending on crop type, it is thought that this is due more to associated cultivation practices and microclimates, rather than to any particular preference for the crops themselves. The times of planting and harvesting, for example, seem to play an important role in the species found in a particular crop (Holland & Luff, 2000 [90]).

Cultivation Timing and Techniques The carabid species found in high abundances in spring and autumn planted crops are known to differ. Similarly, cultivation techniques have an effect on the species found in particular fields. The most abundant species found in spring planted fields, autumn planted fields and in those that have been ploughed, or where minimum tillage has been practiced are listed in Table 2.2 (Holland & Luff, 2000 [90]).

Organic Versus Conventional Agriculture Kromp (1999 [102]) reviewed many studies in which the abundance and species richness of carabids were found to be higher in organically farmed land, as opposed to conventionally farmed land. In Austria, for example, the species *Poecilus versicolor, Dyschirius globosus* and *Harpalus aeneus* were often found to be associated with organic farming techniques, while *Pterostichus melanarius* was found mainly in conventional farmland. In these studies it was believed that practices such irrigation, drainage, mowing, intensive grazing, the addition of mineral fertilizers and liquid manure accounted for the observed reductions in carabid species on conventional farms.

A later review comparing organic and conventional agriculture showed more ambiguous results. In the studies reporting increased diversity in organic farming systems, this was attributed more to crop rotation and differences in habitat caused by specific cultivation practices, than to agrochemical input levels per se (Holland & Luff, 2000 [90]).

Then, more recently, it was found that where landscape features remained similar, there were few differences in carabid assemblages between organic and conventional farms (Purtauf *et al.*, 2005 [145]).

In fact, although high levels of agrochemical input are obviously detrimental, it is now believed that the biodiversity benefits of organic farming may be due less to a lack of agrochemicals and more to the associated increases in heterogeneity created by other organic practices (Benton *et al.*, 2003 [11]).

Important Aspects of Heterogeneity Field size is an important aspect of heterogeneity, as far as carabids are concerned. This is because it is much harder for carabids to recolonize large fields after cultivation, due to the long distances involved. Also, recolonization is aided by there being a high diversity of crop or land use types within a single area. This is due to the fact that cultivation practices take place at different times in different crops, meaning that, at any one time, there is likely to be undisturbed habitat available for carabids to shelter in, while cultivation practices are taking place elsewhere (Kromp, 1999 [102]).

Another aspect of heterogeneity important for carabids is the presence of non-cropped habitat. While carabids live in crops during the summer, they are known to use field margins to hibernate in (Pollard, 1968 [140]; Sotherton, 1985 [161]). Where this is possible, carabids are less vulnerable to ploughing,

Table 2.2: The most abundant carabid species in different types of cultivation.

Spring Planted	**Autumn Planted**
Amara bifrons	*Asaphidion flavipes*
Amara fulva	*Agonum dorsale*
Bembidion lampros	*Agonum muelleri*
Bembidion obtusum	*Agonum sexpunctatum*
Bembidion quadrimaculatum	*Amara* spp.
Calathus ambiguus	*Carabus auratus*
Calathus erratus	*Carabus cancellatus*
Calathus fuscipes	*Carabus granulatus*
Calathus melanocephalus	*Carabus purpurascens*
Clivina fossor	*Harpalus rufipes*
Harpalus rufipes	*Loricera pilicornis*
Harpalus griseus	*Nebria brevicollis*
Pterostichus melanarius	*Pterostichus cupreus*
Pterostichus niger	*Pterostichus lepidus*
Trechus quadristriatus	

Ploughing	**Minimum Tillage**
Agonum placidum	*Asaphidion flavipes*
Agonum dorsale	*Agonum cupreum*
Amara quenseli	*Agonum dorsale*
Amara torrida	*Agonum muelleri*
Bembidion aeneum	*Agonum sexpunctatum*
Bembidion guttula	*Bembidion bimaculatum*
Bembidion lampros	*Bembidion lampros*
Bembidion lunulatum	*Bembidion obtusum*
Bembidion obtusum	*Bembidion quadrimaculatum*
Bembidion quadrimaculatum	*Bembidion rupicola*
Bembidion tetracolum	*Calathus fuscipes*
Clivina fossor	*Carabus auratus*
Demetrias atricapillus	*Carabus monilis*
Harpalus rufipes	*Carabus violaceus*
Loricera pilicornis	*Cyclotrachelus sodalis*
Nebria brevicollis	*Harpalus affinis*
Pterostichus lucublandus	*Harpalus rufipes*
Pterostichus melanarius	*Loricera pilicornis*
Trechus quadristriatus	*Nebria brevicollis*
	Pterostichus cupreus
	Pterostichus madidus
	Pterostichus melanarius
	Pterostichus niger
	Notiophilus biguttatus

harrowing and insecticide application, which are most likely to take place during the autumn and winter (Holland & Luff, 2000 [90]). Also field margins may be very important as breeding sites for many species (Desender & Alderweireldt, 1988 [42]; Thomas *et al.*, 1991 [169]), while species that live in patches of woodland will use field margins as dispersal corridors (Burel & Baudry, 1989 [16]).

However, some species of carabid, like *Harpalus* spp. and *Pterostichus* spp., do not need to make use of field margins in this way. They are less vulnerable to the effects of autumn and winter cultivation practices, as they are large and are able to bury themselves deep enough to avoid them (Luff, 1980 [113]).

The presence of weeds within cultivations, an aspect of within-field heterogeneity, is also known to be important for carabids (Gersdorf, 1937 [80]; Heydemann, 1953 [85]; Tischler, 1958 [171]; Kirchner, 1960 [98]; Rivard, 1964 [146]). More specifically, Kromp (1990 [101]) found that where weeds were present, indicating a more extensive form of agriculture, *Amara* spp. were often found in high abundance.

2.5.1.5 Range and Dispersal

Generally, in agricultural areas, carabids live within 60 m of the field boundaries (Holland *et al.*, 1999 [91]), as they prefer the cover of weedy areas and can find higher numbers of phytophagous prey there (Wilson & Aebischer, 1995 [188]; Coombes & Sotherton, 1986 [36]).

They can; however, move much greater distances when required. For instance, they can move from their overwintering sites in the field margins, several hundred meters into the surrounding crop (Coombes & Sotherton, 1986 [36]; Holopainen, 1995 [92]).

Carabids are known to form metapopulations (den Boer, 1990a [40]) and are unevenly distributed within and between agricultural fields, depending on local conditions (Hengeveld, 1979 [84]). The size of the metapopulations are not thought to be limited by dispersal ability, but by the location of food sources. Carabids usually set up burrows and foraging areas in one place and seldom move out of a 20 m^2 range, unless the food resources are depleted there. Range size is; however, correlated to body size, and the ranges of some larger species can reach a number of hectares (Thomas *et al.*, 1998 [168]).

Certain landscape features may aid or have an inhibiting effect on dispersal. Boundaries between fields, such as hedgerows, roads, tracks and stone walls may limit dispersal between fields. However, where carabids cannot cross a linear feature, they will disperse along its length (Mader *et al.*, 1990 [120]). Duelli *et al.*, (1990 [51]) found that a tarmac road of 6 m in width reduced the movement of individuals by 60 %, while a dirt road reduced movement by 49 %.

Strips of non-cropped habitat are thought to aid dispersal (Burel, 1996 [17]; Petit & Usher, 1998 [138]), allowing carabids to recolonize areas where their numbers have been reduced (den Boer, 1990b [41]). Where there are many linear features together and they cross each other forming nodes, the larger areas of semi-natural habitat this creates may be very beneficial to carabids (Holland & Luff, 2000 [90]).

2.5.2 Pitfall Trapping

Pitfall traps, sometimes called Barber traps, are the most common method used to study carabids, when working in agro-ecosystems (Duelli *et al.*, 1999 [49]). They may also be used to study other groups of active, surface-living invertebrates, including other families of Coleoptera and Arachnids.

Pitfall traps consist of collecting cups, buried up to their rims in soil and part filled with a preserving fluid such as ethylene glycol. They can be fitted with lids, which help to deter scavengers and prevent small mammals or reptiles being caught by accident (Sutherland, 1996 [165]). Lids can be made from flat squares of wood with a leg at each corner. They are buried in the soil around the collecting cup and stand 1 cm above the rim of the trap.

Although pitfall traps are widely used when studying carabids, the results obtained from them do not adequately reflect population sizes. They are generally biased towards certain species, particularly the larger and more active ones. For this reason it is difficult to obtain reliable data on absolute species abundances using pitfall traps. Abundance data collected using pitfall traps is therefore better referred to as activity density data (Thiele, 1977 [167]). However, pitfall traps can be used effectively to determine the dominant species present in a habitat (Luff, 1987 [114]), to measure relative abundance when comparing different areas and to estimate the species richness and diversity of carabid assemblages (Luff, 1996 [115]).

2.6 Cluster Analysis

Cluster analysis allows study sites to be grouped on a dendrogram according to similarities in species composition and relative abundance. The sites that are most similar form clusters. Areas located in the same cluster are more similar than sites in different clusters (Tryfos, 1998 [176]).

There are numerous methods of cluster analysis and many different algorithms may be used. To start with, the input matrices can contain either abundance data or incidence data. Then the level of similarity or ecological distance can be measured in a number of different ways (Kindt & CoeTree, 2005 [97]).

Agglomerative clustering methods, which include the unweighed pair-wise group average (UPWGA) algorithm, produce a hierarchy of clusters on a dendrogram. Agglomerative clustering starts with as many clusters as there are sites, then as it proceeds, it allocates them to progressively larger clusters. The UPWGA algorithm joins clusters according to the average distance between all the members of a cluster (Kindt & CoeTree, 2005 [97]).

The Bray-Curtis dissimilarity is one of the most commonly used measures for quantifying differences in species composition and relative abundance. However, it is a dissimilarity measure rather than a distance measure, as it does not satisfy the triangle inequality axiom (Legendre & Legendre, 1998 [108]).

2.7 Ordination Methods

Another good way of visualizing patterns in relative abundance data is to use ordination methods. The program CANOCO is commonly used in ecology and can perform many different kinds of ordination (Lepš & Šmilauer, 2003 [109]).

Indirect gradient analysis is a type of ordination used to explore and visualize the information present in large data sets, such as the data matrices obtained when studying relative species abundances. Patterns in such multivariate data are extremely difficult to visualize. While two variables may show a correlation that can be visualized as a cloud of points on a two dimensional graph, correlations between three or more variables are a different matter. Each new variable must be plotted in its own separate spatial dimension. This means that as variables are added to the analysis, they form data clouds, which exist in as many different dimensions as there are variables (Palmer, 2010 [132]).

Correspondence analysis (CA) is used for indirect gradient analysis, while canonical correspondence analysis (CCA), is used for direct gradient analysis. Direct gradient analysis allows the inclusion of environmental variables in the analysis, as well as species data. The species abundance data become the dependent variables, and can be examined in relation to patterns seen in environmental variables, which become the independent variables. Additionally in CCA, certain variables, such as local environmental variables, can be used as co-variables, thereby removing their effects from the analysis. This allows the influences of other variables of interest to be seen more clearly, without the interference created by less interesting variables (Lepš & Šmilauer, 2003 [109]).

The procedure used for CCA is the same as that used for CA, except that there have been extra steps added to the algorithm (Palmer, 1993 [131]).

2.7.0.1 Correspondence Analysis

The basic algorithm for CA uses reciprocal averaging. Arbitrary numbers or site scores are first assigned to each sample. Then species scores are calculated as the weighted average of the site scores (the weight being the abundance of the species in each sample). Then the species scores are restandardized either from 0 to 100 or by subtracting the mean and dividing by the standard deviation. After this, new site scores are allocated. These are the weighted average of the species scores for all species in the sample, with the weights again being the species abundances. This process is repeated until there are no obvious changes in the species and site scores between iterations. At the end of this procedure the first CA axis is produced. Higher CA axes are then calculated in the same way, except that the linear effects of the previous axes are factored out (Palmer, 1993 [131]).

2.7.0.2 Canonical Correspondence Analysis

In CCA, the calculated site scores are used in a multiple linear least squares regression, which is determined from the weighted averages of the species scores. These are used as the dependent variables and the environmental data are used as the independent variables. The regression equation is then used to assign new site scores called LC (linear combination) scores. The LC scores are then used to produce the CCA axes (Palmer, 1993 [131]). In CCA, high eigenvalues are associated with long and strong environmental gradients (Gauch, 1982 [79]).

On CCA triplots, the positions of samples and species can be shown as points, and the environmental gradients as arrows. The lengths of the arrows show the relative importance of the different environmental gradients. The positions of the arrows show how well the environmental variables are correlated with the species composition axes. Correlations between different environmental variables are shown by the angles of the arrows relative to one another. The positions of the samples relative to the arrows show what kind of environmental conditions are present at the sampling sites. Then, the locations of the species relative to the arrows show the species preferences regarding environmental conditions (Palmer, 1993 [131]).

The eigenvalue associated with each axis equals the correlation coefficient between the species scores and the site scores. The levels of the eigenvalues for the first two CCA axes indicate how informative the resulting plot will be. High eigenvalues show a high degree of correspondence between species and sites. Generally, eigenvalues of 0.4 or over allow for niche separation of the species data. A Monte Carlo permutation test can be used to determine the significance of the influence exerted by each of the independent variables. The percentage variance in the species data that is explained by each independent variable shows how much influence each variable exerts (ter Braak *et al.*, 1995 [166]).

2.8 Species Richness Estimators

Species richness is the number of species of a particular taxon found in a given site. While it is rarely possible to determine the absolute species richness of a site, there are many methods available for estimating species richness. The results of these estimates can then be compared in order to determine the relative species richness of different sites (Magurran, 2004 [121]).

2.8.0.3 Rarefaction

Rarefaction uses accumulation curves, moving from right to left, to estimate species richness. It allows sites that have been sampled to different degrees to be compared fairly, meaning that all the data obtained in the study can be used. It estimates what the species richness of a site would be if the level of sampling was reduced to the lowest level that occurred in all sites. In this way, sites that experienced high levels of trap loss can be compared to sites where more traps were recovered (Magurran, 2004 [121]).

2.8.0.4 Nonparametric Estimators

The Chao 1 estimator uses the species present in the sample, which are only represented by one or two individuals, to produce an estimate of species richness, while the Chao 2 estimator includes information about how species are distributed between samples (Chao, 1984 [27]; Colwell & Coddinton, 1994 [34]).

The ACE estimator, developed by Lee and Chao (1994 [106]), is a coverage estimated used for plant data. It uses the abundances of species represented by over ten individuals, while the related ICE estimator is an incidence based method, which uses the abundances of species represented by ten or less individuals.

The Jackknife 1 estimator uses the number of species that occur in a single sample to estimate species richness, while the Jackknife 2 takes the number of species found in both one and two samples into account (Burnham & Overton, 1978 [19]; Heltshe & Forrestor, 1983 [83]).

The Bootstrap estimator is related to the Jackknife, but can be applied more widely, as it uses only the number of observed species in its calculation (Efron, 1979 [56]).

2.9 Diversity Indices

The Simpson's diversity index is a nonparametric index, as it makes no assumptions about species abundance distributions. It describes the variance of the species abundance distribution, taking into account both species richness and evenness (Simpson, 1949 [158]). It is probably the most robust and meaningful diversity index (Magurran, 2004 [121]). While it is normally reported in the reciprocal form ($1/D$), this has variance problems, so the complement ($1 - D$) (Lande, 1996 [104]) will be used instead.

Whittaker's measure of β-diversity (β_W) describes the variation among samples taken from each study field. This can also be thought of as how different one sample is to another. It shows the number of times that the richness in the whole field is greater than the average richness of each sample. As different samples were taken at different times in the season, this measure indicates the level of change over time, as well as the level of variation between different sampling sites in the field (Anderson *et al.*, 2011 [3]; Magurran, 2004 [121]).

The Shannon index (*H'*) is a popular diversity index, but has the disadvantage of assuming that all species in a site have been sampled at least once, something that can lead to errors (Magurran, 2004 [121]). In this study; however, the pattern of results obtained by the Shannon index closely mirrored those obtained by the Simpson's index, suggesting that the level of error was small, allowing meaningful comparisons to be made between the study fields. When the Shannon index is calculated for many different sites, or in this case study fields, the resulting data set is usually normally distributed. This allows the use of parametric statistics on such datasets (Magurran, 2004 [121]).

Margalef's diversity index (D_{Mg}), although technically a species richness index, takes into account the number of samples obtained for each study field. For this reason it may be used to compare fields in which different numbers of traps were recovered. This means that all the data obtained in the study can be used when calculating this index (Clifford & Stephenson, 1975 [30]).

2.10 Evenness

Evenness describes how similar the numbers of individuals of each species are in a given site. Communities that are dominated by only a few species will have low levels of evenness, while communities in which all species are present in similar numbers, will have high levels of evenness. Evenness can be measured using the Shannon evenness measure (*J'*), which is calculated from the Shannon diversity index (*H'*). *J'* can be described as the ratio of the diversity to the natural log of the total number of species in all samples (Pielou, 1975 [139]).

2.11 Correlations

A standard correlation tests whether there is an association between two variables. The Pearson product--moment correlation, a parametric test, produces an r-value of between -1 and 1, which indicates the strength of the association between the two variables. A low r-value shows that the two variables being tested are negatively correlated, so high levels of one variable are associated with low levels of the other variable. A high r-value shows that the two variables are positively correlated, so a high level of one variable is associated with a high level of the other variable. The p-value indicates whether or not the correlation is significant. The Spearman rank-order correlation is the nonparametric version of this test, which may be used if the data sets do not conform to the assumptions of parametric testing (Dytham, 2003 [54]).

2.12 Project Aims

The aim of this project is to compare closely situated sites of heterogeneous and homogeneous agriculture. Comparisons between sites will be made regarding:

1. the relative abundance of higher invertebrate taxa and Coleoptera families.
2. the relative abundance, species composition, species richness and diversity of carabid species.
3. the diversity and percentage cover of wild plant morphospecies.
4. different aspects of landscape heterogeneity, which will be identified using landscape analysis.

Finally this project aims to determine which aspects of landscape heterogeneity have the greatest influence on carabid communities.

Chapter 3

Methods

3.1 Study Area

The study area was located close to the town of Lamia, in the Spercheios valley, Fthiotida, Central Greece (38°53′52.32′′N, 22°15′49.58′′E). A map and satellite picture of this area are presented in Figure 3.1. The area covered around 75 km^2 and contained mixed cultivation, some pastureland, as well as many areas of interspersed woodland and wasteland.

The study area was chosen because it contained sites of small-scale, heterogeneous agriculture, of the type typical to much of Greece, in close proximity to sites of larger scale, more homogeneous agriculture.

3.2 Study Sites

From within the study area, six study sites were then chosen. These sites were paired so that sites of heterogeneous agriculture (a) could be compared to closely situated sites of more homogeneous agriculture (b). Heterogeneous sites had small field sizes, large amounts of non-cropped habitat and high levels of land use diversity. Homogeneous sites; however, had larger field sizes, smaller amounts of non-cropped habitat and lower levels of land use diversity. See Table 3.1.

The sizes of the study sites varied and their shapes were irregular, as their outlines marked the places that were considered most heterogeneous or homogeneous when compared to each other and to the surrounding landscape. Figure 3.2 shows the relative positions of the six different study sites.

The paired heterogeneous and homogeneous sites were matched regarding their average elevation and their distances from man-made or natural landscape features. These were villages, roads, rivers, streams and large areas of woodland or wasteland. This meant that the paired sites were as similar as possible to each other in every way apart from their heterogeneity. The data for matching these sites were obtained using Google Earth and are presented in Appendix 1.

Table 3.1: Characteristics of heterogeneous (a) and homogeneous (b) study sites. Land use diversity calculated with the Simpson's Index.

Study Site	**1a**	**1b**	**2a**	**2a**	**3a**	**3b**
Field Size (ha)	0.18	0.50	0.03	1.00	0.50	0.87
Non-Cropped Habitat (ha) / 10 ha	3.24	0.44	3.83	0.03	5.56	2.15
Land Use Diversity	0.86	0.36	0.81	0.03	0.80	0.68

Table 3.2: Agrochemical input information used to match study fields in heterogeneous (a) and homogeneous (b) study sites.

Study Field	**Insecticide**	**Fertilizer**
Maize (a)	None	10-20-10, lime
Maize (b)	None	23-8-6, 0.5Zn
Olives (a)	None	None
Olives (b)	None	None
Wheat (a)	None	None
Wheat (b)	None	None
Cotton (a)	Phosalone	11-15-15
Cotton (b)	Phosalone	11-15-15

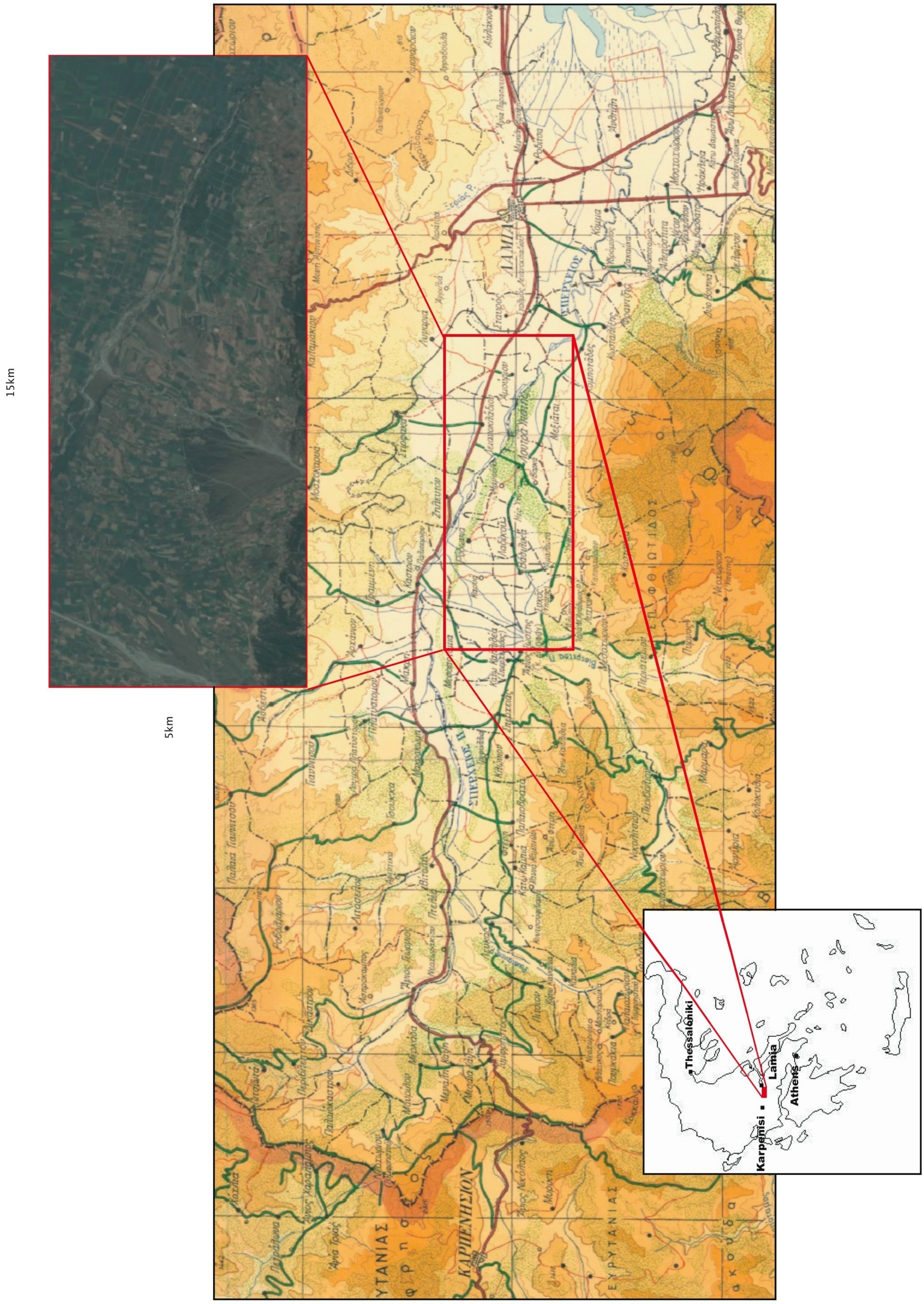


Figure 3.1: Map and satellite picture of the study area.

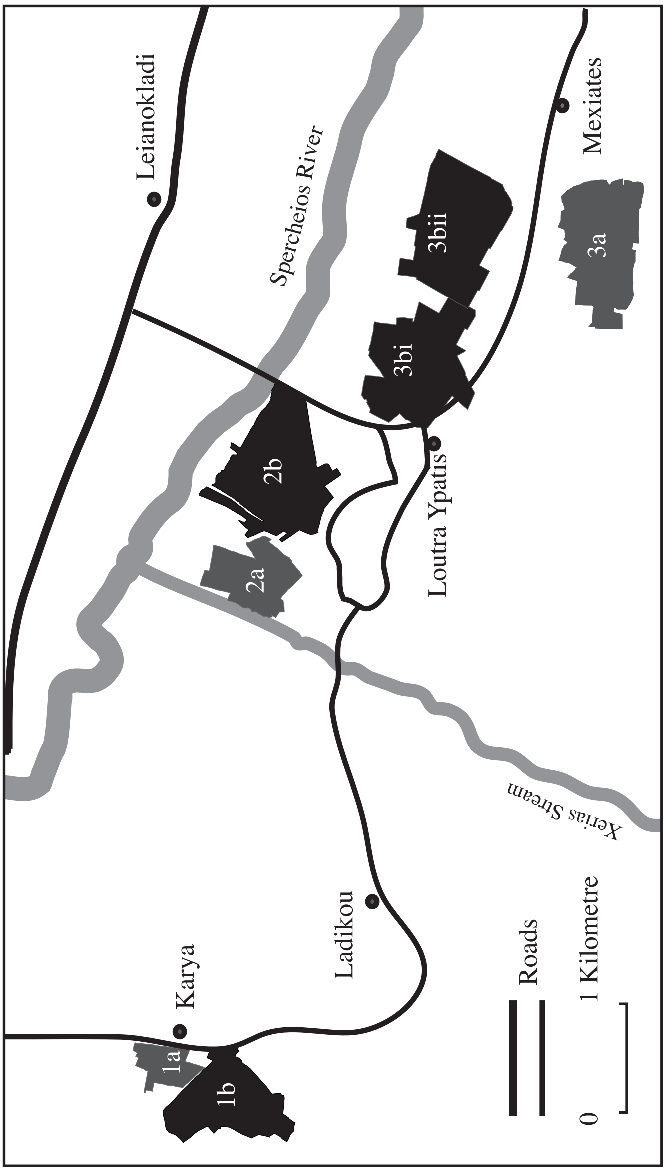


Figure 3.2: The locations of the matched heterogeneous (a) and homogeneous (b) study sites.

Table 3.3: Crop husbandry information used to match study fields in heterogeneous (a) and homogeneous (b) study sites.

Study Field	**Previous Crop**	**Harvest**	**Irrigation**
Maize (a)	Maize	Mid September	Yes
Maize (b)	Maize	Mid September	Yes
Olives (a)	NA	NA	No
Olives (b)	NA	NA	No
Wheat (a)	Alfalfa	Early June	No
Wheat (b)	Alfalfa	Early June	No
Cotton (a)	Cotton	Late October	Yes
Cotton (b)	Cotton	Late October	Yes

3.3 Study Fields

From within the heterogeneous and homogeneous study sites, study fields pairs were chosen for comparison. This was done by inspecting the fields on the ground and by interviewing the landowners regarding the agricultural practices used in the fields. Initially, ten study fields were chosen, five in the heterogeneous sites and five in the homogeneous sites. The field pairs were matched as closely as possible according to their crop type, their previous crop type, their times of planting and harvesting, their agrochemical treatment and the presence or absence of irrigation. The crops grown in the five field pairs were alfalfa, maize, olives, wheat and cotton. However, invertebrate sampling in the alfalfa fields had to be abandoned because the frequency of harvesting in these fields destroyed the traps before they could be collected. For this reason, data from these fields will not be presented. While it was not important to match the time of harvest or previous crop type for the two olive cultivations, the study fields were matched so that the trees were of similar ages. The agrochemical input information used in matching the study fields is shown in Table 3.2 and other crop husbandry information in Table 3.3. Photographs of the eight study fields are shown in Figures 3.3 to 3.10, while the positions of the study fields within the study sites are shown with red dots on the maps beginning on Page 168.

Figure 3.3: Maize study field in heterogeneous site 1a.

Figure 3.4: Maize study field in homogeneous site 1b.

Figure 3.5: Olive study field in heterogeneous site 2a.

Figure 3.6: Olive study field in homogeneous site 2b.

Figure 3.7: Wheat study field in heterogeneous site 3a.

Figure 3.8: Wheat study field in homogeneous site 3bi.

Figure 3.9: Cotton study field in heterogeneous site 3a.

Figure 3.10: Cotton study field in homogeneous site 3bii.

3.4 Landscape Analysis

3.4.1 Study Site Maps

Categorical maps of each study site were made using satellite photographs and by visiting the sites. The satellite photographs were taken from an eye altitude of 1.5 km. The maps made from these photographs show the positions of all the fields and land use patches, the identities of the different land use types and the positions of the sampling fields. Each land use type is represented by a polygon of a different colour. These maps are presented in an appendix beginning on Page 168. Because of the size of homogeneous site 3b, this area was divided in two, and two separate maps were made. The map of site 3bi shows the area around the wheat study field, while the map of site 3bii shows the area around the cotton study field.

3.4.2 Data Matrices

The crop and land use maps of each of the different study sites were then converted into data matrices. Equally sized rectangular grids were placed on top of the maps. These grids were made up of 25 m^2 cells and were used to compare the heterogeneous and homogeneous sites. 25 m^2 grid cells were used as their areas are close to the average range size (20 m^2) of many carabid species. The land use type present in every grid cell was recorded as a different integer, producing the data matrices. Two separate data matrices were produced for each area, one covered an area of 10 ha, the other covered an area of 50 ha.

3.4.3 Calculation of FRAGSTATS Metrics

The data matrices were then input into the program FRAGSTATS, which calculated metrics at three different levels, the patch level, the class level and the landscape level. In total, taking into account all of the different land use types, 399 different calculations were made.

The patch level metrics provided data regarding the individual study fields. The class level metrics provided data regarding the various land use types in the study areas, while the landscape level metrics provided data covering entire study areas. The metrics used at each of these different levels are listed and described in Table 3.4. The algorithms of the metrics (McGarigal *et al.*, 2002 [123]) are provided in an appendix beginning on Page 171.

Two different sizes of data matrix were used to calculate the metrics. This was because of the difference in size between the heterogeneous and homogeneous sites. Using a 10 ha matrix on a homogeneous site, resulted in the loss of large amounts of data from the larger sites. However, using a 50 ha matrix on a heterogeneous site meant that varying amounts of unidentified background were recorded, causing the actual size of the analyzed sites to differ. For this reason two separate comparisons were made. The first comparison using the 10 ha matrices, compared class and landscape level metrics that would vary in value depending on the size of the site being examined. At the class level, this was the number of patches of each land use type. At the landscape level, these metrics were land use richness and the Simpson's diversity index. All the other metrics were calculated using the 50 ha grids, so that all of the data collected from the larger homogeneous sites could be used in the comparisons.

As FRAGSTATS produced landscape-scale data for each study site, replication of the landscape analysis within each site was not possible. Only one data point was obtained per site, per metric. This meant that the significance of differences between landscape metrics could not be tested between heterogeneous and homogeneous sites. Dividing the sites into smaller grids would have reduced the scale of the analysis too much to produce meaningful results at the landscape level.

3.5 Invertebrate Sampling

Invertebrate sampling took place in 2007, starting in May, once the crop plants had become established and would not be easily damaged. It concluded in October when the maize and wheat fields were ploughed. The samples were taken using pitfall traps. These were plastic cups, 7.3 cm in diameter, part filled with ethylene glycol and covered with wooden lids. 10 traps were set in each study field with 10 m distance between them. Only 10 traps were used per study field because some of the fields in the heterogeneous sites were very small and narrow, only 20 m wide in the case of the maize study field. This meant that these fields would not be rapidly depleted of invertebrates as the sampling period

Table 3.4: The landscape metrics calculated by FRAGSTATS.

Patch Level Metrics	
FRAGSTATS Metric	**Description**
Area	Study field area (ha).
Proximity Index	Proximity of study fields to others of the same crop type.
Similarity Index	Proximity of study fields to others of similar land use types.
Class Level Metrics	
Percentage of Landscape	Percentage of the area occupied by each land use type.
Number of Patches	Number of fields of each land use type.
Contagion Index	Contagion of fields of each land use type.
Aggregation Index	Aggregation of fields of each land use type.
Interspersion / Juxtaposition Index	Interspersion / juxtaposition of each land use type.
Connectance Index	Connectivity of each land use type.
Landscape Level Metrics	
Number of Patches	The number of fields in each study area.
Largest Patch Index	The dominant land use type in each study area.
Patch Area Distribution	Average field size in each study area.
Proximity Index Distribution	Average proximity to fields of the same land use type.
Similarity Index Distribution	Average proximity to fields of a similar land use type.
Contagion Index	Average contagion of all land use types.
Aggregation Index	Average aggregation of all land use types.
Interspersion / Juxtaposition Index	Average interspersion / juxtaposition of all land use types.
Land Use Richness	Richness of land use types.
Simpson's Diversity Index	Diversity of land use types.

progressed. In each of the field pairs, the traps were placed 5 m from the field boundaries so that the same type of habitat was being sampled regardless of the field size. The traps were emptied after a 15 day period and were then reset.

Not all field pairs were sampled during every 15 day period. This was because access to the fields depended on the farming practices taking place at the time. Irrigation, harvesting and spraying would prevent access to the fields and the setting of traps. In all, 440 traps were set and 380 were recovered. Initially a pair of alfalfa fields were also sampled for invertebrates, but the frequency of harvesting meant that the traps were destroyed before they could be collected, so sampling was not continued after the first sampling period. Details of the sampling procedure followed are provided in Table 3.5.

The recovered invertebrate samples were first sorted according to their higher taxa. Then the Coleoptera were identified to family level and the Carabidae to species or subspecies level. The books used for the initial identifications were Harde & Severa (2000 [81]), Luff (2007 [116]), Trautner & Geigenmüller (1987 [174]) and Unwin (1984 [181]). The family and species level identifications were then checked by experts in those groups. Subsamples containing individuals of each captured family and species were provided for checking within the department in Athens. Then a small number of unidentified specimens were sent to the Natural History Museum in London for final verification. See Acknowledgements on Page ix for names and affiliations.

In all, only six individuals were not identifiable to species level. However, a number more had questionable identities. The first five unidentified individuals belonged to the same species in the genus *Harpalus*. Then there was one individual that could only be cautiously identified as belonging to the subgenus *Bembidion (Philochthus)*. See results in Section 4.2.8.4. In addition to these; however, the identities of individuals belonging to the species *Carterus rufipes*, *Harpalus atratus* and *Harpalus smaragdinus* were not 100 % verified.

3.6 Plant and Environmental Sampling

Plant and environmental sampling took place between May and October in 2008. It was conducted during the same weeks of the year as the invertebrate sampling. This meant that the same number of plant, environmental and invertebrate samples were taken for each study field pair.

For the plant samples, a 25 cm x 25 cm quadrat was placed at each pitfall trap site to sample plant percentage cover. 10 quadrat samples were taken per field, placed at 10 m intervals. From within each quadrat the percentage cover of each plant species was recorded. Also a sample of each plant species was taken, photographed and preserved. The plants were then identified to morphospecies and given a code number, so that one species could be distinguished from another.

Environmental data were also collected from the study fields. This was done 10 times for each field, during every sampling trip. One sample was taken at each invertebrate and plant sampling site. The environmental data collected comprised:

- soil moisture.
- soil temperature.
- soil pH.
- light intensity at ground level.

The soil moisture, pH and light intensity measurements were taken using a combined moisture, pH and light meter, the electrodes of which were placed in the upper 5 cm of soil. The pH meter function was calibrated using a range of buffers. This allowed the readings obtained from the meter to be converted to more accurate pH levels. Soil temperature measurements were taken using a soil thermometer, also placed in the upper 5 cm of soil. The time of day in which each field was sampled was alternated. This meant that the fields were not consistently sampled at times of low temperature and light in the morning, or conversely during high temperature and light levels later in the day. In this way the comparisons of average soil temperates and light intensity were fair. Soil samples were then taken from each of the study fields, from 3 points that had been previously sampled for invertebrates and plants. These samples were analyzed for their organic matter content. This was done via the Loss-on-Ignition test, using a similar procedure to that of Schulte & Hopkins (1996 [151]). 2 g of dry soil were weighed into a crucible, placed in a muffle furnace for 1 hour at 400°C, then reweighed at the end of the process. Loss-on-ignition was then calculated for each sample using the following equation:

$$LOI\ (g\ kg^{-1}) = \frac{dry\ soil\ weight - soil\ weight\ after\ combustion}{dry\ soil\ weight} \times 1,000$$

Soil type was analyzed using a test sieve shaker with the following sieve mesh sizes: 2 mm, 1 mm, 500 μm, 250 μm, 125 μm and 63 μm. 50 g samples of dry soil were placed in the shaker for 15 minutes. The resulting soil fractions were weighed, and the program Gradistat (Blott & Pye, 2001 [13]) was used to determine the textural group of the soil and the percentages of sand and mud in each of the samples.

3.7 Data Analysis

Comparisons between study fields in the heterogeneous and homogeneous sites used the data obtained from 40 successful traps out of each field. The traps compared always came from the same chronological sampling period. So if a trap from one study field was destroyed, then data from its chronological equivalent in the other site were removed from the analysis. Although this led to some data loss, it meant that comparisons between fields were always fair, as the data compared came from the same level of sampling effort and from the same times in the season.

Comparisons between crop types used the data taken from both fields of that crop type. 40 traps were taken from the field in the heterogeneous site, 40 from the field in the homogenous area. This meant that comparisons between crop types used the data obtained from 80 traps for each of the different crop types.

3.7.1 Relative Abundance

To start with, the total numbers of invertebrates in each trap and in each study field were calculated. The former created data sets that were tested using the Anderson-Darling test, showing that none of them followed a normal distribution. This meant that Mann-Whitney U tests were used to determine the significance of differences between the study fields in the heterogeneous and homogeneous sites. Finally, the mean number of invertebrates per trap was also calculated for each study field.

The total number of invertebrates trapped in each crop type was also determined and compared. Then Kruskal-Wallis and Mann-Whitney U tests were used to determine the significance of differences between the crop types. Then finally, the mean number of invertebrates per trap was calculated for each of the different crop types.

The total abundance of individuals from each higher invertebrate taxon was calculated for each study field. Then the total number of individuals per trap was found. Again these data sets were tested using the Anderson-Darling test and were found not to follow a normal distribution. The data for the total numbers per trap were tested using the Mann-Whitney U test, to see if there were any significant differences between heterogeneous and homogeneous sites. Finally, the mean number of individuals of each higher taxon were calculated for each of the study fields.

Comparisons of higher taxa abundance were also made between crop types. The total number of individuals found in each crop type was calculated. Kruskal-Wallis tests were used to determine the significance of the differences in total numbers per trap. Then the mean number of individuals of each taxon per trap was calculated for each of the different crop types.

Finally, the same procedure was used with both the Coleoptera family data sets and the carabid species data sets.

3.7.2 The Number of Taxa

The number of higher invertebrate taxa found in the study fields of the heterogeneous and homogeneous sites were also compared. The total number of taxa trapped in each field was determined. Then the number of taxa per trap was found, so that Mann-Whitney U tests could be used to test the significance of any differences between fields. The same procedure was also used to compare the number of different Coleoptera families and the number of different carabid species in heterogeneous and homogeneous sites.

Comparisons were also made between crop types, using the Kruskal-Wallis test and the Mann-Whitney U test. Non-parametric statistics were used in almost all the comparisons made in this study. This was because the assumptions of parametric testing were nearly always violated by the data sets. The data often had unequal variances and were not normally distributed. The use of non-parametric testings; however, made it less likely to find significant differences between areas. This is a problem, which could have been solved by having larger data sets (Dytham, 2003 [54]).

3.7.3 Cluster Analysis

Cluster analysis was performed in Past using the UPWGA algorithm and the Bray-Curtis dissimilarity. This allowed difference in species composition between study fields and sampling trips to be examined. These analyses used abundance data sets for the carabid species, plant morphospecies, Coleoptera families and higher invertebrate taxa.

For all of the invertebrate data sets, supersamples were created by summing the data from groups of samples. The data from 7 traps from each sampling trip were summed, for each of the study fields. This allowed differences between sampling trips to be examined, along with differences due to heterogeneity and crop type.

The next step was to combine the data from 40 successful traps, taken from each study field. These data were used as larger supersamples. This allowed attention to be focussed on differences due to crop type and heterogeneity, rather than due to the time of year that the samples were taken in.

As the plant communities changed rapidly throughout the season, differences due to the sampling trip, were not of interest. So for these data, only one cluster analysis was performed. For this, the abundance data from 50 quadrats per field was summed, allowing differences attributable to heterogeneity and crop type to be examined.

3.7.4 Ordination

Firstly, indirect gradient analysis (correspondence analysis) was performed on the data obtained with 40 traps from each study field. This was used to to see how species composition varied regarding the different study fields, heterogeneous and homogeneous sites.

The species data were log transformed in order to down-weight highly abundant species. Hill's scaling was used in the analysis so that the spread of samples would give an indication of the variation between samples in each study field. It also meant that the species points for the species sampled in each field were scattered around the sample points for those fields (ter Braak *et al.*, 1995 [166]).

Next, direct gradient analysis (canonical correspondence analysis) was used to examine the effects of the environmental variables and crop type on the carabid assemblages. Monte Carlo permutation tests were performed on the variables, using 499 permutations, to determine which variables explained the highest levels of variance in the species data. The influence of crop type was then excluded, by performing another CCA, this time using these variables as covariables. This allowed the influence of environmental variables on carabid species composition to be determined independently.

Then the landscape metrics were included in the CCA. During this process the most influential environmental variables and the crop type variables were treated as covariables, while the landscape metrics became the independent variables. This removed the effects of the environmental and crop data and allowed the influences of the landscape metrics to be identified.

As many landscape metrics were calculated, see Table 3.4, half of the highly correlated metrics were removed from the analysis. This was done by finding the highly correlated metric pairs, then removing one of the metrics of each pair. Which metric of the pair was removed depended on the other metrics already included in the analysis and on their relative levels of influence. This ensured that at least one metric for all unrelated aspects of heterogeneity remained in the analysis. The most influential metrics regarding the carabid species data were determined with a Monte Carlo permutation test using 499 permutations.

3.7.5 Estimates of Species Richness

Species richness was estimated using a number of different methods (Magurran, 2004 [121]). This was done using the program EstimateS (Colwell, 2009 [33]). When rarefaction was performed, it used all of the data obtained in the study. This meant that for each field, the data from different numbers of traps were used. For the other estimates; however, only the data obtained from 40 traps from each field were used. This meant that the data came from the same number of traps for each field.

The first of the estimates to be calculated was the Chao 1 (S_{Chao} 1). This was used to estimate the species richness of the carabid assemblages and takes the following form:

$$S_{Chao}\ 1 = S_{obs} + \frac{F_1^2}{2F_2}$$

Where:

- S_{obs} = the total number of species in the sample.
- F_1 = the number of species represented by 1 individual.
- F_2 = the number of species represented by 2 individuals.

The Chao 2 estimator (S_{Chao} 2) was also calculated for the carabid assemblages. This estimator can be written as follows:

$$S_{Chao}\ 2 = S_{obs} + \frac{Q_1^2}{2Q_2}$$

Where:

- Q_1 = the number of species that occur in 1 sample only.
- Q_2 = the number of species that occur in 2 samples.

Coverage estimates were then performed on the plant morphospecies data (Chao & Lee, 1992 [28]). These were of two types. The first was the abundance-based coverage estimate (S_{ACE}), which was calculated using the following equation (Chazdon *et al.*, 1998 [29]):

$$S_{ACE} = S_{abund} + \frac{S_{rare}}{C_{ACE}} + \frac{F_1}{C_{ACE}}\ \gamma^2_{ACE}$$

Where:

- $$\gamma^2_{ACE} = max\left[\frac{S_{rare}}{C_{ACE}}\frac{\sum_{i=1}^{10} i(i-1)F_i}{(N_{rare})(N_{rare}-1}) - 1, 0\right]$$

- S_{rare} = the number of rare species (≤ 10 individuals).
- S_{abund} = the number of abundant species (> 10).
- N_{rare} = the total number of individuals that are rare species.
- F_i = the total number of species with i individuals.
- F_1 = the number of singletons.
- $C_{ACE} = 1 - F_1/N_{rare}$.

The second was the incidence-based coverage estimate (S_{ICE}), which was calculated using the following equation:

$$S_{ICE} = S_{freq} + \frac{S_{infr}}{C_{ICE}} + \frac{Q_1}{C_{ICE}}\ \gamma^2_{ICE}$$

Where:

- $$\gamma^2_{ICE} = max\left[\frac{S_{infr}}{C_{ICE}} \frac{m_{infr}}{(m_{infr}-1)} \frac{\sum_{j=1}^{10} j(j-1)Q_j}{(N_{infr})^2} - 1, 0\right]$$
- S_{infr} = the number of infrequent species (found in ≤ 10 samples).
- S_{freq} = the number of frequent species (found in > 10 samples).
- m_{imfr} = the number of samples with at least one infrequent species.
- N_{infr} = the total number of occurrences of infrequent species.
- Q_j = the total number of species in j samples.
- Q_1 = the number of uniques.
- $C_{ICE} = 1 - Q_1/N_{infr}$.

The Jackknife 1 and 2 estimators (S_{Jack} 1 & S_{Jack} 2) were then calculated for both carabid and plant data using the following equations (Burnham & Overton, 1978 [19]; Heltshe & Forrestor, 1983 [83]):

$$S_{Jack}\ 1 = S_{obs} + Q_1\left(\frac{m-1}{m}\right)$$

$$S_{Jack}\ 2 = S_{obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$$

Where:

- m = the number of samples.
- Q_1 = the number of species found in only 1 sample.
- Q_2 = the number of species found in 2 samples.

Next the Bootstrap estimator (S_{boot}) was calculated for both the plant and carabid data, using the following method:

$$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}} (1-p_k)^m$$

Then, finally, rarefaction, using Colman's random placement method (Coleman, 1981 [31]; Coleman *et al.*, 1982 [32]) was used on the carabid data. Using rarefaction allowed the richness in study fields where fewer traps were recovered to be compared to study fields where more data had been collected.

3.7.6 Diversity and Evenness

Diversity and evenness indices were calculated for the carabid species data and the plant morphospecies data. For the carabid data, all the indices except Margalef's index, were calculated using data taken from 40 traps out of each study field. For the plant data; however, where all samples were successful, the data from all 50 quadrats were used. Then heterogenous and homogeneous sites were compared.

To compare diversity and evenness between crop types, the data taken from both fields of the same crop type were combined. This meant that comparisons were made using the data from 80 traps per crop type in the case of the carabid data, or from 100 quadrats per crop type in the case of the plant data.

The Simpson's diversity index (D) (Simpson, 1949 [158]) was used to calculate the diversity of carabid species and the diversity of plant morphospecies. Then D was converted to the complement ($1 - D$). The following equation was used for the calculation of D:

$$D = \sum_{i=1}^{S} \left(\frac{n_i[n_i - 1]}{N[N - 1]} \right)$$

Where:

- S = the number of species.
- n_i = the total number of individuals of a given species.
- N = the total number of individuals of all species.

Whittaker's measure of β-diversity (β_W) (Whittaker, 1960 [186]) was calculated for the carabid species data. It was not calculated for the plant morphospecies data, as the level of difference between samples taken at different times in the season was great enough to mask any differences due to sample location. The calculation was performed using the following equation:

$$\beta_W = \gamma \,/\, \overline{\alpha}$$

Where:

- γ = the total number of species trapped in an area (in this case the study field).
- $\overline{\alpha}$ = the average species richness of all the samples in the area.

The Shannon index (H') was also calculated (Shannon & Weaver, 1949 [154]) using the carabid species data and the plant morphospecies data. This was done using the following equation:

$$H' = -\sum p_i \;\; ln \;\; p_i$$

Where:

- p_i = the proportion of individuals found in the ith species.

Correlations were then performed using the results of the Shannon index and each of the different landscape metrics. In the majority of cases, both variables conformed to the assumptions of parametric statistics, so the Pearson product-moment correlation was used. If one of the data sets did not meet the assumptions of parametric testing, then the Spearman's rank correlation was used.

The final diversity index to be calculated was Margalef's diversity index (D_{Mg}) (Magurran, 2004 [121]). This index allows areas with different sample numbers to be compared, so all of the data obtained in the study was used. This was calculated using the following equation:

$$D_{Mg} = \frac{(S - 1)}{lnN}$$

Where:

- S = the number of species recorded.

- N = the total number of individuals in the sample.

Evenness was calculated for the carabid and plant data sets using Shannon's evenness measure (F') (Pielou, 1975 [139]). This was calculated using the following equation:

$$F' = H'/lnS$$

Where:

- H' = the Shannon diversity index.
- S = the number of species in all samples.

Table 3.5: Sampling Procedure.

Sampled Field (Study Site)	15 day Sampling Period	No. of Traps Set	No. of Successful Traps	No. of Traps Used in Data Analysis
Maize (Heterogeneous Site 1a)	7th June - 22nd June	10	10	10
	23rd June - 8th July	10	10	9
	9th July - 24th July	10	10	9
	9th Aug - 24th Aug	10	9	8
	8th Sept - 23rd Sept	10	4	4
	Totals / Field	**50**	**43**	**40**
Maize b (Homogeneous Site 1b)	7th June - 22nd June	10	10	10
	23rd June - 8th July	10	10	9
	9th July - 24th July	10	9	9
	9th Aug - 24th Aug	10	9	8
	8th Sept - 23rd Sept	10	7	4
	Totals / Field	**50**	**45**	**40**
Olives a (Heterogeneous Site 1a)	5th May - 20th May	10	8	7
	22nd May - 6th June	10	10	9
	23rd June - 8th July	10	10	9
	9th July - 24th July	10	10	9
	25th July - 9th Aug	10	10	6
	8th Oct - 23rd Oct	10	10	0
	Totals / Field	**60**	**58**	**40**
Olives b (Homogeneous Site 1b)	5th May - 20th May	10	10	7
	22nd May - 6th June	10	10	9
	23rd June - 8th July	10	10	9
	9th July - 24th July	10	10	9
	25th July - 9th Aug	10	10	6
	8th Oct - 23rd Oct	10	9	0
	Totals / Field	**60**	**59**	**40**
Wheat a (Heterogeneous Site 3a)	5th May - 20th May	10	10	10
	23rd June - 8th July	10	10	8
	9th July - 24th July	10	10	8
	9th Aug - 24th Aug	10	8	7
	23rd Sept - 8th Oct	10	9	7
	8th Oct - 23rd Oct	10	0	0
	Totals / Field	**60**	**47**	**40**
Wheat b (Homogeneous Site 3bi)	5th May - 20th May	10	10	10
	23rd June - 8th July	10	8	8
	9th July - 24th July	10	10	8
	9th Aug - 24th Aug	10	7	7
	23rd Sept - 8th Oct	10	10	7
	8th Oct - 23rd Oct	10	7	0
	Totals / Field	**60**	**52**	**40**
Cotton a Heterogeneous Site 3a	22nd May - 6th June	10	10	10
	7th June - 22nd June	10	9	9
	9th July - 24th July	10	6	5
	8th Sept - 23rd Sept	10	10	10
	23rd Sept - 8th Oct	10	7	6
	Totals / Field	**50**	**42**	**40**
Cotton b (Homogeneous Site 3bii)	22nd May - 6th June	10	10	10
	7th June - 22nd June	10	10	9
	9th July - 24th July	10	5	5
	8th Sept - 23rd Sept	10	10	10
	23rd Sept - 8th Oct	10	10	6
	Totals / Field	**50**	**45**	**40**

Chapter 4

Results and Discussion

4.1 Landscape Analysis

4.1.1 Patch Level Metrics

For some patch level metrics, there were consistent patterns regarding heterogeneous and homogeneous sites. For others, the patterns held for study sites 1 and 2, but not for one of the comparisons made in study site 3.

4.1.1.1 Area

Study fields in the heterogeneous sites were all much smaller than those in the homogeneous sites. This was because field size was one of the criteria used when heterogeneous and homogeneous sites were initially chosen using satellite pictures. The sizes of the study fields are given in Table 4.1. There did not appear to be any correlation between the size of the study fields and patterns in plant or invertebrate abundance, richness or diversity. Average field size at the landscape level, the patch area distribution did; however, appear to have an influence on patterns in carabid species composition. See Section 4.87.

Table 4.1: The area of each of the study fields.

		Area (ha)	
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	0.08	4.76
2	Olives	0.14	10.37
3	Wheat	0.36	1.81
3	Cotton	0.72	2.16

4.1.1.2 Proximity Index

The proximity indices for study fields in heterogeneous sites were usually lower than those in homogeneous sites. See Table 4.2. This was true for all study field pairs, except for the wheat, in study site 3. In homogeneous site 3bi, the proximity index was relatively low. It can been seen in the map of this site, shown in Figure 3, that although the wheat study field was located near a number of other wheat fields, these were at more of a distance than the closest wheat fields in heterogeneous site 3a, which were adjacent to the study field. See Figure 2.

Table 4.2: The proximity indices for each of the study fields.

		Proximity Index	
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	16	663
2	Olives	280	1316
3	Wheat	50	19
3	Cotton	4	347

4.1.1.3 Similarity Index

Similarity showed a clear and consistent pattern regarding heterogeneity. See Table 4.3. Study fields in heterogeneous sites all had lower similarity indices than those in homogeneous sites. Table 4.4 gives the similarity weightings used to calculate the indices. For each pair of land use types being compared, a similarity weighting of between 0 and 1 was allocated. A weighting of 0 showed that the two land use types were as different as possible to each other. A weighting of 1 showed that the two land use types were as similar as possible to each other. The land use types represented by the letters A-R are identified in Table 4.5.

Table 4.3: The similarity indices for each of the study fields.

Similarity Index			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	111	769
2	Olives	396	1787
3	Wheat	276	886
3	Cotton	52	466

Table 4.4: The similarity weightings given to each land use type (A-R).

	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**
A	1																	
B	0	1																
C	0.2	0.3	1															
D	0	0.5	0.3	1														
E	0.8	0.2	0.3	0.2	1													
F	0.8	0	0	0	0.2	1												
G	0.5	0.2	0.2	0.2	0.2	0.8	1											
H	0.2	0.2	0.2	0.2	0.2	0.3	0.3	1										
I	0.2	0.2	0.3	0.2	0.5	0.2	0.2	0.2	1									
J	0	0.5	0.3	0.5	0.2	0	0.2	0.2	0.2	1								
K	0	0.8	0.3	0.5	0.2	0	0.2	0.2	0.2	0.5	1							
L	0.8	0.2	0.3	0.2	0.5	0.2	0.2	0.2	0.5	0.2	0.2	1						
M	0.2	0.5	0.3	0.5	0.2	0	0.2	0.2	0.2	0.5	0.5	0.3	1					
N	0.2	0	0.2	0	0.2	0.2	0.2	0.2	0.2	0	0.2	0.2	0.2	1				
O	0.2	0.2	0.3	0.2	0.5	0.2	0.2	0.2	0.5	0.2	0.2	0.5	0.2	0.2	1			
P	0	0.5	0.3	0.5	0.2	0	0.2	0.2	0.2	0.5	0.5	0.2	0.2	0	0.2	1		
Q	0.8	0.2	0.3	0.2	0.5	0.2	0.2	0.2	0.5	0.2	0.2	0.8	0.2	0.2	0.5	0.2	1	
R	0.8	0.2	0.3	0.2	0.5	0.2	0.2	0.2	0.5	0.2	0.2	0.8	0.2	0.2	0.5	0.2	0.8	1

Table 4.5: The letters used to represent the land use types in Table 4.4.

Code Letter	**Land Use Type**	**Code Letter**	**Land Use Type**
A	Woods & Hedges	**J**	Cotton
B	Wheat	**K**	Barley
C	Maize	**L**	Olives
D	Alfalfa	**M**	Hay
E	Plums	**N**	Tracks & Roads
F	Wasteland	**O**	Kiwi Fruit
G	Fallow	**P**	Vegetables & Herbs
H	Gardens & Buildings	**Q**	Almonds
I	Vines	**R**	Walnuts

4.1.2 Class Level Metrics

The class level metrics also showed some clear differences between heterogeneous and homogeneous sites. Many of these metrics showed consistent patterns regarding heterogeneity. A number though, showed different patterns for one or both of the comparisons made in study site 3.

Only the results of the most influential class level metrics are presented in this section. The results of all the calculated class level metrics can be seen in an appendix beginning on Page 175.

4.1.2.1 Percentage of Landscape

Figures 4.1 to 4.7 show the percentage land use in each of the study sites. Heterogeneous sites were usually more evenly divided into different land use types than homogeneous sites. Homogeneous sites tended to be dominated by just one land use type. There was an exception for site 3, however. Heterogeneous site 3a contained large areas of olive cultivations and few other land use types. This made site 3a appear more like a homogeneous site. See Figure 4.5. Conversely homogeneous site 3bi was fairly evenly divided between land use types, making it appear more like a heterogeneous site. See Figure 4.6.

Table 4.6 shows the percentages of the study sites covered by study crops (the crop present in the study field). For this metric, a consistent pattern was seen. In all comparisons, there were higher percentages of study crops in the homogeneous sites. However, the percentage of study crop in site 3bi, where the wheat field was located, was relatively low for a homogeneous site.

Table 4.7 shows the percentages of the study sites covered by woods & hedges. Generally there were higher percentages of woods & hedges in the heterogeneous sites. However, the olive comparison broke the pattern, as a smaller percentage of woods & hedges was seen in the heterogeneous site than in the homogeneous site, although the difference between the two sites was not great.

Table 4.6: The percentage of the landscape covered by the study crop types.

Percentage of Landscape - Study Crops			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	12.1	49.0
2	Olives	25.7	65.1
3	Wheat	3.7	18.0
3	Cotton	11.9	46.3

Table 4.7: The percentage of the landscape covered by woods & hedges.

Percentage of Landscape - Woods & Hedges			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	13.1	4.9
2	Olives	4.8	5.1
3	Wheat	20.6	13.0
3	Cotton	20.6	10.3

Table 4.8 shows the percentages of the study sites left as fallow. Here there was a clear pattern, with heterogeneous sites having greater percentages of fallow than homogeneous sites. The percentage of fallow was ranked joint second in the list of most influential landscape metrics regarding carabid species composition. See Section 4.87.

Table 4.9 shows the percentages of the study sites left as wasteland. Here there was a mixed pattern regarding heterogeneity. For the olive and wheat comparisons, there were large areas of wasteland in the homogeneous sites. However, the other homogeneous sites contained no wasteland. The percentage of fallow plus wasteland was found to be the most influential metric of all regarding carabid species composition. Again see results in Section 4.87.

Table 4.10 shows the percentage of each study site covered by non-cropped habitat. Non-cropped habitat comprised woods & hedges, fallow and wasteland. There was a consistent pattern seen for this metric. Heterogeneous sites always had greater percentages of non-cropped habitat than homogeneous sites.

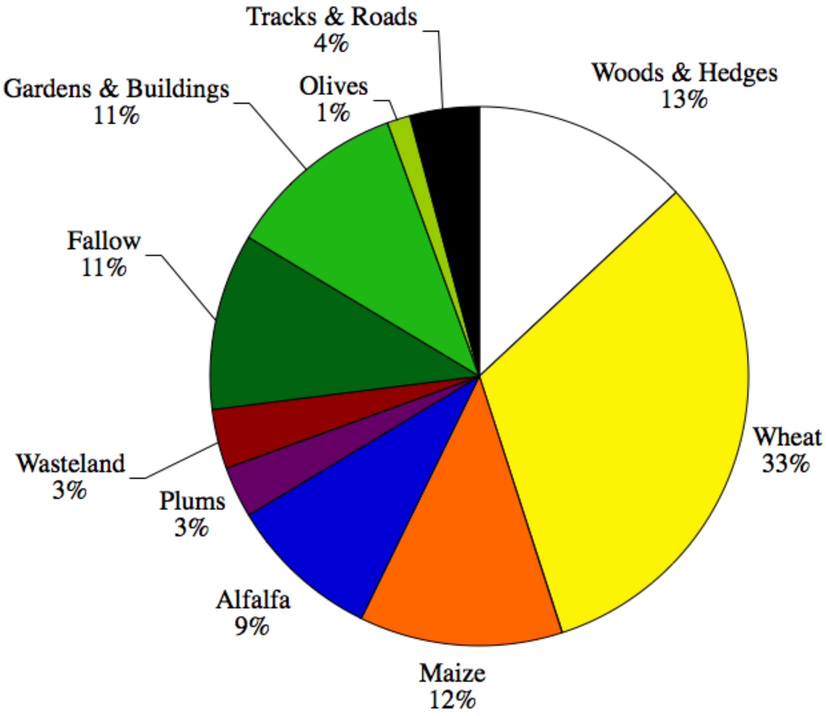


Figure 4.1: The percentage of the landscape covered by each land use type in heterogeneous site 1a, containing the maize study field.

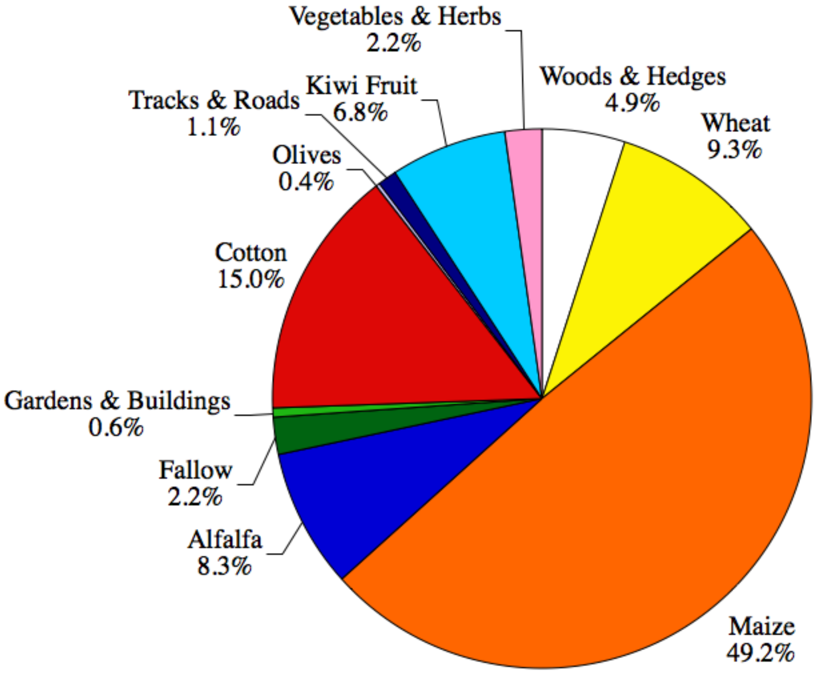


Figure 4.2: The percentage of the landscape covered by each land use type in homogeneous site 1b, containing the maize study field.

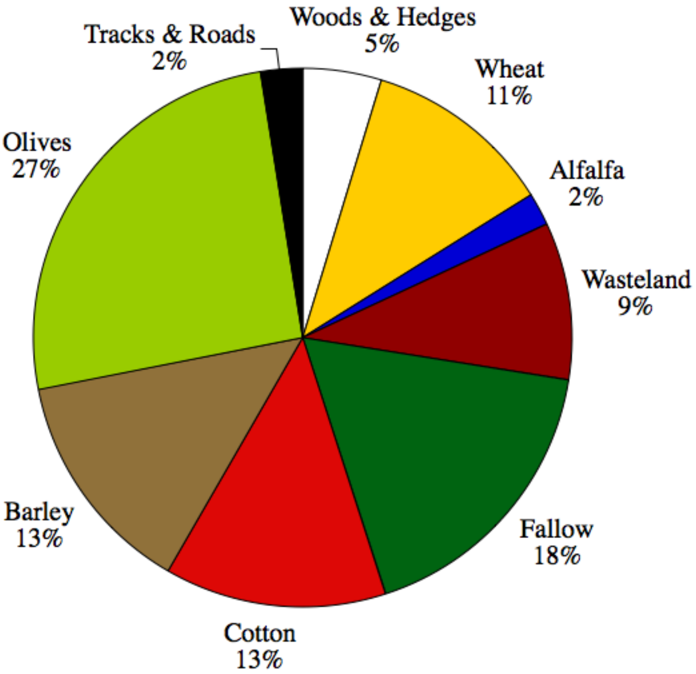


Figure 4.3: The percentage of the landscape covered by each land use type in heterogeneous site 2a, containing the olive study field.

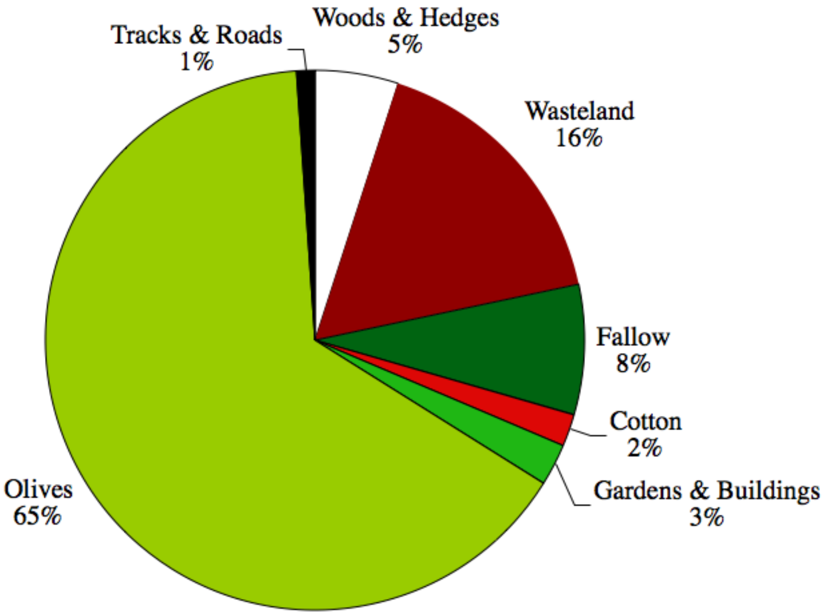


Figure 4.4: The percentage of the landscape covered by each land use type in homogeneous site 2b, containing the olive study field.

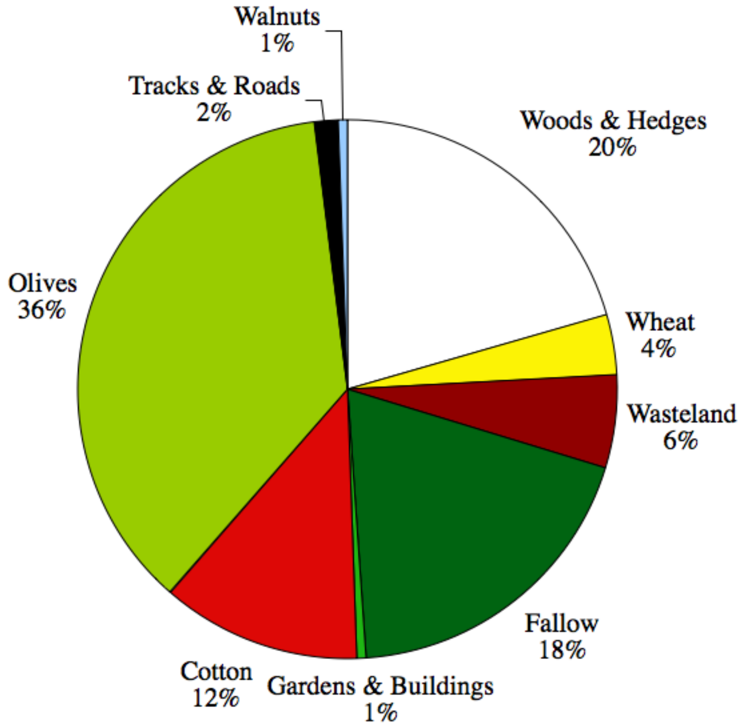


Figure 4.5: The percentage of the landscape covered by each land use type in heterogeneous site 3a, containing the wheat and cotton study fields.

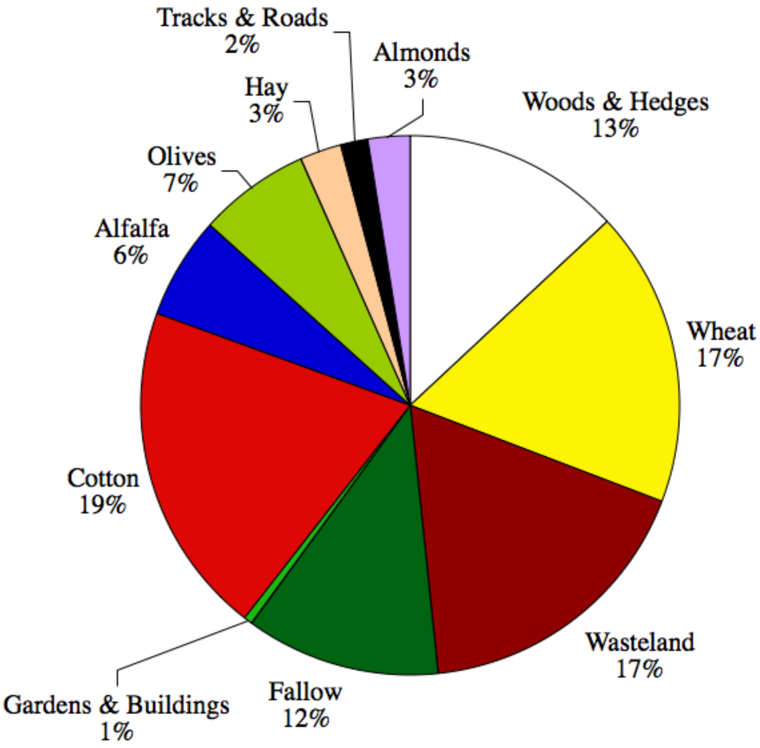


Figure 4.6: The percentage of the landscape covered by each land use type in homogeneous site 3bi, containing the wheat study field.

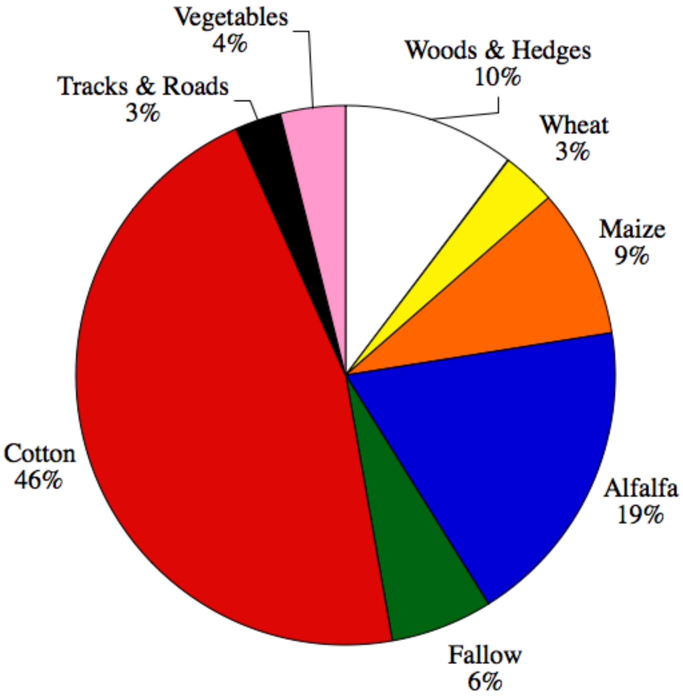


Figure 4.7: The percentage of the landscape covered by each land use type in homogeneous site 3bii, containing the cotton study field.

Table 4.8: The percentage of the landscape left as fallow.

Percentage of Landscape - Fallow			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	10.7	2.2
2	Olives	17.5	7.8
3	Wheat	19.1	11.6
3	Cotton	19.1	6.2

Table 4.9: The percentage of the landscape left as wasteland.

Percentage of Landscape - Wasteland			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	3.5	0.0
2	Olives	9.2	16.5
3	Wheat	5.6	17.4
3	Cotton	5.6	0.0

Table 4.10: The percentage of the landscape left as non-cropped habitat.

Percentage of Landscape - Non-Cropped			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	27.3	7.1
2	Olives	31.5	29.4
3	Wheat	45.2	41.9
3	Cotton	45.2	16.5

4.1.2.2 Number of Patches

This metric shows the number of fields or patches of each land use type in each of the study sites. It also shows how fragmented each land use type is. The greater the number of patches, the more fragmented the land use type.

Overall there were more habitat patches in the heterogeneous sites than in the homogeneous sites. This was expected, as the heterogeneous sites all had smaller fields than the homogeneous sites. However, the patterns varied when the numbers of patches of specific land use types were compared.

Table 4.11 shows the number of patches of study crops present in each study site. These were greater in heterogeneous sites, for study sites 1 and 2. However, this was not the case for study site 3. In heterogeneous site 3a, the numbers of patches of study crops were lower than in both homogeneous sites.

Table 4.11: The number of patches of the study crops.

Number of Patches - Study Crops			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	11	2
2	Olives	8	1
3	Wheat	2	3
3	Cotton	3	4

Table 4.12 shows the number of patches of woods & hedges in each study site. These were higher in the heterogeneous sites, except for the site around the wheat study field in study site 3, where the reverse was true.

Table 4.12: The number of patches of woods & hedges.

Number of Patches - Woods & Hedges			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	20	6
2	Olives	37	3
3	Wheat	7	15
3	Cotton	7	6

The numbers of patches of fallow; however, did show a clear pattern regarding heterogeneity. In all study sites, there were more patches of fallow in heterogeneous sites than in homogeneous sites. See Table 4.13.

Table 4.13: The number of patches of fallow.

Number of Patches - Fallow			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	8	1
2	Olives	5	0
3	Wheat	8	1
3	Cotton	8	2

The numbers of patches of wasteland also showed a clear pattern regarding heterogeneity. In all study sites, there were more patches of wasteland in heterogeneous sites than in homogeneous sites. See Table 4.14.

Table 4.14: The number of patches of wasteland.

Number of Patches - Wasteland			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	6	0
2	Olives	8	0
3	Wheat	4	3
3	Cotton	4	0

The numbers of patches of non-cropped habitat were higher in heterogeneous sites, except in the sites surrounding the wheat study fields. Here the numbers of patches were equal in heterogeneous and homogeneous sites. See Table 4.15.

Table 4.15: The number of patches of non-cropped habitat.

Number of Patches - Non-Cropped			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	34	7
2	Olives	50	3
3	Wheat	19	19
3	Cotton	19	8

4.1.2.3 Contagion Index

Table 4.16 shows the contagion indices for the study crops. These were lower for heterogeneous sites in study sites 1 and 2 and for the cotton comparison in study site 3. For the wheat comparison in study site 3; however, contagion was higher in the heterogeneous site. This was due to the presence of a number of contiguous wheat fields in this site. See Figure 2.

Table 4.17 shows the contagion indices for patches of woods & hedges. These did not show a clear pattern regarding heterogeneity. For the maize and wheat comparisons, higher levels of this metric were seen in the heterogeneous site. For the olive and cotton comparisons; however, higher levels of this metric were seen in the homogeneous site.

Table 4.18 shows the contagion of fallow. This was lower in heterogeneous sites, except for site 3, in the wheat comparison. Here contagion was higher in the heterogeneous site.

Table 4.19 shows the contagion of wasteland. For the maize comparison, this was higher in the heterogeneous site. For the other comparisons, higher contagion was seen in the homogeneous sites.

Table 4.16: The contagion indices for each of the study crop types.

Contagion Index - Study Crops			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	0.68	0.93
2	Olives	0.31	0.94
3	Wheat	0.84	0.67
3	Cotton	0.91	0.92

Table 4.17: The contagion indices for patches of woods & hedges.

Contagion Index - Woods & Hedges			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	0.26	0.18
2	Olives	0.08	0.16
3	Wheat	0.21	0.14
3	Cotton	0.21	0.41

Table 4.18: The contagion indices for patches of fallow.

Contagion Index - Fallow			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	0.76	0.87
2	Olives	0.24	0.88
3	Wheat	0.83	0.62
3	Cotton	0.83	0.89

Table 4.19: The contagion indices for patches of wasteland.

Contagion Index - Wasteland			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	0.62	0.00
2	Olives	0.29	0.88
3	Wheat	0.74	0.92
3	Cotton	0.74	0.92

4.1.2.4 Interspersion / Juxtaposition Index

Table 4.20 shows the interspersion / juxtaposition indices for the study crops. These were greater in heterogeneous sites for study sites 1 and 2, meaning that here the study crops were well mixed within other land use types. See Figure 1. However, this was not the case in study site 3, where the reverse was true. In heterogeneous site 3a, the wheat and cotton fields were fairly clustered and not interspersed with other land use types. See Figure 2.

The interspersion / juxtaposition indices for patches of woods & hedges showed the same pattern. In the heterogeneous sites, these were greater for study sites 1 and 2, but lower for study site 3. See results in Table 4.21.

Table 4.20: The interspersion / juxtaposition indices for each of the study crop types.

Interspersion / Juxtaposition Index - Study Crops			
Study Site	**Crop Type**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	73	38
2	Olives	85	41
3	Wheat	17	32
3	Cotton	15	21

Table 4.21: The interspersion / juxtaposition indices for patches of woods & hedges.

Interspersion / Juxtaposition Index - Woods & Hedges			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	91	84
2	Olives	81	79
3	Wheat	74	86
3	Cotton	74	88

The interspersion / juxtaposition indices for fallow were greater in heterogeneous sites, except for the site around the wheat study field in site 3. See results in Table 4.22. This metric was one of the most influential regarding carabid species composition. The results of the CCA ranked it joint third in the list of most influential landscape metrics. See results in Section 4.87.

Table 4.22: The interspersion / juxtaposition indices for patches of fallow.

Interspersion / Juxtaposition Index - Fallow			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	71	64
2	Olives	82	3
3	Wheat	18	24
3	Cotton	18	7

The interspersion / juxtaposition indices for wasteland are shown in Table 4.23. They were greater in heterogeneous sites for study sites 1 and 2, but in study site 3 they were greater in the homogeneous sites.

Table 4.23: The interspersion / juxtaposition indices for patches of wasteland.

Interspersion / Juxtaposition Index - Wasteland			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	62	0
2	Olives	53	39
3	Wheat	16	36
3	Cotton	16	36

4.1.2.5 Aggregation Index

The aggregation indices for study crops were lower in the heterogeneous sites, except in site 3 for the wheat comparison, where they were equal. See Table 4.24. Again this was due to there being a number of other wheat fields in close proximity to the study field in heterogeneous site 3a. See Figure 2.

Table 4.25 shows the aggregation indices for patches of woods & hedges. These were generally greater in heterogeneous sites than in homogeneous sites, except in study site 2. The heterogeneous site 2a had a very low level of woods & hedges aggregation, due to the small overall area covered by that land use type.

Table 4.26 shows the aggregation indices for patches of fallow. These were generally less in heterogeneous sites, except in site 3, in the sites including and surrounding the wheat study fields, where the opposite situation was seen.

Table 4.27 shows the aggregation indices for patches of wasteland. These data show no clear pattern regarding the heterogeneous and homogeneous sites. For the olive and wheat comparisons, homogeneous sites had higher levels of wasteland aggregation than all other sites.

Table 4.24: The aggregation indices for each of the study crop types.

Aggregation Index - Study Crops			
Study Site	**Crop Type**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	87	97
2	Olives	64	98
3	Wheat	92	92
3	Cotton	95	97

Table 4.25: The aggregation indices for patches of woods & hedges.

Aggregation Index - Woods & Hedges			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	64	33
2	Olives	23	51
3	Wheat	65	43
3	Cotton	65	62

Table 4.26: The aggregation indices for patches of fallow.

Aggregation Index - Fallow			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	89	95
2	Olives	70	93
3	Wheat	90	86
3	Cotton	90	93

Table 4.27: The aggregation indices for patches of wasteland.

Aggregation Index - Wasteland			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	81	0
2	Olives	61	96
3	Wheat	90	97
3	Cotton	90	0

4.1.2.6 Connectance Index

The connectance of study crops showed a mixed pattern regarding heterogeneity. For the maize and wheat comparisons, higher connectance levels for study crops were seen in the heterogeneous sites. For the olive and cotton comparisons; however, higher connectance levels were seen in the homogeneous sites. See Table 4.28.

Table 4.29 shows the connectance indices for patches of woods & hedges. These were lower in heterogeneous sites, expect for study site 3, in the wheat comparison. Here this metric was higher in the heterogeneous site. The fact that this metric was generally higher in homogeneous sites seems strange. It may have been due to the scale the landscape analysis was performed at. As the grid squares used in the analysis were 5 m x 5 m, field margins that were less than 2.5 m wide would not have registered as connected. So heterogeneous sites, which had smaller fields and correspondingly narrower field margins, would have had lower connectance.

The connectances of both fallow and wasteland; however, were always higher in heterogeneous sites. These two metrics showed clear patterns regarding heterogeneity. See Tables 4.30 and 4.31

Table 4.28: The connectance indices for each of the study crop types.

Connectance Index - Study Crops			
Study Site	**Crop Type**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	6.1	0.0
2	Olives	1.5	30.0
3	Wheat	50.0	4.4
3	Cotton	4.8	13.2

Table 4.29: The connectance indices for patches of woods & hedges.

Connectance Index - Woods & Hedges			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	4.3	5.1
2	Olives	0.3	0.6
3	Wheat	11.4	1.3
3	Cotton	11.4	16.7

Table 4.30: The connectance indices for patches of fallow.

Connectance Index - Fallow			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	10.7	0.0
2	Olives	0.8	0.0
3	Wheat	4.0	3.9
3	Cotton	4.0	0.0

Table 4.31: The connectance indices for patches of wasteland.

Connectance Index - Wasteland			
Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**
1	Maize	80.5	0.0
2	Olives	2.6	0.0
3	Wheat	8.3	0.0
3	Cotton	8.3	0.0

4.1.3 Landscape Level Metrics

There were also some clear differences between heterogeneous and homogeneous sites at the landscape level. However, again one or both of the comparisons made in study site 3 often produced different patterns to those seen in study sites 1 and 2.

4.1.3.1 Number of Patches

To start with, the total number of land use patches in each study site were calculated. For all comparisons, these were greater in the heterogeneous sites than in the homogeneous sites. This meant that overall the land use types were more fragmented in heterogeneous sites than they were in homogeneous sites. This can be seen in the results presented in Table 4.32. This pattern is unsurprising, as the number and size of fields was one of the most important factors considered when heterogeneous and homogeneous sites were chosen.

Table 4.32: The number of patches in each of the study sites.

Number of Patches			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	69	14
2	Olives	68	5
3	Wheat	37	29
3	Cotton	37	19

4.1.3.2 Largest Patch Index

The largest patch index was also calculated for each of the study sites. This measured the size of the largest field or land use patch within the study sites. The figures, presented in Table 4.33, were lower in the heterogeneous sites for study sites 1 and 2, but lower in the homogeneous site for study site 3. This was due to the presence of many small olive fields in study site 3a. These were situated so close to one another that, in many cases, they would have been counted as a single field or habitat patch. See Figure 2.

Table 4.33: The largest patch indices for each of the study sites.

Largest Patch Index (ha)			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	19.3	23.7
2	Olives	5.6	25.7
3	Wheat	19.7	15.3
3	Cotton	19.7	5.9

4.1.3.3 Patch Area Distribution

The patch area distribution, or average field size, was a factor that was taken into account when the heterogeneous and homogeneous sites were chosen by eye from the satellite photographs. Therefore, it was unsurprising that this metric was consistently lower in the heterogeneous sites. This metric was found to be one of the most influential landscape metrics regarding carabid species composition. It was ranked joint third in the list of most influential metrics identified by the CCA. See results in Section 4.87. Table 4.34 shows the patch area distributions for each of the study sites.

4.1.3.4 Proximity Index Distribution

The results in Table 4.35 show the proximity index distributions for each of the study sites. These were the average proximity indices for all patches in the study sites. They indicate how far each patch was situated from another of the same land use type. The proximity index distributions were much lower in the heterogeneous sites for study sites 1 and 2, meaning that fields in the heterogeneous sites were

Table 4.34: The patch area distributions for each of the study sites.

Patch Area Distribution (ha)			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	0.18	0.50
2	Olives	0.03	1.00
3	Wheat	0.50	0.83
3	Cotton	0.50	0.87

situated further from those of the same land use type. This was not the case in study site 3, however. Here proximity was higher in the heterogeneous site than in the homogeneous sites. This was probably due to the presence of many small olive fields in site 3a, all situated close to one another. Also there were a number of wheat fields situated in close proximity to each other in this site. See Figure 2.

Table 4.35: The proximity index distributions for each of the study sites.

Proximity Index Distribution			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	18	41
2	Olives	7	114
3	Wheat	134	121
3	Cotton	134	130

4.1.3.5 Similarity Index Distribution

The similarity index distribution shows the average similarity for the fields or habitat patches in each of the study sites. That meant how close each field or land use patch was to another of a similar land use type. There were low levels of this metric in the heterogeneous sites of study sites 1 and 2, but low levels in the homogeneous sites of study site 3. See Table 4.36. Again study site 3 broke the pattern, probably due to the large proportion of olive fields in site 3a, leading to a high level of overall similarity, despite the small-scale nature of the farming. See Figure 2.

Table 4.36: The similarity index distributions for each of the study sites.

Similarity Index Distribution			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	148	411
2	Olives	107	2,535
3	Wheat	2,016	1,288
3	Cotton	2,016	315

4.1.3.6 Contagion Index

The next metric to be calculated was the contagion index. At the landscape level this meant the average contagion of all land use types. The levels of this metric, shown in Table 4.37, were generally lower in heterogeneous sites than in homogeneous sites, except in study site 3, in the sites including and surrounding the wheat study fields. Here the opposite situation was seen. Again this would have been due to the presence of numerous, small olive fields in study site 3a, located so close to one another that they would have appeared contiguous. See Figure 2.

Table 4.37: The contagion indices for each of the study sites.

Contagion Index			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	41	57
2	Olives	29	64
3	Wheat	50	45
3	Cotton	50	53

4.1.3.7 Aggregation Index

Average aggregation indices were then calculated for each of the study sites. For all study sites, these were lower in the heterogeneous sites than in the homogeneous sites. See Table 4.38. This meant that the homogeneous sites had large areas of land covered by the same land use type, forming clumps within the landscape. Heterogeneous sites; however, had their land use types spread more evenly throughout the landscape. This metric was ranked joint second in the list of most influential landscape metrics regarding carabid species composition. See results in Section 4.87.

Table 4.38: The aggregation indices for each of the study sites.

Aggregation Index			
Study Site	**Study Site**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	85	92
2	Olives	62	94
3	Wheat	85	88
3	Cotton	85	92

4.1.3.8 Interspersion / Juxtaposition Index

When the average interspersion / juxtaposition indices for all patches in the study sites were compared, no clear pattern was seen. As far as the heterogeneous sites were concerned, higher levels of this index were seen in study site 1, equal levels in study site 2 and lower levels in study site 3. The results seen for study area 3 are particularly unusual, as heterogeneous sites would have been predicted to have higher levels of interspersion / juxtaposition.

Table 4.39: The interspersion / juxtaposition indices for each of the study sites.

Interspersion / Juxtaposition Index			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	68	57
2	Olives	59	59
3	Wheat	50	54
3	Cotton	50	60

4.1.3.9 Land Use Richness

The richness of land use types was then calculated for each of the study sites. See Table 4.40. For study sites 1 and 2, richness was greater in heterogeneous sites than in homogeneous sites. In study site 3, in the sites including and surrounding the wheat study fields, richness was greater in the homogeneous site. In the sites including and surrounding the cotton study fields, richness was equal in the two sites. Again site 3 shows a different pattern to that expected, as heterogeneous sites would be predicted to have higher levels of land use richness.

Table 4.40: Land use richness in each of the study sites.

Land Use Richness /10 ha			
Study Site	**Study Fields**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	10	8
2	Olives	9	3
3	Wheat	7	8
3	Cotton	7	7

4.1.3.10 Land Use Diversity

The final landscape level metric to be calculated was patch diversity. See Table 4.41. This was the diversity of different crops or land use types, calculated using the Simpson's diversity index. For all of the study sites, diversity was seen to be greater in the heterogeneous sites than in the homogeneous sites. These results were almost exactly what would have been expected when comparing heterogeneous and homogeneous sites. Although the levels in the wheat comparison in study site 3 where closer than would have been predicted.

Table 4.41: Land use diversity in each of the study sites.

Simpson's Diversity Index /10 ha			
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**
1	Maize	0.86	0.36
2	Olives	0.81	0.03
3	Wheat	0.80	0.78
3	Cotton	0.80	0.58

4.1.4 Overview of the Landscape Analysis Results

The results of the landscape analysis show that, on the whole, fields or habitat patches in the heterogeneous sites were smaller, more numerous and were usually situated further from fields of the same or similar land use types than those in homogeneous sites. There was also generally both a greater richness and a greater diversity of land use types in the heterogeneous sites.

For the most part, study crops in heterogeneous sites covered less area, were less contiguous, less aggregate, less connected and more interspersed than those in homogeneous sites.

Heterogeneous sites also contained larger amounts of natural and semi-natural habitat than did homogeneous sites. Such habitat was also generally more interspersed, juxtaposed and more fragmented in the heterogeneous sites.

However, the comparisons made between study sites 3a and 3b, those concerning the sites around the wheat and cotton study fields, often showed different results to those just described. In study site 3, the metrics listed in Table 4.42 either showed the opposite pattern to that seen in study sites 1 and 2, or the levels seen in areas 3a and 3b were very similar. For this reason the distinction between heterogeneous and homogeneous sites in study site 3 is less clear than for study sites 1 and 2. In fact, for many metrics, the heterogeneity classifications of sites 3a and 3b could be reversed. This is something that should be considered when looking at the results of the invertebrate and plant sampling.

Table 4.42: The landscape metrics that showed different results for study site 3.

Metric Level	**Metric Name**
Patch	Proximity Index
Class	Number of Patches of Study Crops
Class	Interspersion / Juxtaposition of Study Crops
Class	Aggregation of Study Crops
Class	Contagion of Study Crops
Class	Connectance of Study Crops
Class	Connectance of Woods & Hedges
Class	Interspersion / Juxtaposition of Wasteland
Class	Percentage of Wasteland
Landscape	Proximity Index Distribution
Landscape	Similarity Index Distribution
Landscape	Contagion
Landscape	Interspersion / Juxtaposition
Landscape	Richness

4.2 Invertebrates

4.2.1 The Relative Abundance of Invertebrates

Figure 4.8 shows the relative abundance of invertebrates in the different study fields. When heterogeneous and homogeneous sites were compared, there were seen to be higher abundances in the homogeneous sites for all of the comparisons. This may have been due to the study fields in those sites being much larger than those in heterogeneous sites. See Section 4.1.1. As crop type will usually determine which invertebrate species are found in a field, large fields of a continuous crop type will probably support higher abundances of species preferring the conditions created by that crop.

Table 4.43 shows that there were also higher mean abundances per trap in the homogeneous sites. Additionally, there were significantly higher abundances per trap in the homogeneous sites for both the wheat and cotton fields. However, it must be remembered that the wheat and cotton fields in the homogeneous sites were located in sites that the landscape analysis often found to be highly heterogeneous. See Section 4.1.4. So for these fields significantly higher abundances were found in the sites of highest heterogeneity.

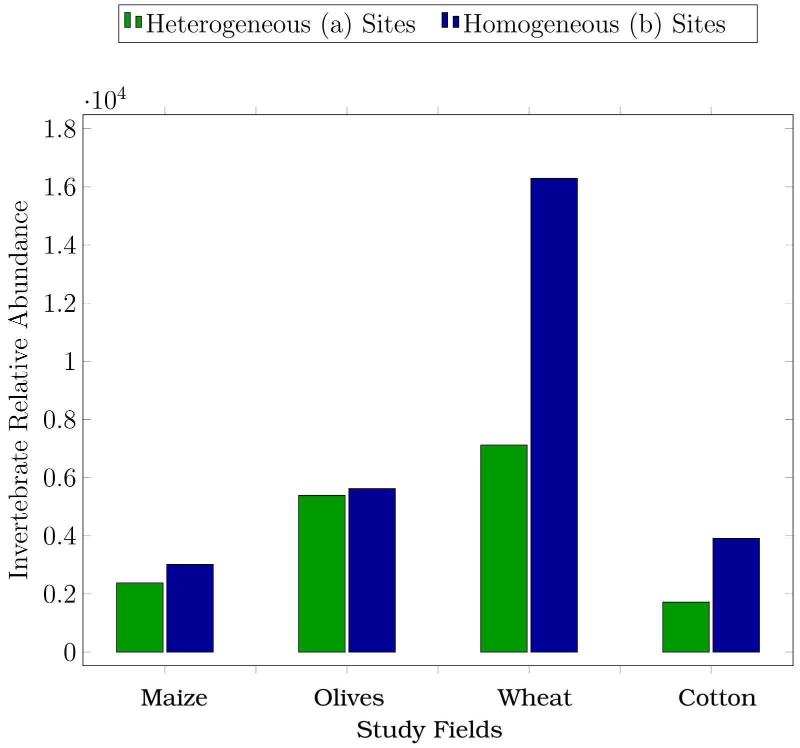


Figure 4.8: The total number of invertebrates trapped in each study field.

Table 4.43: The mean numbers of invertebrates per trap in each study field. Also the results of the Mann-Whitney U tests.

Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
		Mean Number of Individuals			
1	Maize	60	75	858	0.5823
2	Olives	135	140	854	0.6101
3	**Wheat**	178	407	1,214	**0.0001**
3	**Cotton**	43	98	1,198	**0.0001**

Figure 4.9 shows the relative abundance of invertebrates in each of the crop types. The wheat study fields had by far the highest levels of abundance, followed by the olive, cotton and maize fields. The results of the Kruskal-Wallis test showed that there was a highly significant difference in abundance between crop types (H = 103.94, p = <0.0001).

The mean numbers of invertebrates found per trap are shown in Table 4.44, along with the results of the pairwise Mann-Whitney U tests. These statistics show that there were highly significant differences in abundance between all crop types, except between the cotton and the maize.

The wheat study fields may have had higher abundance because for a large part of the sampling period they provided a relatively undisturbed environment. After harvest in early June, the stubble was left undisturbed until the autumn. In addition to this, the wheat fields were never affected by irrigation, or by pesticide or herbicide application.

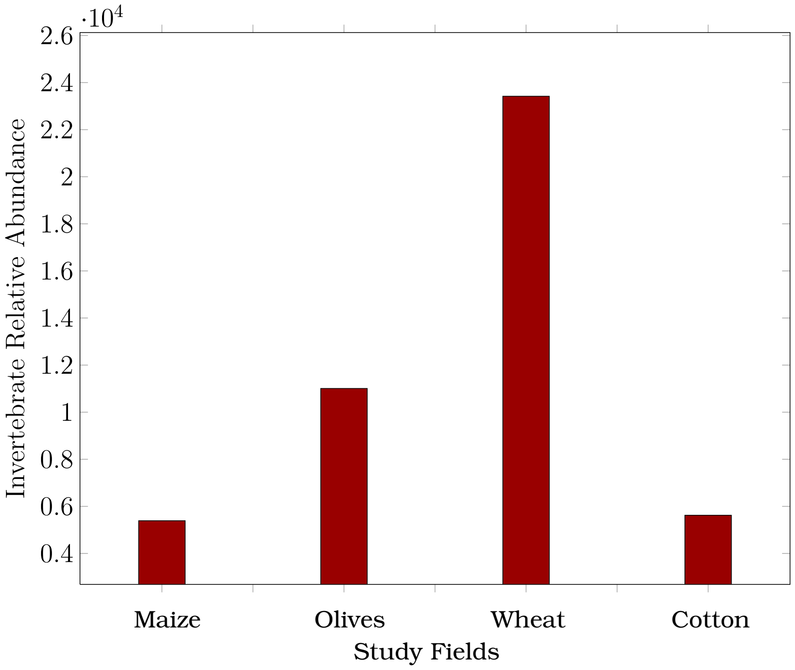


Figure 4.9: The total number of invertebrates trapped in each crop type.

Table 4.44: The mean numbers of invertebrates per trap in each crop type. Also the results of the pairwise Mann-Whitney U tests.

Crop Types	**Mean Abundance**		**U-statistic**	**P-value**
Maize vs. Olives	67	138	4,587	**<0.0001**
Maize vs. Wheat	67	293	5,625	**<0.0001**
Maize vs. Cotton	67	70	3091	0.7114
Olives vs. Wheat	138	293	4,678	**<0.0001**
Olives vs. Cotton	138	70	1,785	**<0.0001**
Wheat vs. Cotton	293	70	771	**<0.0001**

4.2.2 The Number of Higher Invertebrate Taxa

Figure 4.10 shows the total number of higher invertebrate taxa trapped in each of the study fields. Greater numbers of taxa were found in the heterogeneous sites for the maize and olive comparisons in study sites 1 and 2. For the wheat comparison in study site 3, the total number of taxa was greater in the homogeneous site. For the cotton comparison in study site 3, the total numbers of taxa were the same in heterogeneous and homogeneous sites. The pattern of these results reflects those seen for many of the landscape metrics. See Section 4.1.4. This indicates that the landscape metrics identified in Table 4.42 may influence the number of invertebrate taxa found in the study sites.

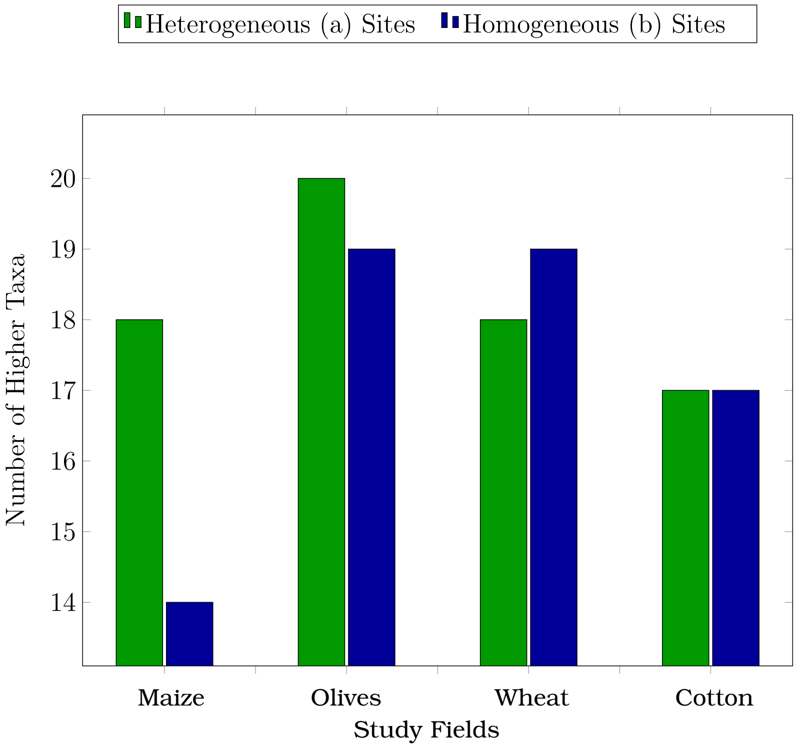


Figure 4.10: The total number of higher invertebrate taxa trapped in each study field.

Table 4.45 shows the mean number of higher invertebrate taxa per trap, as well as the results of the Mann-Whitney U tests used in significance testing. When mean numbers of taxa are considered, higher levels were seen in all heterogeneous sites. However none of the differences between heterogeneous and homogeneous sites were found to be significant.

Table 4.45: The mean number of higher invertebrate taxa per trap in each of the study fields.

Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
		Mean Number of Taxa			
1	Maize	6.43	5.65	616	0.0767
2	Olives	9.03	8.40	649	0.1471
3	Wheat	8.83	8.25	655	0.1645
3	Cotton	6.90	6.53	727	0.4839

It appears that crop type had a greater influence than heterogeneity on the number of higher invertebrate taxa. Figure 4.15 shows the total number of higher invertebrate taxa trapped in each crop type. The greatest number of higher taxa was trapped in the olive study fields, followed by the wheat, cotton and maize fields.

Table 4.70 shows the mean number of higher taxa trapped in each crop type. The results of the Kruskal-Wallis test show that there was a highly significant difference between the different crop types (H = 78.93, p = <0.0001). Then the pairwise Mann-Whitney U tests found highly significant differences between the maize and olive fields, the maize and wheat fields, the olive and cotton fields, as well as the wheat and cotton fields. However, the maize and cotton fields were not significantly different from each other, nor were the olive and wheat fields. See Table 4.70.

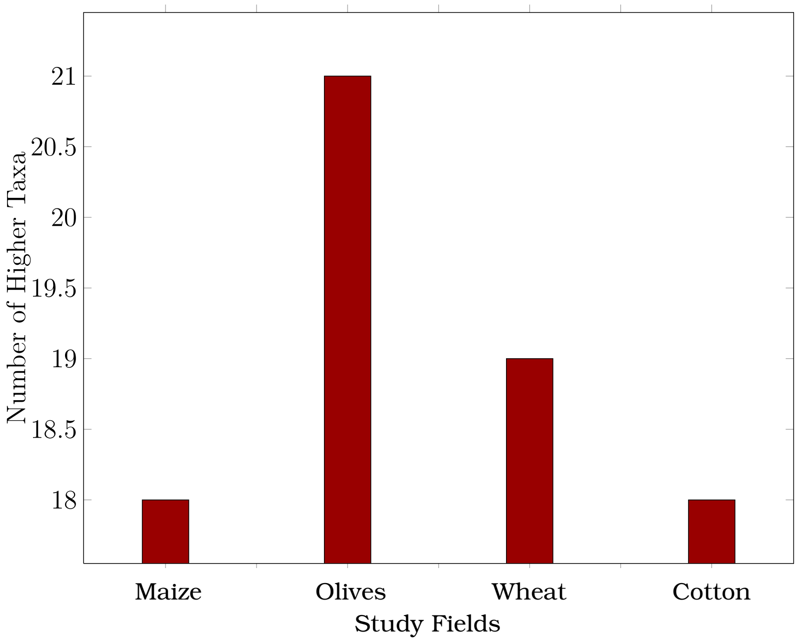


Figure 4.11: The total number of higher invertebrate taxa trapped in each crop type.

Table 4.46: The mean number of higher invertebrate taxa per trap in each crop type. Also the results of the pairwise Mann-Whitney U tests.

Crop Types	**Mean No. of Higher Taxa**		**U-statistic**	**P-value**
Maize vs. Olives	6.04	8.71	5,385	**<0.0001**
Maize vs. Wheat	6.04	8.54	5,235	**<0.0001**
Maize vs. Cotton	6.04	6.71	3,769	0.0524
Olives vs. Wheat	8.71	8.54	3,017	0.5353
Olives vs. Cotton	8.71	6.71	1,669	**<0.0001**
Wheat vs. Cotton	8.54	6.71	1,821	**<0.0001**

4.2.3 The Relative Abundance of Higher Invertebrate Taxa

This section looks at the relative abundance of higher invertebrate taxa trapped during the study. Table 4.47 presents the total number of individuals trapped in 40 successful traps in each study field, throughout the sampling period. The Hymenoptera were by far the most abundant group, with just over fifteen thousand individuals. These were followed by the Collembola, with nearly twelve thousand individuals and the Coleoptera, with around seven thousand individuals. The least abundant groups were the Mantodea, Oligochaeta and the Thysanura. These figures probably reflected the ease with which pitfall traps sampled each of these taxa, rather than providing any meaningful indication of relative abundance.

Table 4.47: The number of individuals of each higher invertebrate taxon trapped in all of the study fields throughout the sampling period.

Taxon	**Number of Individuals**
Acari	2,046
Araneae	2,660
Blattodea	220
Chilopoda	87
Coleoptera	7,111
Collembola	11,925
Dermaptera	347
Diplopoda	317
Diplura	98
Diptera	1,148
Hemiptera	305
Hymenoptera	15,157
Isopoda	1,300
Lepidoptera	46
Mantodea	5
Oligochaeta	6
Opiliones	983
Orthoptera	1,783
Pulmonata	36
Scorpiones	49
Thysanura	11
Total	45,640

4.2.3.1 Maize Study Fields - Study Site 1

Table 4.48 shows the relative abundance of each taxon sampled in the maize study fields. For many taxa, these numbers differed greatly between heterogeneous and homogeneous sites. Eighteen different taxa were recorded in the heterogeneous site, fourteen in the homogeneous site. The Blattodea, Diplura, Oligochaeta and Pulmonata were absent from the homogeneous site. Fifteen of the eighteen taxa present in the maize fields had higher abundances in the heterogeneous site. On the other hand, only three of the taxa had higher abundances in the homogeneous site.

Table 4.49 shows the mean abundance of higher invertebrate taxa trapped in the maize study fields. It shows that there were significantly higher numbers of four taxa in the heterogeneous site. These were the Diptera, Hemiptera, Hymenoptera and Isopoda. In the homogeneous site; however, only one taxon, the Dermaptera, was found to have a significantly higher level of abundance.

Table 4.48: The number of individuals of each higher invertebrate taxon trapped in the maize study fields throughout the sampling period.

Maize Study Fields		
Higher Taxon	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Acari	40	9
Araneae	323	281
Blattodea	5	0
Chilopoda	5	1
Coleoptera Adults	1,016	2,086
Collembola	64	1
Dermaptera	16	196
Diplopoda	4	3
Diplura	5	0
Diptera	141	65
Hemiptera	47	9
Hymenoptera	475	183
Isopoda	70	16
Lepidoptera	9	7
Oligochaeta	1	0
Opiliones	7	19
Orthoptera	151	135
Pulmonata	2	0

Table 4.49: The mean number of individuals of each higher invertebrate taxon trapped in the maize study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Mean Abundance of Higher Invertebrate Taxa				
Maize Study Fields				
Invertebrate Taxon	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Acari	1.00	0.23	778	0.8337
Araneae	8.08	7.03	782	0.8650
Blattodea	0.13	0.00	760	0.7039
Chilopoda	0.13	0.03	720	0.4473
Coleoptera Adults	25.40	52.15	991	0.0673
Collembola	1.60	0.03	719	0.4354
Dermaptera	0.40	4.90	1,287	**<0.0001**
Diplopoda	0.10	0.08	781	0.8572
Diplura	0.13	0.00	780	0.8493
Diptera	3.53	1.63	577	**0.0316**
Hemiptera	1.18	0.23	560	**0.0209**
Hymenoptera	11.88	4.58	460	**0.0011**
Isopoda	1.75	0.40	506	**0.0048**
Lepidoptera	0.23	0.18	800	1.0000
Oligochaeta	0.03	0.00	780	0.8493
Opiliones	0.18	0.48	804	0.9761
Orthoptera	3.78	3.38	717	0.4295
Pulmonata	0.05	0.00	760	0.7039

4.2.3.2 Olive Study Fields - Study Site 2

Table 4.50 shows the relative abundance of each taxon sampled in the olive study fields. Again, for many taxa, these numbers differed between heterogeneous and homogeneous sites. Twenty taxa were recorded in the heterogeneous site, nineteen in the homogeneous site. The Oligochaeta were missing from the heterogeneous site, the Pulmonata and the Thysanura from the homogeneous site. Eleven of the twenty-one taxa present in the olive fields had higher abundances in the heterogeneous site. On the other hand, only eight of the taxa had higher abundances in the homogeneous site, while two taxa had equal abundance in heterogeneous and homogeneous sites.

Table 4.50: The number of individuals of each higher invertebrate taxon trapped in the olive study fields throughout the sampling period.

Olive Study Fields		
Higher Taxon	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Acari	185	185
Araneae	508	419
Blattodea	98	70
Chilopoda	41	15
Coleoptera Adults	219	670
Collembola	445	1,474
Dermaptera	35	20
Diplopoda	124	18
Diplura	2	3
Diptera	90	90
Hemiptera	22	118
Hymenoptera	2,968	2,360
Isopoda	589	91
Lepidoptera	3	5
Mantodea	4	1
Oligochaeta	0	1
Opiliones	28	33
Orthoptera	5	4
Pulmonata	17	0
Scorpiones	3	42
Thysanura	2	0

Table 4.51 shows the mean abundance of higher invertebrate taxa trapped in the olive study fields. It shows that there were significantly higher numbers of three taxa in the heterogeneous site. These were the Chilopoda, the Diplopoda and the Isopoda. Significantly higher numbers of three taxa were also found in the homogeneous site. These were the Coleoptera, the Hemiptera and the Scorpiones.

Table 4.51: The mean number of individuals of each higher invertebrate taxon trapped in the olive study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Mean Abundance of Higher Invertebrate Taxa				
Olive Study Fields				
Invertebrate Taxon	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Acari	4.63	4.63	737	0.5419
Araneae	12.70	10.48	746	0.6101
Blattodea	2.45	1.75	792	0.9362
Chilopoda	1.03	0.38	580	**0.0340**
Coleoptera Adults	5.48	16.75	1219	**0.0001**
Collembola	11.13	36.85	639	0.1236
Dermaptera	0.88	0.50	722	0.4533
Diplopoda	3.10	0.45	380	**0.0001**
Diplura	0.05	0.08	801	1.0000
Diptera	2.25	2.25	875	0.4777
Hemiptera	0.55	2.95	1289	**<0.0001**
Hymenoptera	74.20	59.00	811	0.9203
Isopoda	14.73	2.28	399	**0.0001**
Lepidoptera	0.08	0.13	840	0.7039
Mantodea	0.10	0.03	740	0.5687
Oligochaeta	0.00	0.03	820	0.8493
Opiliones	0.70	0.83	724	0.4654
Orthoptera	0.13	0.10	836	0.7339
Pulmonata	0.43	0.00	620	0.0836
Scorpiones	0.08	1.05	1,115	**0.0024**
Thysanura	0.05	0.00	760	0.7039

4.2.3.3 Wheat Study Fields - Study Site 3

Table 4.52 shows the relative abundance of each taxon sampled in the wheat study fields. Again, for many taxa, these numbers differed between heterogeneous and homogeneous sites. Eighteen taxa were recorded in the heterogeneous site, nineteen in the homogeneous site. Eight of the taxa had higher relative abundance in the heterogeneous site, while eleven had greater abundance in the homogeneous site. This is the opposite situation to that seen for the maize and olive comparisons and may be due to the differences in landscape metrics seen for study area 3. See Section 4.1.4. These results may indicate that heterogeneity has some influence on the relative abundance of higher invertebrate taxa.

Table 4.53 shows the mean abundance of higher invertebrate taxa trapped in the wheat study fields. The heterogeneous site had significantly higher numbers of two taxa. These were the Diplopoda and the Diplura. The homogeneous site, on the other hand, had significantly higher numbers of four different taxa. These were the Acari, the Collembola, the Hymenoptera and the Isopoda. Again this is the opposite situation to that seen in study sites 1 and 2.

Table 4.52: The number of individuals of each higher invertebrate taxon trapped in the wheat study fields.

Wheat Study Fields		
Higher Taxon	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Acari	548	767
Araneae	416	357
Blattodea	33	8
Chilopoda	10	6
Coleoptera Adults	1,404	593
Collembola	1,617	8,138
Dermaptera	2	6
Diplopoda	70	9
Diplura	83	4
Diptera	111	133
Hemiptera	41	21
Hymenoptera	2,603	5,924
Isopoda	129	207
Lepidoptera	4	7
Opiliones	9	67
Orthoptera	31	33
Pulmonata	5	10
Scorpiones	0	4
Thysanura	7	2

Table 4.53: The mean number of individuals of each higher invertebrate taxon trapped in the wheat study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Mean Abundance of Higher Invertebrate Taxa				
Wheat Study Fields				
Invertebrate Taxon	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Acari	13.70	19.18	1,045	**0.0188**
Araneae	10.40	8.93	725	0.4715
Blattodea	0.83	0.20	723	0.4593
Chilopoda	0.25	0.15	754	0.6599
Coleoptera Adults	35.10	14.83	639	0.1236
Collembola	40.43	203.45	1,135	**0.0013**
Dermaptera	0.05	0.15	861	0.5619
Diplopoda	1.75	0.23	506	**0.0048**
Diplura	2.08	0.10	548	**0.0155**
Diptera	2.78	3.33	803	0.9840
Hemiptera	1.03	0.53	619	0.0819
Hymenoptera	65.08	148.10	1,241	**<0.0001**
Isopoda	3.23	5.18	1,010	**0.0434**
Lepidoptera	0.10	0.18	859	0.5755
Opiliones	0.23	1.68	951	0.1471
Orthoptera	0.78	0.83	862	0.5552
Pulmonata	0.13	0.25	878	0.4593
Scorpiones	0.00	0.10	860	0.5687
Thysanura	0.18	0.05	719	0.4413

4.2.3.4 Cotton Study Fields - Study Site 3

Table 4.54 shows the relative abundance of each taxon sampled in the cotton study fields. There were seventeen different taxa found in both the heterogeneous and homogeneous sites. The Diplura were absent from the heterogeneous site, the Pulmonata from the homogeneous site. Nine of the taxa had higher abundance in the heterogeneous site, while eight of the taxa had higher abundance in the homogeneous site.

Table 4.54: The number of individuals of each higher invertebrate taxon trapped in the cotton study fields throughout the sampling period.

Cotton Study Fields		
Higher Taxon	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Acari	310	2
Araneae	179	177
Blattodea	4	2
Chilopoda	5	4
Coleoptera Adults	103	821
Collembola	117	69
Dermaptera	1	71
Diplopoda	86	3
Diplura	0	1
Diptera	165	353
Hemiptera	41	6
Hymenoptera	434	210
Isopoda	19	179
Lepidoptera	1	10
Oligochaeta	2	2
Opiliones	96	724
Orthoptera	153	1,271
Pulmonata	2	0

Table 4.55 shows the mean abundance of higher invertebrate taxa trapped in the cotton study fields. In the heterogeneous site, three different taxa had significantly higher numbers. These were the Acari, the Collembola and the Diplopoda. In the homogeneous site, four different taxa had significantly higher numbers than in the heterogeneous site. These were the Coleoptera, Dermaptera, Diptera and the Orthoptera. Again the opposite situation is seen in study site 3 to that seen in study sites 1 and 2. This may be due to the influence of the landscape metrics discussed in Section 4.1.4.

Table 4.55: The mean number of individuals of each higher invertebrate taxon trapped in the cotton study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Mean Abundance of Higher Invertebrate Taxa				
Cotton Study Fields				
Invertebrate Taxon	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Acari	7.75	0.05	301	**<0.0001**
Araneae	4.48	4.43	651	0.1527
Blattodea	0.10	0.05	760	0.7039
Chilopoda	0.13	0.10	818	0.8650
Coleoptera Adults	2.58	20.53	1,371	**<0.0001**
Collembola	2.93	1.73	586	**0.0394**
Dermaptera	0.03	1.78	1,107	**0.0033**
Diplopoda	2.15	0.08	474	**0.0017**
Diplura	0.00	0.03	820	0.8493
Diptera	4.13	8.83	1,120	**0.0021**
Hemiptera	1.03	0.15	620	0.0836
Hymenoptera	10.85	5.25	761	0.7039
Isopoda	0.48	4.48	966	0.1118
Lepidoptera	0.03	0.25	881	0.4413
Oligochaeta	0.05	0.05	800	1.000
Opiliones	2.40	18.10	936	0.1936
Orthoptera	3.83	31.78	1,043	**0.0198**
Pulmonata	0.05	0.00	760	0.7039

4.2.3.5 Summary

Overall the results seen for the relative abundance of higher invertebrate taxa show a similar pattern to those seen for the landscape metrics identified in Table 4.42. This suggests that heterogeneity may have some influence on the relative abundance of higher invertebrate taxa.

Table 4.56 shows the mean abundance per trap of the higher invertebrate taxa in each crop type. Fifteen of the taxa showed a highly significantly difference in abundance between crop types. See the results of the Kruskal-Wallis tests also presented in the table below. These results suggest that crop type has a greater influence than heterogeneity on the abundance of higher invertebrate taxa.

Table 4.56: The mean number of individuals of each higher invertebrate taxon trapped in the different crop types throughout the sampling period. Also the results of the Kruskal-Wallis test.

Mean Abundance of Higher Invertebrate Taxa in Each Crop Type						
Taxon	**Maize**	**Olives**	**Wheat**	**Cotton**	**H-statistic**	**P-value**
Acari	0.61	4.63	16.44	3.90	102	**<0.0001**
Araneae	7.55	11.59	9.66	4.45	57	**<0.0001**
Blattodea	0.06	2.10	0.51	0.08	40	**<0.0001**
Chilopoda	0.08	0.70	0.20	0.11	15	**0.0017**
Coleoptera Adults	38.75	11.11	24.96	11.55	51	**<0.0001**
Collembola	0.81	23.99	121.94	2.33	149	**<0.0001**
Dermaptera	2.65	0.69	0.10	0.90	15	**0.0018**
Diplopoda	0.09	1.78	0.99	1.11	23	**<0.0001**
Diplura	0.06	0.06	1.09	0.01	8	0.0568
Diptera	2.58	2.25	3.05	6.48	36	**<0.0001**
Hemiptera	0.70	1.75	0.78	0.59	23	**<0.0001**
Hymenoptera	8.23	66.60	106.59	8.05	187	**<0.0001**
Isopoda	1.08	8.50	4.20	2.48	63	**<0.0001**
Lepidoptera	0.20	0.10	0.14	0.14	0.7	0.8756
Mantodea	0.00	0.06	0.00	0.00	0.7	0.8732
Oligochaeta	0.01	0.01	0.00	0.05	0.3	0.9523
Opiliones	0.33	0.76	0.95	10.25	36	**<0.0001**
Orthoptera	3.58	0.11	0.80	17.80	90	**<0.0001**
Pulmonata	0.03	0.21	0.19	0.03	2	0.5359
Scorpiones	0.00	0.56	0.05	0.00	12	**0.0093**
Thysanura	0.00	0.03	0.11	0.00	2	0.6571

Figure 4.12 shows a dendrogram produced by cluster analysis of the invertebrate higher taxa abundance data. It was made using the Bray-Curtis dissimilarity measure and the UPWGA algorithm. The data from 7 traps per sampling trip were combined to form supersamples. These were labelled with the name of the crop, the letter (a) for a heterogeneous site, or the letter (b) for a homogeneous site. Then the numbers (1-6) were added to refer to the sampling trip. The Cophenetic correlation coefficient for this analysis was 0.7638.

The most similar supersamples were those that came from the olive study field in the homogeneous site and the wheat study field in the heterogeneous site. However, this latter field was located in a site found to be homogeneous in a number of important aspects identified by the landscape analysis.

Otherwise the data appeared to cluster by crop type, rather than by heterogeneity, or by sampling trip. Other less similar clusters were composed primarily of supersamples taken from the same study field, or from supersamples taken from the same crop type. This suggests that crop type is the most important influence on the invertebrate data. However, the similarity of the wheat_a and olive_b supersamples suggests that there may be some underlying influence of heterogeneity.

The time at which samples were taken did not appear to have an influence on the relative abundance of the higher invertebrate taxa. If that had been the case, then samples from the same sampling trip would have been expected to form clusters.

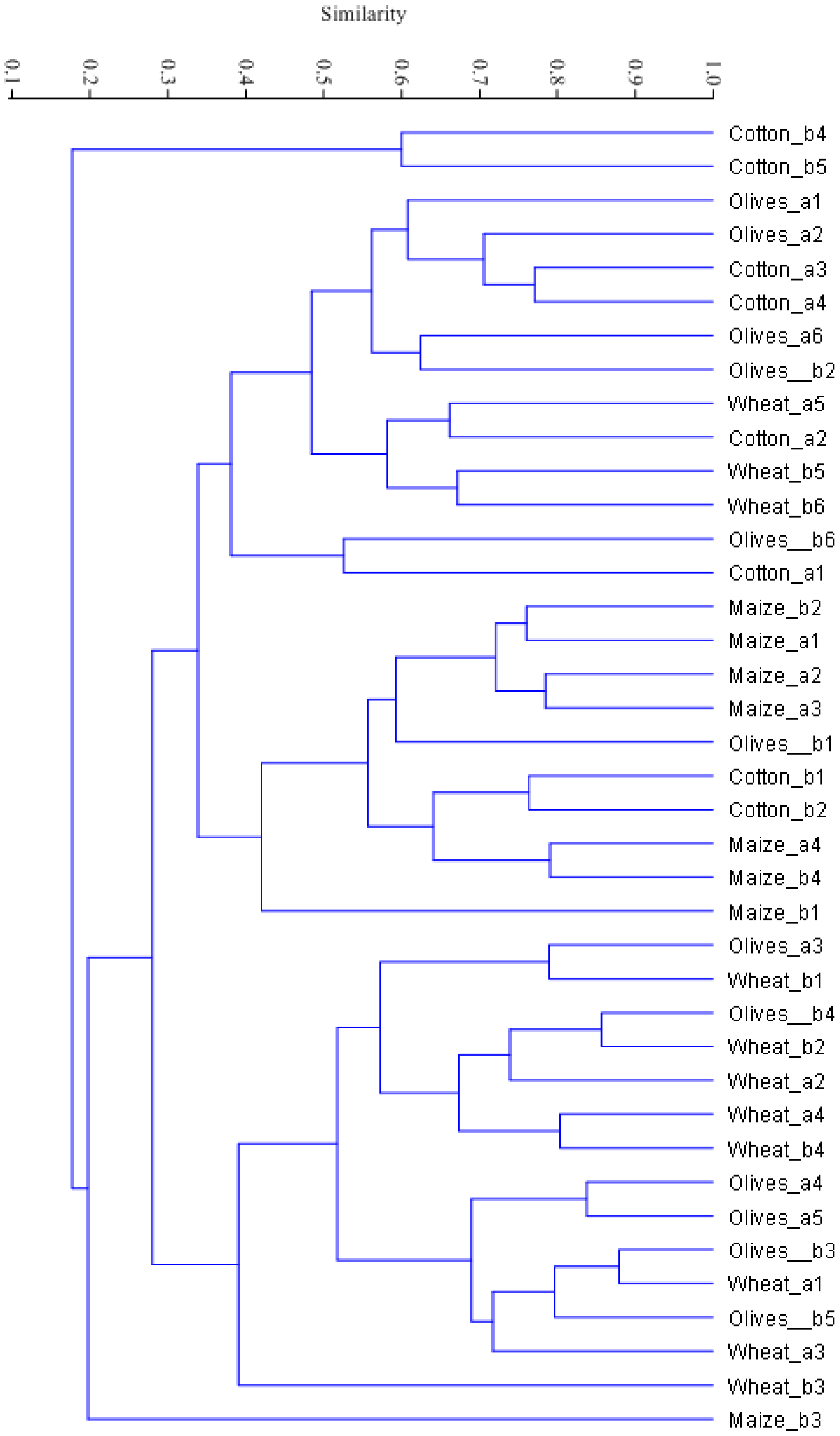


Figure 4.12: Cluster analysis of invertebrate higher taxa abundance data. Data divided by sampling trip.

When data from 40 traps per study field were combined to form one supersample for each field, the dendrogram in Figure 4.13 was produced. Again the Bray-Curtis dissimilarity measure and the UPWGA algorithm were used. The Cophenetic correlation coefficient was 0.8680. For this analysis, each supersample was labeled with the crop name and either the letter (a) for a heterogeneous site, or the letter (b) for a homogeneous site. Here clustering by crop type can be seen fairly clearly. The two maize fields formed a similar cluster, as did the two cotton fields. The clustering of the olive and wheat fields; however, showed that there was perhaps some influence of heterogeneity. The olives_b supersample was most similar to the wheat_a supersample. The sites these fields were located in both had low levels of heterogeneity, according to the landscape metrics listed in Table 4.42.

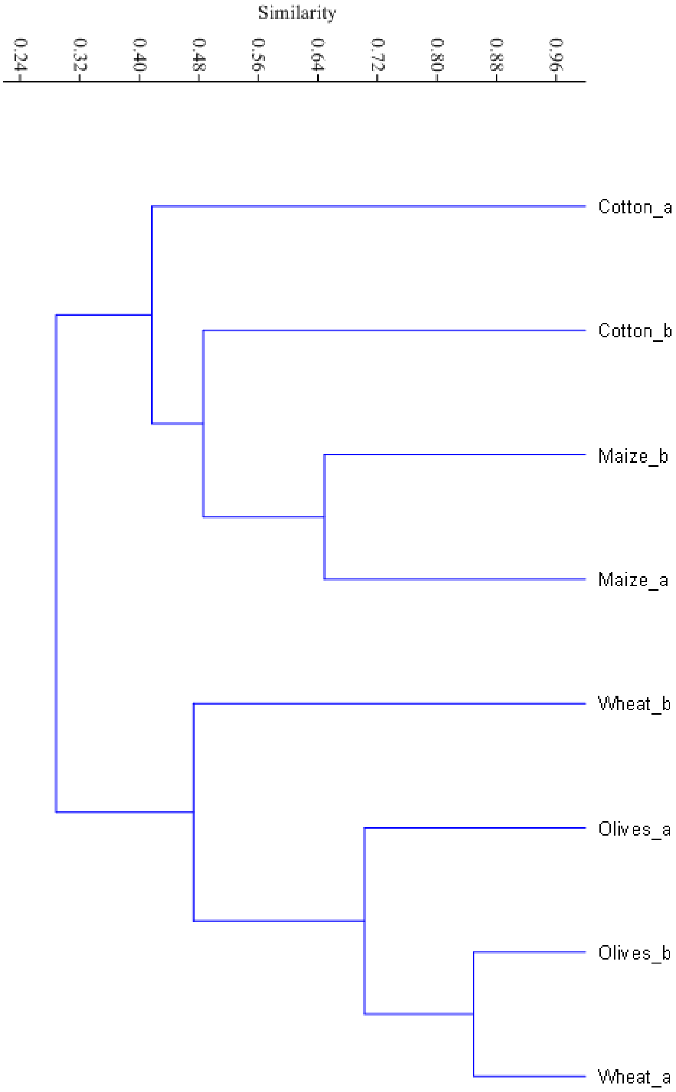


Figure 4.13: Cluster analysis of invertebrate higher taxa abundance data. Data taken from entire sampling period.

4.2.4 The Number of Coleoptera Families

Figure 4.14 shows the total number of Coleoptera families trapped in each of the study fields. For all crop types except the olives, family numbers were higher in the heterogeneous sites. For the olive study fields, total family numbers were equal in heterogeneous and homogeneous sites.

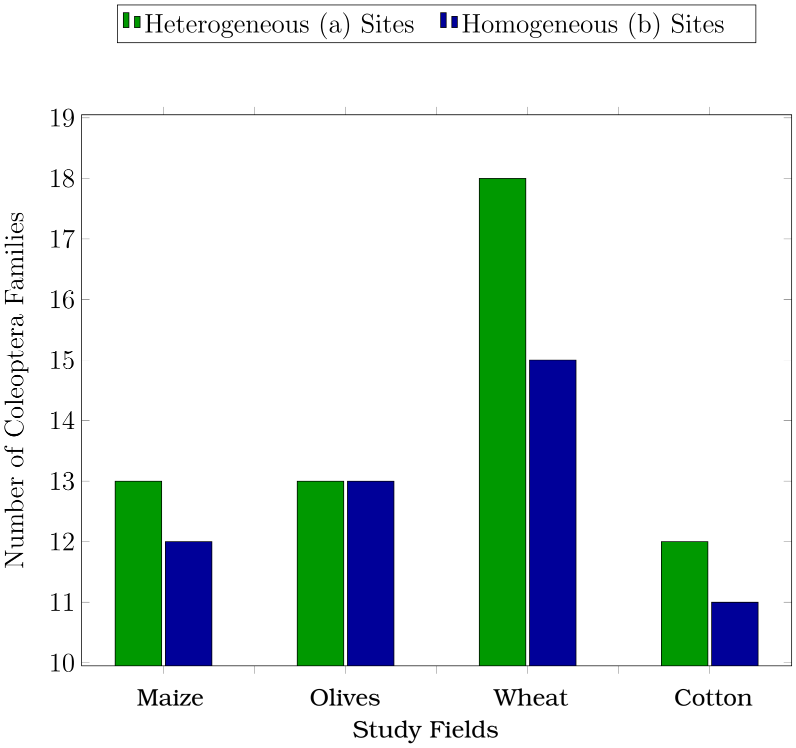


Figure 4.14: The total number of Coleoptera families trapped in each study field.

Table 4.57 shows the mean numbers of Coleoptera families per trap, along with the results of the Mann-Whitney U tests used in significance testing. The mean numbers showed a slightly different pattern to the total number of families per study field. The mean numbers of families were higher in heterogeneous sites for the maize and wheat study fields, but higher in homogeneous sites for the olive and cotton study fields. The cotton study fields were the only fields to show a significant difference between heterogeneous and homogeneous sites. For these fields, there were significantly more families seen per trap in the homogeneous site. This may suggest that some of the landscape metrics identified in Table 4.70 had an influence on the number of Coleoptera families found in this site. On the whole though, Coleoptera families did not appear to be strongly influenced by the level of farmland heterogeneity.

Table 4.57: The mean number of Coleoptera families per trap in each of the study fields.

Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**p-value**
		Mean Number of Families			
1	Maize	2.60	2.35	689	0.2846
2	Olives	2.43	3.00	931	0.2113
3	Wheat	3.38	3.33	776	0.8181
3	**Cotton**	1.23	2.25	1,183	**0.0002**

It appears that crop type had a greater influence than heterogeneity on the number of Coleoptera families sampled. Figure 4.15 shows the total number of Coleoptera families trapped in each crop type. The maize, olive and cotton study fields all had fifteen families trapped in them, while the wheat study fields had a total of twenty families trapped in them.

The mean number of families found per trap in each of the crop types are presented in Table 4.58. The Kruskal-Wallis test showed that there was a significant difference in family numbers between the different crop types (H = 27.88, p = <0.0001). Then the pairwise Mann-Whitney U tests, the results of which are also presented in Table 4.58, showed that the maize fields were significantly different to the wheat fields and the cotton fields. The cotton fields were also significantly different to both the olive and wheat fields. However, the maize and wheat fields were not significantly different to the olive fields.

The large numbers of families found in the wheat fields may have been caused by these fields being undisturbed for a large part of the sampling period. These fields were harvested in early June, then the stubble was left undisturbed until the autumn. Also these fields were never irrigated or sprayed with pesticides or herbicides.

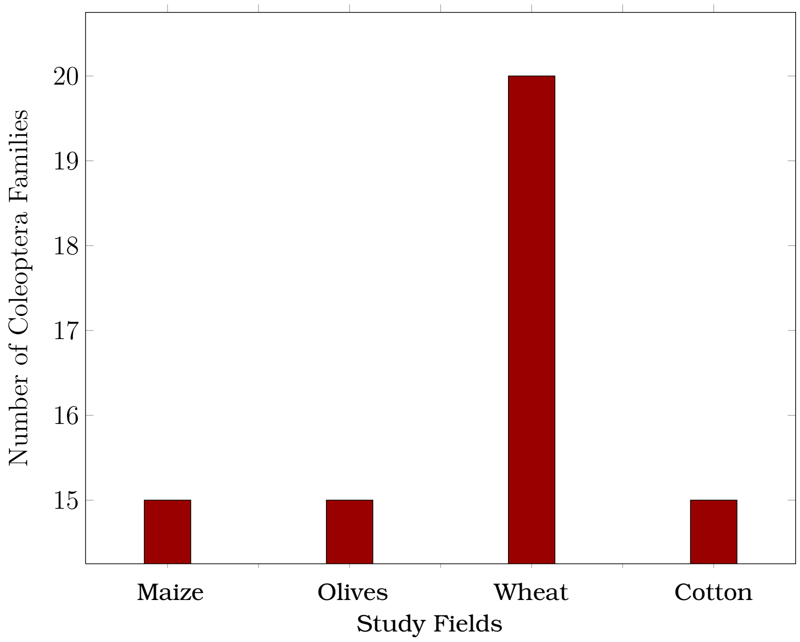


Figure 4.15: The total number of Coleoptera families trapped in each crop type.

Table 4.58: The mean number of Coleoptera families per trap in each crop type. Also the results of the pairwise Mann-Whitney U tests.

Crop Types	**Mean No. of Families**		**U-Statistic**	**P-Value**
Maize vs. Olives	2.48	2.71	3,420	0.4533
Maize vs. Wheat	2.48	3.35	3,937	**0.0121**
Maize vs. Cotton	2.48	1.74	2,191	**0.0006**
Olives vs. Wheat	2.71	3.35	3683	0.1010
Olives vs. Cotton	2.71	1.74	2,204	**0.0007**
Wheat vs. Cotton	3.35	1.74	1,792	**<0.0001**

4.2.5 The Relative Abundance of Coleoptera Families

This section looks at the relative abundance of each of the Coleoptera families trapped during the study. Table 4.59 presents the total number of individuals of each Coleoptera family trapped throughout the sampling period, in all of the study fields. The data were taken from the 40 successful traps recovered from each study field. The Carabidae were by far the most abundant family, with over three thousand individuals. These were followed by the Anthicidae, with over two thousand six hundred individuals. The families caught in the largest numbers would have been those that were most active at ground level.

Table 4.59: The number of individuals of each Coleoptera family trapped in all study fields throughout the sampling period.

Family	**Total Number of Individuals**
Anobiidae	1
Anthicidae	2,607
Buprestidae	2
Carabidae	3,108
Cerambycidae	2
Chrysomelidae	6
Cleridae	22
Coccinellidae	12
Cryptophagidae	2
Cucujidae	63
Curculionidae	22
Dermestidae	60
Elateridae	144
Endomychidae	9
Lampyridae	2
Melyridae	89
Nitidulidae	3
Scarabaeidae	49
Silphidae	33
Sphaeriidae	27
Staphylinidae	270
Tenebrionidae	578
Total	7,111

4.2.5.1 Maize Study Fields - Study Site 1

Table 4.60 shows the relative abundance of each Coleoptera family sampled in the maize study fields. There were thirteen families found in the heterogeneous site and twelve in the homogeneous site. The Coccinellidae and the Tenebrionidae were missing from the heterogeneous site. The Curculionidae, Melyridae and Sphaeriidae were missing from the homogeneous site. Seven of the fifteen families present in the maize fields had higher abundances in the heterogeneous site. On the other hand, eight of the families had higher abundances in the homogeneous site. The fact that a greater number of families had higher abundances in the homogeneous site may have been due to the much higher soil moisture levels found in that study field. Or perhaps this was due to the greater size of the study field in the homogeneous site.

Table 4.61 shows that significantly higher numbers of Staphylinidae were found in the heterogeneous site, while in the homogeneous site the Anthicidae were significantly more abundant.

Table 4.60: The number of individuals of each Coleoptera family trapped in the maize study fields throughout the sampling period.

Maize Study Fields		
Carabid Family	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Anthicidae	45	1,272
Carabidae	820	906
Chrysomelidae	2	1
Coccinellidae	0	2
Cucujidae	7	1
Curculionidae	2	0
Dermestidae	5	11
Elateridae	3	7
Endomychidae	3	4
Melyridae	2	0
Nitidulidae	2	1
Scarabaeidae	2	5
Sphaeriidae	1	0
Staphylinidae	68	12
Tenebrionidae	0	4

Table 4.61: The mean number of individuals of each Coleoptera family trapped in the maize study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Relative Abundance of Coleoptera Families				
Maize Study Fields				
Coleoptera Family	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Anthicidae	1.13	31.80	1,024	**0.0316**
Carabidae	20.50	22.65	906	0.3125
Chrysomelidae	0.05	0.03	780	0.8493
Coccinellidae	0.00	0.05	840	0.7039
Cucujidae	0.18	0.03	680	0.2501
Curculionidae	0.05	0.00	760	0.7039
Dermestidae	0.13	0.28	805	0.9681
Elateridae	0.08	0.18	842	0.6965
Endomychidae	0.08	0.10	820	0.8572
Melyridae	0.05	0.00	780	0.8493
Nitidulidae	0.05	0.03	800	1.0000
Scarabaeidae	0.05	0.13	821	0.8415
Sphaeriidae	0.03	0.00	780	0.8493
Staphylinidae	1.70	0.30	513	**0.0058**
Tenebrionidae	0.00	0.10	840	0.7039

4.2.5.2 Olive Study Fields - Study Site 2

Table 4.62 shows the relative abundance of each Coleoptera family sampled in the olive study fields. There were thirteen families sampled in the heterogeneous site and thirteen in the homogeneous site. The families present in the heterogeneous site, but not in the homogeneous site were the Buprestidae and the Cleridae. The Coccinellidae and the Cryptophagidae on the other hand, were absent from the heterogeneous site. Only six families were found in higher abundance in the heterogeneous site, while eight families were found in higher abundance in the homogeneous site.

Table 4.63 shows the mean abundance of each family sampled in the olive study fields. The Tenebrionidae were found in significantly higher numbers in the homogeneous site.

Table 4.62: The number of individuals of each Coleoptera family trapped in the olive study fields throughout the sampling period.

Olive Study Fields		
Higher Taxon	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Anthicidae	7	35
Buprestidae	1	0
Carabidae	103	56
Cleridae	1	0
Coccinellidae	0	2
Cryptophagidae	0	1
Cucujidae	24	26
Curculionidae	4	5
Dermestidae	3	3
Elateridae	3	19
Melyridae	5	3
Silphidae	10	9
Scarabaeidae	11	14
Staphylinidae	33	30
Tenebrionidae	8	449

Table 4.63: The mean number of individuals of each Coleoptera family trapped in the olive study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Relative Abundance of Coleoptera Families				
Olive Study Fields				
Coleoptera Family	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Anthicidae	0.18	0.88	983	0.0801
Buprestidae	0.03	0.00	780	0.8493
Carabidae	2.58	1.40	613	0.0719
Cleridae	0.03	0.00	780	0.8493
Coccinellidae	0.00	0.05	840	0.7039
Cryptophagidae	0.00	0.03	820	0.8493
Cucujidae	0.60	0.65	825	0.8103
Curculionidae	0.10	0.13	784	0.8808
Dermestidae	0.08	0.08	800	1.0000
Elateridae	0.08	0.48	928	0.2225
Melyridae	0.13	0.08	799	0.9920
Scarabaeidae	0.28	0.35	856	0.5961
Silphidae	0.25	0.23	721	0.4473
Staphylinidae	0.83	0.75	623	0.0891
Tenebrionidae	0.20	11.23	1,408	**<0.0001**

4.2.5.3 Wheat Study Fields - Study Site 3

Table 4.64 shows the relative abundance of each Coleoptera family sampled in the wheat study fields. There were eighteen families found in the heterogeneous site, fifteen in the homogeneous site. Fourteen of these families were found in greater abundance in the heterogeneous site, while six were found in greater abundance in the homogeneous site. These fields contained the largest number of families of all the study fields. The families present in the heterogeneous site, but not in the homogeneous site were the Buprestidae, the Cerambycidae, the Chrysomelidae, the Endomychidae and the Lampyridae. The families present in the homogeneous site, but not in the heterogeneous site were the Anobiidae and the Coccinellidae.

When the mean number of families per trap was considered, there were no significant differences seen for any families between heterogeneous and homogeneous sites. See Table 4.65.

Table 4.64: The number of individuals of each Coleoptera family trapped in the wheat study fields throughout the sampling period.

Wheat Study Fields		
Higher Taxon	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Anobiidae	0	1
Anthicidae	362	206
Buprestidae	1	0
Carabidae	895	239
Cerambycidae	2	0
Chrysomelidae	1	0
Cleridae	10	7
Coccinellidae	0	2
Cucujidae	2	1
Curculionidae	3	6
Dermestidae	24	13
Elateridae	12	5
Endomychidae	1	0
Lampyridae	2	0
Melyridae	71	8
Scarabaeidae	2	8
Silphidae	5	9
Sphaeriidae	13	12
Staphylinidae	59	54
Tenebrionidae	20	80

Table 4.65: The mean number of individuals of each Coleoptera family trapped in the wheat study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Relative Abundance of Coleoptera Families				
Wheat Study Fields				
Coleoptera Family	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Anobiidae	0.00	0.03	820	0.8493
Anthicidae	9.05	5.15	675	0.2301
Buprestidae	0.03	0.00	780	0.8493
Carabidae	22.38	5.98	678	0.2420
Cerambycidae	0.05	0.00	780	0.8493
Chrysomelidae	0.03	0.00	780	0.8493
Cleridae	0.25	0.18	780	0.8493
Coccinellidae	0.00	0.05	840	0.7039
Cucujidae	0.05	0.03	780	0.8493
Curculionidae	0.08	0.15	859	0.5755
Dermestidae	0.60	0.33	814	0.8966
Elateridae	0.30	0.13	696	0.3271
Endomychidae	0.03	0.00	780	0.8493
Lampyridae	0.05	0.00	760	0.7039
Melyridae	1.78	0.20	621	0.0854
Scarabaeidae	0.05	0.20	862	0.5552
Silphidae	0.13	0.23	860	0.5687
Sphaeriidae	0.33	0.30	806	0.9601
Staphylinidae	1.48	1.35	938	0.1868
Tenebrionidae	0.50	2.00	942	0.1738

4.2.5.4 Cotton Study Fields - Study Site 3

Table 4.78 shows the relative abundance of each Coleoptera family sampled in the cotton study fields. There were twelve families found in the heterogeneous site, eleven in the homogeneous site. Six of these were found in greater abundance in the heterogeneous site, while seven were found in greater abundance in the homogeneous site. The families present in the heterogeneous site, but not in the homogeneous site were the Chrysomelidae, the Coccinellidae, the Dermestidae and the Sphaeriidae. The families present in the homogeneous site, but not in the heterogeneous site were the Cryptophagidae, the Curculionidae and the Endomychidae.

Table 4.67 shows that the differences in mean abundance between heterogeneous and homogeneous sites were highly significant for the Anthicidae, the Carabidae and the Elateridae. All these families were found in higher mean abundances in the homogeneous site.

Table 4.66: The number of individuals of each Coleoptera family trapped in the cotton study fields throughout the sampling period.

Cotton Study Fields		
Carabidae Species	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Anthicidae	52	628
Carabidae	14	75
Chrysomelidae	2	0
Cleridae	2	2
Coccinellidae	6	0
Cryptophagidae	0	1
Cucujidae	1	1
Curculionidae	0	2
Dermestidae	1	0
Elateridae	4	91
Endomychidae	0	1
Scarabaeidae	5	2
Sphaeriidae	1	0
Staphylinidae	11	3
Tenebrionidae	1	16

Table 4.67: The mean number of individuals of each Coleoptera family trapped in the cotton study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Relative Abundance of Coleoptera Families				
Cotton Study Fields				
Coleoptera Family	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**P-value**
Anthicidae	1.30	15.70	1,298	**<0.0001**
Carabidae	0.35	1.88	1,135	**0.0013**
Chrysomelidae	0.05	0.00	780	0.8493
Cleridae	0.05	0.05	819	0.8572
Coccinellidae	0.15	0.00	720	0.4473
Cryptophagidae	0.00	0.03	820	0.8493
Cucujidae	0.03	0.03	800	1.0000
Curculionidae	0.00	0.05	840	0.7039
Dermestidae	0.03	0.00	780	0.8493
Elateridae	0.10	2.28	1,155	**0.0006**
Endomychidae	0.00	0.03	820	0.8493
Scarabaeidae	0.13	0.05	759	0.6965
Sphaeriidae	0.03	0.00	780	0.8493
Staphylinidae	0.28	0.08	737	0.5485
Tenebrionidae	0.03	0.40	801	1.0000

4.2.5.5 Summary

There was no clear pattern regarding landscape heterogeneity and the relative abundance of Coleoptera families. The wheat and cotton comparisons did show a similar pattern as those obtained for the landscape metrics in Table 4.42. However, this was not the case for the maize and olive comparisons.

Table 4.68 shows the mean abundance per trap of Coleoptera families in each crop type. Only five of the families showed highly significant differences in abundance between crop types. This can be seen in the results of the Kruskal-Wallis tests, which are also presented in the table below. It seems that crop type had a greater level of influence on the relative abundance of Coleoptera families than heterogeneity.

Table 4.68: The number of individuals of each Coleoptera family trapped in each crop type throughout the sampling period. Also the results of the Kruskal-Wallis test.

Mean Abundance of Coleoptera Families in Each Crop Type						
Taxon	**Maize**	**Olives**	**Wheat**	**Cotton**	**H-statistic**	**P-value**
Anobiidae	0.00	0.00	0.01	0.00	0.03	0.9986
Anthicidae	16.46	0.53	7.10	8.50	47.11	**<0.0001**
Buprestidae	0.00	0.01	0.01	0.00	0.04	0.9979
Carabidae	21.58	1.99	14.18	1.11	134	**<0.0001**
Cerambycidae	0.00	0.00	0.03	0.00	0.03	0.9986
Chrysomelidae	0.04	0.00	0.01	0.03	0.18	0.9808
Cleridae	0.00	0.01	0.21	0.05	0.25	0.9691
Coccinellidae	0.03	0.03	0.03	0.08	0.11	0.9906
Cucujidae	0.10	0.63	0.04	0.03	17.23	**0.0006**
Curculionidae	0.03	0.11	0.11	0.03	0.95	0.8133
Cryptophagidae	0.00	0.01	0.00	0.01	0.04	0.9979
Dermestidae	0.20	0.08	0.46	0.01	5.32	0.1498
Elateridae	0.13	0.28	0.21	1.19	5.49	0.1392
Endomychidae	0.09	0.00	0.01	0.01	0.18	0.9808
Lampyridae	0.00	0.00	0.03	0.00	0.11	0.9906
Melyridae	0.03	0.10	0.99	0.00	2.82	0.4202
Nitidulidae	0.04	0.00	0.00	0.00	0.11	0.9906
Scarabaeidae	0.09	0.31	0.13	0.09	2.48	0.4789
Silphidae	0.00	0.24	0.18	0.00	4.28	0.2328
Sphaeriidae	0.01	0.00	0.31	0.01	5.05	0.1682
Staphylinidae	1.00	0.79	1.41	0.18	14.5	**0.0023**
Tenebrionidae	0.05	5.71	1.25	0.21	37.86	**<0.0001**

Figure 4.16 is a dendrogram produced by cluster analysis of the Coleoptera family abundance data. It used the Bray-Curtis dissimilarity measure and the UPWGA algorithm. The data from 7 samples per sampling trip were combined to form supersamples. These were labelled with the name of the crop, the letter (a) for the heterogeneous site, or the letter (b) for the homogeneous site. Then the numbers (1-6) referred to the sampling trip. The Cophenetic correlation coefficient was 0.8058.

This figure shows that samples taken from the same crop type, during the same or a subsequent sampling trip were most similar in terms of their Coleoptera families. For example, the supersamples Maize_a4 and Maize _b4 were very similar, as were Maize_a1 and Maize_b2. This means that crop type and the date of sampling had more influence than heterogeneity regarding these data.

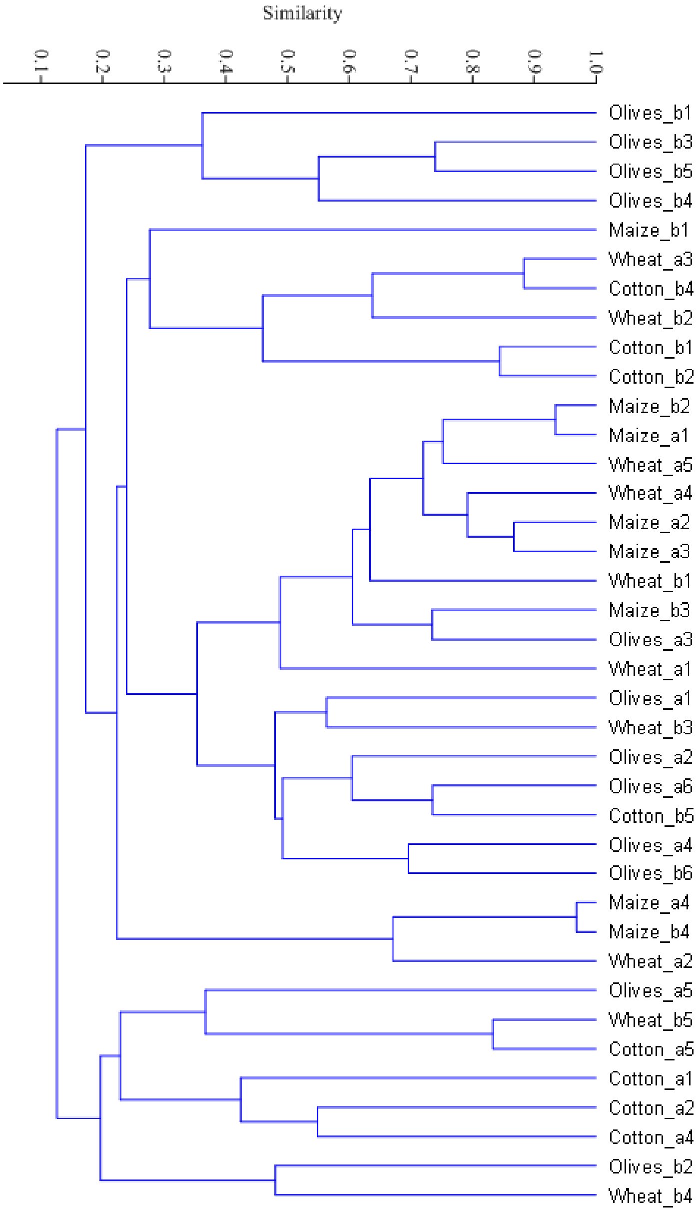


Figure 4.16: Cluster analysis of the Coleoptera family abundance data. Data divided by sampling trip.

Figure 4.17 shows a dendrogram in which each supersample corresponds to the data taken from one field throughout the sampling season. It used the Bray-Curtis dissimilarity measure and the UPWGA algorithm. Again the supersamples were labeled with the crop type and the letter (a) for a heterogeneous site, or the letter (b) for a homogeneous site. The Cophenetic correlation coefficient was 0.8632.

This figure does not show consistent clustering regarding either heterogeneity or crop type. The two olive supersamples are the only field pairs to cluster together according to crop type, but they are not very similar. The most similar supersamples, Maize_a and Wheat_a were taken from the maize field in the heterogeneous site and the wheat field, which was located in an area found to be fairly homogeneous. This suggests that heterogeneity does not have a great influence on the Coleoptera family data.

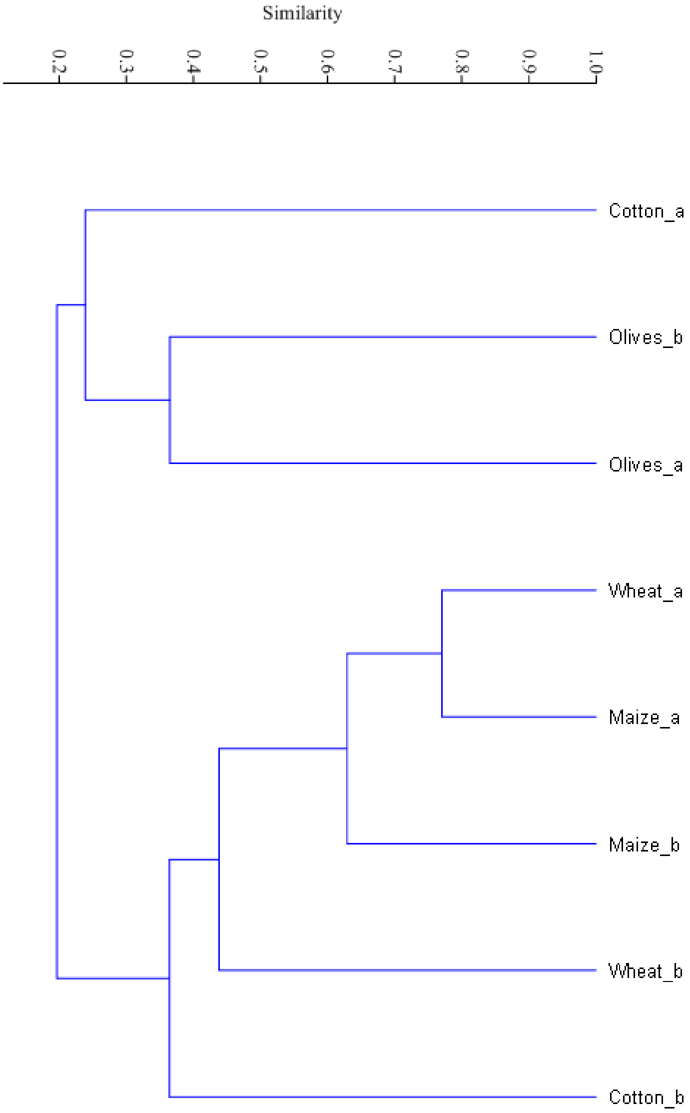


Figure 4.17: Cluster analysis of Coleoptera family abundance data. Data taken from entire sampling period.

4.2.6 The Number of Carabid Species

Figure 4.18 shows the total number of carabid species trapped in each of the study fields. Species numbers were higher in the homogeneous sites for the olive, wheat and cotton comparisons. However, for the maize comparison, the number of species was higher in the heterogeneous site.

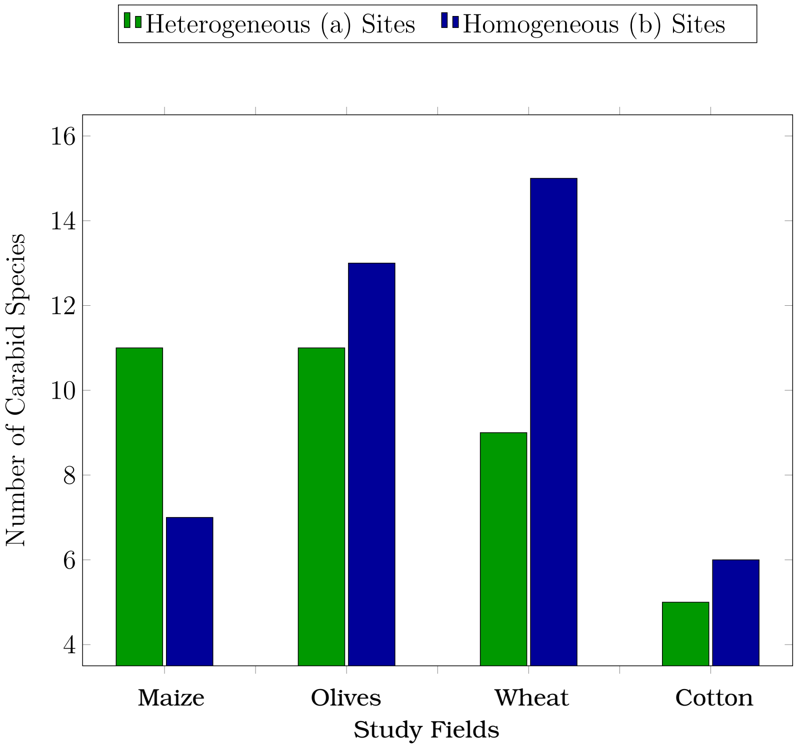


Figure 4.18: The total number of carabid species trapped in each study field.

Table 4.69 shows the mean number of species per trap caught in each study field. It also shows the results of the Mann-Whitney U tests, which were used to test the significance of the differences between heterogeneous and homogeneous sites. When mean species numbers were considered, higher species numbers were always seen in the sites most often found by the landscape analysis to have the highest levels of heterogeneity (sites 1a, 2a and 3b).

The only significant difference in species numbers was seen for the cotton comparison, where there was a greater number of species in the homogeneous site (U = 1190, p = 0.0002). However this site had high heterogeneity according to many of the landscape metrics identified in Section 4.1.4.

Table 4.69: Mean number of carabid species per trap in each of the study fields.

Study Site	**Study Field**	**Heterogeneous Site (a)**	**Homogeneous Site (b)**	**U-statistic**	**p-value**
		Mean Number of Species			
1	Maize	2.45	2.15	674	0.2263
2	Olives	1.18	0.93	645	0.1362
3	Wheat	1.25	1.58	762	0.7188
3	**Cotton**	0.15	0.93	1190	**0.0002**

Figure 4.19 shows the total number of carabid species trapped in each of the crop types. The Kruskal--Wallis test showed that there was a significant difference in species numbers between the crop types (H = 90, p = <0.0001). Then the pairwise Mann-Whitney U tests found that the wheat and olive fields were the only crop types not significantly different from one another. All the other crop types had significantly different species numbers. See Table 4.70. The olive study fields had the highest species numbers, closely followed by the wheat study fields. This was probably because these crops bore the closest resemblance to the natural forest and grassland habitats of many of the carabid species. These crop types also had no agrochemical input and were unirrigated. The lowest species numbers where seen in the cotton study fields, while the maize study fields had moderate species numbers. These crops were both fertilized, irrigated and the cotton fields were treated with insecticide.

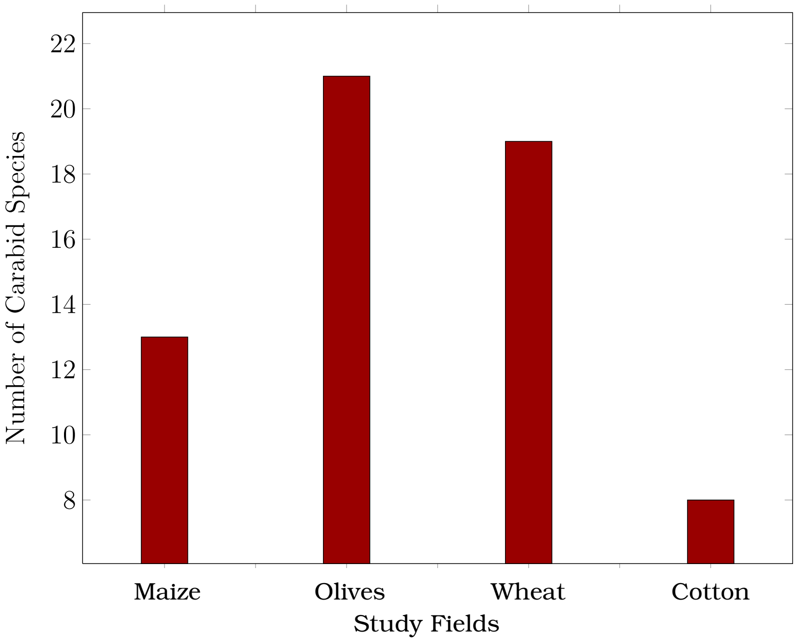


Figure 4.19: The total number of carabid species trapped in each crop type.

Table 4.70: The mean number of carabid species per trap in each crop type. Also the results of the pairwise Mann-Whitney U tests.

Crop Types	**Mean No. of Species**		**U-statistic**	**P-value**
Maize vs. Olives	2.30	1.05	4,082	**0.0026**
Maize vs. Wheat	2.30	1.41	1,597	**<0.0001**
Maize vs. Cotton	2.30	0.54	589	**<0.0001**
Olives vs. Wheat	1.05	1.41	3,465	0.3681
Olives vs. Cotton	1.05	0.54	2,318	**0.0026**
Wheat vs. Cotton	1.41	0.54	2,040	**0.0001**

4.2.7 The Relative Abundance of Carabid Species

The following section gives information about each of the carabid species sampled. It also examines their relative abundances regarding the different study fields. Table 4.71 shows the total numbers of each carabid species trapped during the study. *Harpalus (Pseudoophonus) rufipes* was found in the greatest numbers, followed by *Microlestes luctuosus* and *Pterostichus (Platysma) niger*.

Table 4.71: The number of individuals of each carabid species trapped in all study fields throughout the sampling period.

Carabid Species	**Total Number of Individuals**
Acinopus picipes	2
Amara aenea	4
Amara similata	12
Bembidion (Philochthus) sp.	1
Brachinus (Brachynidius) explodens	7
Calathus (Bedelinus) circumseptus	1
Calathus korax	62
Calathus (Neocalathus) melanocephalus	5
Carabus (Oreocarabus) preslii	3
Carabus (Pachystus) græcus	25
Carterus rotundicollis	1
Carterus rufipes	8
Cylindera germanica	99
Dixus obscurus	17
Harpalus atratus	1
Harpalus dimidiatus	4
Harpalus (Pseudoophonus) rufipes	1,368
Harpalus smaragdinus	2
Microlestes luctuosus	851
Olisthopus fuscatus	2
Ophonus diffinis	1
Ophonus (Hesperophonus) azureus	1
Pachycarus (Mystropterus) cyaneus	14
Pangus scaritides	1
Poecilus cupreus	51
Pterostichus (Platysma) niger	280
Tapinopterus taborskyi	44
Trechus quadristriatus	2
Zabrus (Pelor) græcus	36
Juveniles	203
Total	3,108

Table 4.72 shows the relative abundance of each carabid species trapped in the maize study fields. A total of eleven species were found in the heterogeneous site, seven in the homogeneous site. Out of these, eight species were found in higher abundance in the heterogeneous site, only four in the homogeneous site.

Table 4.73 shows the mean abundance of each species in the maize fields. *C. germanica* was found in significantly higher abundance in the homogeneous site, while *P. cupreus* was found in significantly higher numbers in the heterogeneous site. Both of these differences were highly significant. The relative abundances of these species are discussed further later in this Section.

Table 4.72: The number of individuals of each carabid species trapped in the maize study fields throughout the sampling period.

Maize Study Fields		
Carabidae Species	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Amara aenea	2	0
Amara similata	5	0
Brachinus (Brachynidius) explodens	4	0
Calathus korax	51	0
Calathus (Neocalathus) melanocephalus	0	1
Carterus rufipes	0	2
Cylindera germanica	5	93
Harpalus (Pseudoophonus) rufipes	622	716
Pachycarus (Mystropterus) cyaneus	1	0
Poecilus cupreus	47	2
Pterostichus (Platysma) niger	153	82
Tapinopterus taborskyi	1	0
Zabrus (Pelor) graecus	1	1

Table 4.73: The mean number of individuals of each carabid species trapped in the maize study fields throughout the sampling period. Also the results of the Mann-Whitney U tests.

Maize Study Fields				
Carabidae Species	**Mean Abundance Per Trap**		**U-statistic**	**P-value**
	Heterogeneous Site (a)	**Homogeneous Site (b)**		
Amara aenea	0.05	0.00	760	0.7039
Amara similata	0.13	0.00	720	0.4473
Brachinus (Brachynidius) explodens	0.10	0.00	740	0.5687
Calathus korax	1.28	0.00	620	0.0836
Calathus (Neocalathus) melanocephalus	0.00	0.03	820	0.8493
Carterus rufipes	0.00	0.05	840	0.7039
Cylindera germanica	0.13	2.33	1199	**0.0001**
Harpalus (Pseudoophonus) rufipes	15.55	17.90	931	0.2077
Pachycarus (Mystropterus) cyaneus	0.03	0.00	780	0.8493
Poecilus cupreus	1.18	0.05	521	**0.0074**
Pterostichus (Platysma) niger	3.83	2.05	662	0.1835
Tapinopterus taborskyi	0.03	0.00	780	0.8493
Zabrus (Pelor) graecus	0.03	0.03	800	1.0000

Table 4.74 shows the relative abundance of each carabid species trapped in the olive study fields. There were eleven species found in the heterogeneous site, thirteen in the homogeneous site. Nine of these species were found in higher abundance in the heterogeneous site, twelve in the homogeneous site.

Table 4.75 shows the mean abundance of each species in the olive fields. The species *M. luctuosus* was found in significantly higher numbers in the heterogeneous site. The relative abundances of these species will be discussed further later in this Section.

Table 4.74: The number of individuals of each carabid species trapped in the olive study fields throughout the sampling period.

Olive Study Fields		
Carabidae Species	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Amara aenea	0	2
Amara similata	0	5
Brachinus (Brachynidius) explodens	0	2
Calathus korax	0	4
Calathus (Neocalathus) melanocephalus	0	3
Carabus (Oreocarabus) preslii	0	3
Carabus (Pachystus) græcus	3	7
Carterus rufipes	1	0
Dixus obscurus	14	0
Harpalus dimidiatus	4	0
Harpalus smaragdinus	0	1
Microlestes luctuosus	57	0
Olisthopus fuscatus	0	2
Ophonus (Hesperophonus) azureus	1	0
Harpalus (Pseudoophonus) rufipes	0	2
Pachycarus (Mystropterus) cyaneus	5	8
Pangus scaritides	0	1
Poecilus cupreus	1	0
Pterostichus (Platysma) niger	11	0
Trechus quadristriatus	1	0
Zabrus (Pelor) graecus	7	1

Table 4.75: The mean number of individuals of each carabid species trapped in the olive study fields. Also the results of the Mann-Whitney U tests.

Olive Study Fields				
Carabidae Species	**Mean Abundance Per Trap**		**U-statistic**	**P-value**
	Heterogeneous Site (a)	**Homogeneous Site (b)**		
Amara aenea	0.00	0.05	840	0.7039
Amara similata	0.00	0.13	880	0.4473
Brachinus (Brachynidius) explodens	0.00	0.05	840	0.7039
Calathus korax	0.00	0.10	840	0.7039
Calathus (Neocalathus) melanocephalus	0.00	0.08	560	0.5687
Carabus (Oreocarabus) preslii	0.00	0.08	840	0.7039
Carabus (Pachystus) græcus	0.08	0.18	880	0.4473
Carterus rufipes	0.03	0.00	780	0.8493
Dixus obscurus	0.35	0.00	700	0.3371
Harpalus dimidiatus	0.10	0.00	720	0.4473
Harpalus smaragdinus	0.00	0.03	820	0.8493
Harpalus (Pseudoophonus) rufipes	0.00	0.05	840	0.7039
Microlestes luctuosus	1.43	0.15	592	**0.0455**
Olisthopus fuscatus	0.00	0.05	760	0.7039
Ophonus (Hesperophonus) azureus	0.03	0.00	820	0.8493
Pachycarus (Mystropterus) cyaneus	0.13	0.20	803	0.9840
Pangus scaritides	0.00	0.03	820	0.8493
Poecilus cupreus	0.03	0.00	780	0.8493
Pterostichus (Platysma) niger	0.28	0.00	660	0.1802
Trechus quadristriatus	0.03	0.00	780	0.8493
Zabrus (Pelor) graecus	0.18	0.03	720	0.4413

Table 4.76 shows the relative abundance of each carabid species trapped in the wheat study fields. There were nine species recorded in the heterogeneous site, fifteen in the homogeneous site. Six of these species were found in higher abundance in the heterogeneous site, thirteen in the homogeneous site.

Table 4.77 shows the mean abundance of each species in the wheat fields. In the wheat comparison, there were no significant differences between heterogeneous and homogeneous sites for any of the species.

Table 4.76: The number of individuals of each carabid species trapped in the wheat study fields throughout the sampling period.

Wheat Study Fields		
Carabidae Species	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Acinopus picipes	0	2
Amara similata	0	2
Bembidion (Philochthus)	0	1
Brachinus (Brachynidius) explodens	1	0
Calathus (Bedelinus) circumseptus	0	1
Calathus korax	1	5
Calathus (Neocalathus) melanocephalus	0	1
Carabus (Pachystus) græcus	3	12
Carterus rotundicollis	0	1
Carterus rufipes	5	0
Dixus obscurus	3	0
Harpalus atratus	0	1
Harpalus smaragdinus	1	0
Harpalus (Pseudoophonus) rufipes	0	16
Microlestes luctuosus	649	142
Ophonus diffinis	0	1
Pterostichus (Platysma) niger	1	17
Trechus quadristriatus	0	1
Zabrus (Pelor) graecus	17	6

Table 4.77: The mean number of individuals of each carabid species trapped in the wheat study fields. Also the results of the Mann-Whitney U tests.

Wheat Study Fields				
Carabidae Species	**Mean Abundance Per Trap**		**U-statistic**	**P-value**
	Heterogeneous Site (a)	**Homogeneous Site (b)**		
Acinopus picipes	0.00	0.05	840	0.7039
Amara similata	0.00	0.05	840	0.7039
Bembidion (Philochthus)	0.00	0.03	820	0.8493
Brachinus (Brachynidius) explodens	0.03	0.00	780	0.8493
Calathus (Bedelinus) circumseptus	0.00	0.03	820	0.8493
Calathus korax	0.03	0.13	841	0.6965
Calathus (Neocalathus) melanocephalus	0.00	0.03	820	0.8493
Carabus (Pachystus) græcus	0.08	0.30	882	0.4354
Carterus rotundicollis	0.00	0.03	820	0.8493
Carterus rufipes	0.13	0.00	720	0.4473
Dixus obscurus	0.08	0.00	740	0.5687
Harpalus atratus	0.00	0.03	820	0.8493
Harpalus smaragdinus	0.03	0.00	780	0.8493
Harpalus (Pseudoophonus) rufipes	0.00	0.40	940	0.1802
Microlestes luctuosus	16.23	3.55	607	0.0643
Ophonus diffinis	0.00	0.03	820	0.8493
Pterostichus (Platysma) niger	0.03	0.43	942	0.1738
Trechus quadristriatus	0.00	0.03	820	0.8493
Zabrus (Pelor) graecus	0.43	0.15	736	0.5353

Table 4.78 shows the relative abundance of each carabid species trapped in the cotton study fields. There were five species found in the heterogeneous site, six in the homogeneous site. Three of these species were found in higher abundance in the heterogeneous site, five in the homogeneous site.

Table 4.79 shows the mean abundance of each species in the cotton fields. The species *P. (Platysma) niger* and *T. taborskyi* were both found in significantly higher numbers in the homogeneous site. However, this was the area that was often found by the landscape analysis to be the most heterogeneous of the pair. The relative abundances of these species will be discussed further later in this Section.

Table 4.78: The number of individuals of each carabid species trapped in the cotton study fields throughout the sampling period.

Cotton Study Fields		
Carabidae Species	**Total Number of Individuals**	
	Heterogeneous Site (a)	**Homogeneous Site (b)**
Calathus korax	1	0
Cylindera germanica	0	1
Microlestes luctuosus	2	1
Harpalus (Pseudoophonus) rufipes	0	12
Poecilus cupreus	0	1
Pterostichus (Platysma) niger	1	15
Tapinopterus taborskyi	2	41
Zabrus (Pelor) graecus	3	0

Table 4.79: The mean number of individuals of each carabid species trapped in the cotton study fields. Also the results of the Mann-Whitney U tests.

Cotton Study Fields				
Carabidae Species	**Mean Abundance Per Trap**		**U-statistic**	**P-value**
	Heterogeneous Site (a)	**Homogeneous Site (b)**		
Calathus korax	0.03	0.00	780	0.8493
Cylindera germanica	0.00	0.03	820	0.8493
Microlestes luctuosus	0.05	0.03	800	1.0000
Harpalus (Pseudoophonus) rufipes	0.00	0.30	940	0.1802
Poecilus cupreus	0.00	0.03	820	0.8493
Pterostichus (Platysma) niger	0.03	0.38	1,041	**0.0209**
Tapinopterus taborskyi	0.05	1.03	1,050	**0.0164**
Zabrus (Pelor) graecus	0.08	0.00	780	0.8493

4.2.7.1 Summary

Overall, the results for the relative abundance of carabid species show a similar pattern to those seen for the landscape metrics identified in Table 4.42. This suggests that these metrics may have some influence on the relative abundance of carabid species.

Table 4.80 shows the mean abundance per trap of each carabid species in each of the four crop types. Four of these species showed highly significant differences in abundance regarding crop type. This indicates that crop type had a fairly high level of influential on carabid species abundance.

Table 4.80: The number of individuals of each carabid species trapped in each crop type. Also the results of the Kruskal-Wallis test.

Mean Abundance of Carabid Species in Each Crop Type						
Taxon	**Maize**	**Olives**	**Wheat**	**Cotton**	**H-statistic**	**P-value**
Acinopus picipes	0.00	0.00	0.03	0.00	0.11	0.9906
Amara aenea	0.03	0.03	0.00	0.00	0.15	0.9852
Amara similata	0.06	0.06	0.03	0.00	0.41	0.9382
Bembidion (Philochthus)	000	000	0.01	000	0.03	0.9986
Brachinus (Brachynidius) explodens	0.05	0.03	0.01	0.00	0.19	0.9792
Calathus (Bedelinus) circumseptus	0.00	0.00	0.01	0.00	0.03	0.9986
Calathus korax	0.64	0.05	0.08	0.01	1.49	0.6846
Calathus (Neocalathus) melanocephalus	0.01	0.04	0.01	0.00	0.18	0.9808
Carabus (Oreocarabus) preslii	0.00	0.04	0.00	0.00	0.11	0.9906
Carabus (Pachystus) græcus	0.00	0.13	0.19	0.00	3.08	0.3795
Carterus rotundicollis	0.00	0.00	0.01	0.00	0.03	0.9986
Carterus rufipes	0.03	0.01	0.06	0.00	0.33	0.9543
Cylindera germanica	1.23	0.00	0.00	0.01	17.19	**0.0006**
Dixus obscurus	0.00	0.18	0.04	0.00	0.68	0.8779
Harpalus atratus	0.00	0.00	0.01	0.00	0.03	0.9986
Harpalus dimidiatus	0.00	0.05	0.00	0.00	0.45	0.9297
Harpalus smaragdinus	0.00	0.01	0.01	0.00	0.04	0.9979
Microlestes luctuosus	0.00	0.79	9.89	0.04	73.6	**<0.0001**
Olisthopus fuscatus	0.00	0.03	0.00	0.00	0.03	0.9986
Ophonus diffinis	000	000	0.01	000	0.03	0.9986
Ophonus (Hesperophonus) azureus	0.00	0.01	0.00	0.00	0.03	0.9986
Harpalus (Pseudoophonus) rufipes	16.73	0.03	0.20	0.15	136.13	**<0.0001**
Pachycarus (Mystropterus) cyaneus	0.01	0.16	0.00	0.00	2.65	0.4488
Pangus scaritides	0.00	0.01	0.00	0.00	0.03	0.9986
Poecilus cupreus	0.61	0.01	0.00	0.01	6.68	0.0828
Pterostichus (Platysma) niger	2.94	0.14	0.23	0.20	44.77	**<0.0001**
Tapinopterus taborskyi	0.01	0.00	0.00	0.54	6.94	0.0738
Trechus quadristriatus	0.00	0.01	0.01	0.00	0.04	0.9979
Zabrus (Pelor) graecus	0.03	0.10	0.29	0.04	2.34	0.5049

Figure 4.21 is a dendrogram produced by cluster analysis of the carabid species abundance data. It used the Bray-Curtis dissimilarity measure and the UPWGA algorithm. For this, the data from 7 samples per sampling trip were combined to form supersamples. These were labelled with the name of the crop, the letter (a) for a heterogeneous site, or the letter (b) for a homogeneous site. Then the numbers (1-6) referred to the sampling trip. The Cophenetic correlation coefficient was 0.8815.

This figure shows that the most similar supersamples were taken from sites 2a and 3bi containing the olive and wheat crops. These were both sites that the landscape analysis found to be heterogeneous. This suggests that there was some influence of heterogeneity on carabid species abundance. Other less similar clusters; however, were made up of fields of the same crop type, showing the influence of crop type. The date of the sampling trip may also have had a slight influence on carabid species abundance, as some clusters contained samples from the same or subsequent sampling trips.

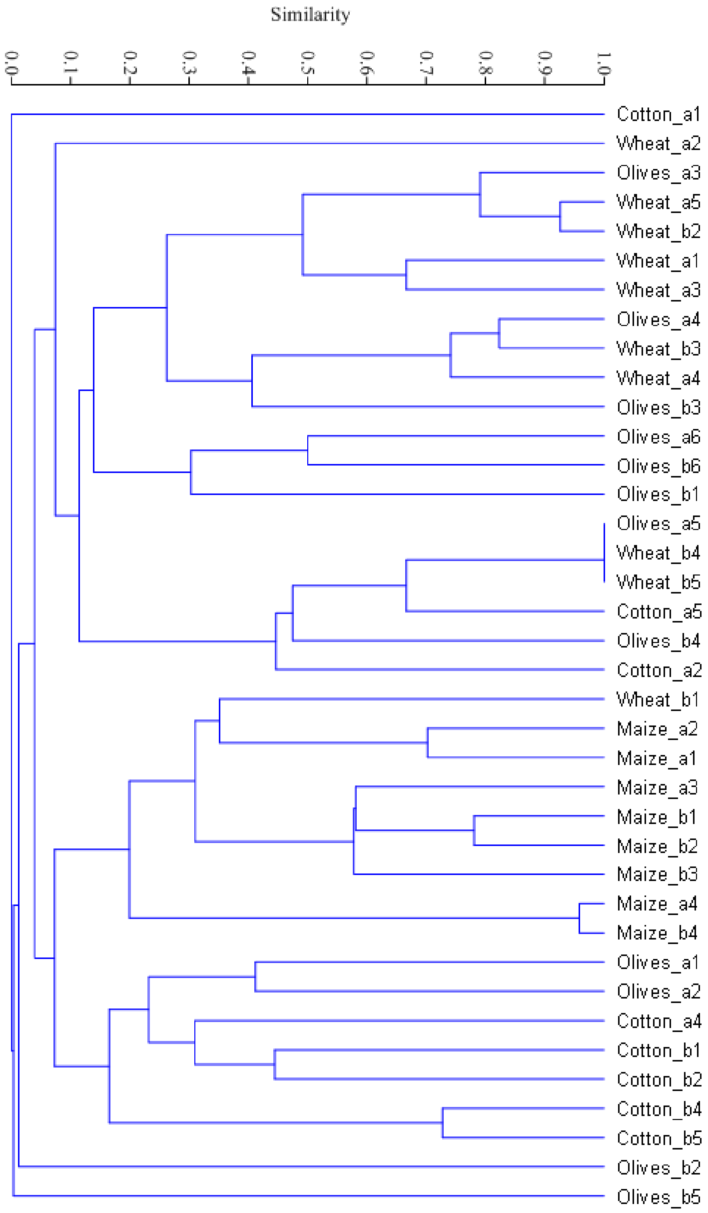


Figure 4.20: Cluster analysis of carabid species abundance data. Data divided by sampling trip.

Figure 4.21 was also produced by cluster analysis of the carabid species abundance data. In this case though, the data for each supersample were taken from 40 successful traps in each study field, throughout the sampling period. It was made using the Bray-Curtis dissimilarity measure and the UPWGA algorithm. The Cophenetic correlation coefficient was 0.9553.

This figure shows that the two maize study fields were the most similar regarding their carabid species. Otherwise there was some clustering based on the levels of heterogeneity. The olive field in the heterogeneous site was found to be similar to the wheat field in site b. This was the site that had high heterogeneity according to many of the calculated metrics. Similarly the olive field in the homogeneous site was found to be similar to the cotton field in site a. This was the site often found by the landscape analysis to be most homogeneous.

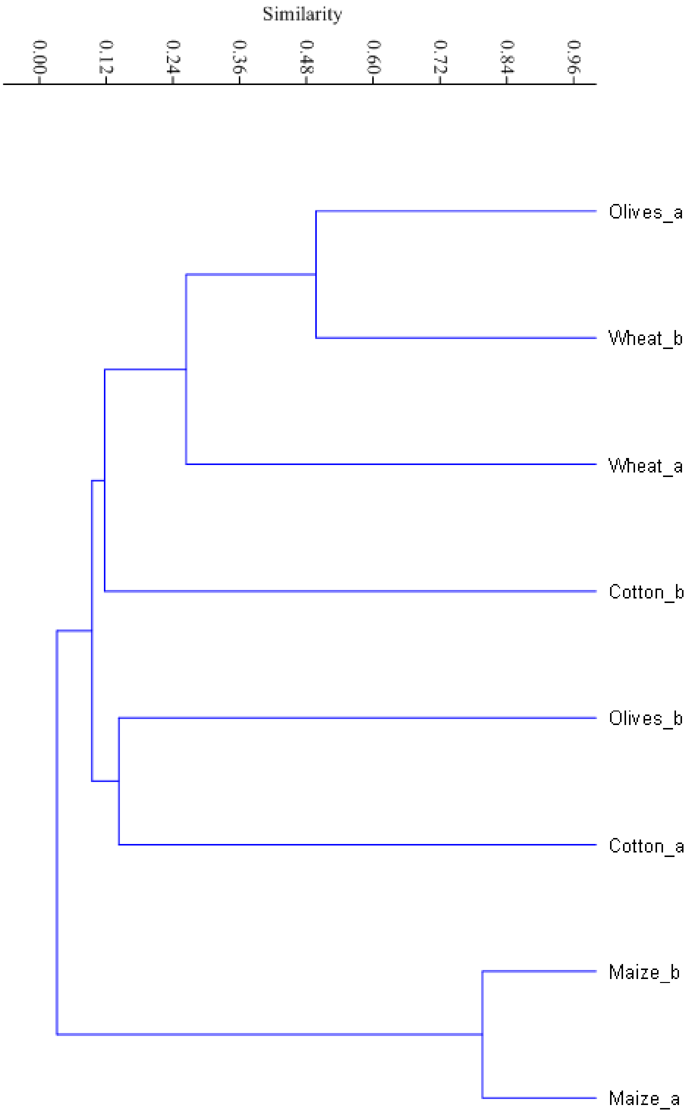


Figure 4.21: Cluster analysis of carabid species abundance data. Data taken from entire sampling period.

4.2.8 The Carabid Species Sampled in the Study

4.2.8.1 *Acinopus picipes*

Acinopus picipes (Olivier, 1795) is a thermophilous species (Notman, 1875 [128]). Its distribution extends from Greece to northern China (Arndt *et al.*, 2011 [6]). It digs burrows under stones and is mostly phytophagous (Trautner & Geigenmüller, 1987 [174]), often eating the seeds of crops and wild plants (Larochelle, 1990 [105]).

In this study *A. picipes* was found only in the wheat study field in the homogeneous site, where two individuals were trapped. This meant that it was present in the study site that was identified by the landscape analysis as having the highest heterogeneity of the pair.

The wheat field would have been suitable for this species, as it was warm, see Table 4.95, with plentiful seed food, which could have been obtained from the crop itself. In fact, the CCA triplot in Figure 4.56 shows that these individuals were found in a very sandy place, with a moderately high temperature. As far as landscape metrics were concerned, Figure 4.58 shows that *A. picipes* was found in a site where there were very few patches of fallow in the 10 ha of land around the study field.

4.2.8.2 *Amara aenea*

Amara aenea (De Geer, 1774) is a xerophilous species, inhabiting mainly grassland, gardens, dunes and wasteland (Luff, 2007 [116]). In agricultural land it is found in arable cultivations, pastureland, clover and alfalfa fields (Thiele, 1977 [167]), where it prefers autumn planted crops (Holland & Luff, 2000 [90]). It is widely distributed from Macaronesia, across Europe and the Mediterranean Region to Western Siberia (Fauna Europaea, 2011 [69]).

The species is thought to be largely phytophagous (Anderson *et al.*, 2000 [4]) and is known to feed on the seeds of agricultural weeds such as shepherd's-purse (*Capsella bursa-pastoris*), chickweed (*Stellaria media*), coltsfoot (*Tussilago farfara*), broadleaf plantain (*Plantago major*), the stinging nettle (*Urtica dioica*) and silver cinquefoil (*Potentilla argentea*) (Lundgren, 2009 [117]). However, it has also been seen to prey on Lepidoptera larvae (Allen & Hagley, 1982 [2]). It is a species that is known to be able to disperse easily (den Boer, 1990 [41]).

Two individuals of *A. aenea* were trapped in the maize study field in the heterogeneous site and two in the olive study field in the homogeneous site.

The CCA plot in Figure 4.56 shows that *A. aenea* was found in places of moderate soil moisture, low temperature and in places with moderate levels of sand and mud in the soil. As far as landscape metrics were concerned, this species was found in sites with moderately high percentages of fallow and wasteland. See Figure 4.58.

4.2.8.3 *Amara similata*

Amara similata (Gyllenhal, 1810) has a near transpalaearctic distribution (Arndt *et al.*, 2011 [6]). It prefers damp areas, especially riverbanks and water meadows (Anderson *et al.*, 2000 [4]), but it will also inhabit arable fields (Popović & Štrbac, 2010 [142]), where it prefers autumn planted crops (Holland & Luff, 2000 [90]). It is a polyphagous species. The adults feed mainly on seeds, which they find by climbing into vegetation. However, it can also prey on invertebrates (Thiele, 1977 [167]). The species is known to have only moderate dispersal ability (den Boer, 1990 [41]).

In this study, 5 individuals of *A. similata* were found in the maize study field in the heterogeneous site and 5 in the olive study field in the homogeneous site. Then 2 individuals were also found in the wheat study field in the homogeneous site. See Figure 4.22. Differences in abundance per trap between heterogeneous and homogeneous sites were not significant.

The CCA triplot in Figure 4.56 shows that *A. similata* was found in areas of moderate soil moisture and temperature, with slightly sandy soil. Figure 4.58 shows that the species was also associated with moderately high levels of landscape level aggregation, something which may have been due to its moderate dispersal ability. Very large expanses of the same crop type would not have been suitable for this species, but areas with moderately high levels of aggregation would probably have provided the right balance between the abundance and diversity of resources.

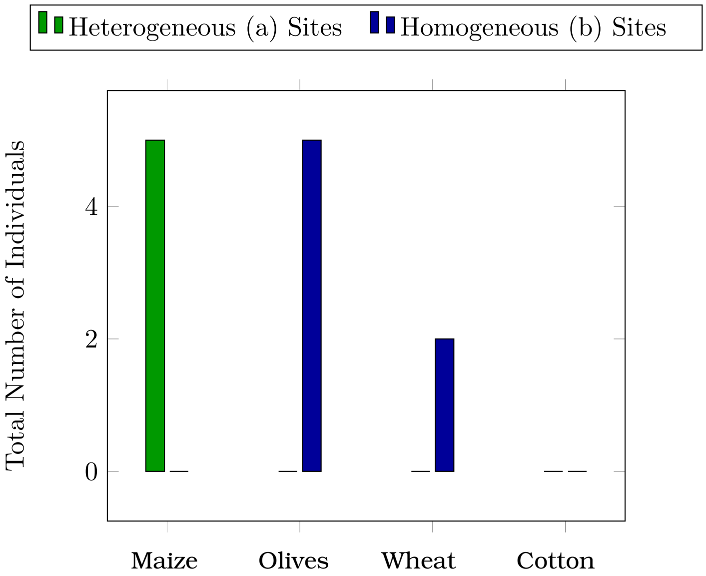


Figure 4.22: Relative abundance of *Amara similata*.

4.2.8.4 *Bembidion (Philochthus)*

An individual cautiously identified as belonging to the subgenus *Bembidion (Philochthus)* was caught in the wheat study field in the homogeneous site. However, according to many of the calculated landscape metrics, this area was the most heterogeneous of the pair.

It was not possible to identify this specimen to species level, but it must have belonged to one of the ten species of *Philochthus* found in Greece. These are *B. (Philochthus) biguttatum*, *B. (Philochthus) decolor*, *B. (Philochthus) judaicum*, *B. (Philochthus) guttula*, *B. (Philochthus) guttuloides*, *B. (Philochthus) inoptatum*, *B. (Philochthus) iricolor*, *B. (Philochthus) lunulatum*, *B. (Philochthus) vicinum* and *B. (Philochthus) escherichii* (Arndt *et al.*, 2011 [6]).

Herbicides are known to be toxic to many species in this genus (Thiele, 1977 [167]). All species in the genus consume animal material. They are active fliers and prefer moist, shady areas (Luff, 2007 [116]). The individual trapped in this study; however, was found in a dry place with a relatively high soil temperature. See Figure 4.56. As far as landscape metrics were concerned, Figure 4.58 shows that the individual was found in a site where there were very few patches of fallow in the 10 ha of land around the sampled field.

4.2.8.5 *Brachinus (Brachynidius) explodens*

Brachinus (Brachynidius) explodens (Duftschmid, 1812) is a species of Bombardier Beetle, which lives mainly in dry grassland and agricultural land, where it may be found in arable cultivations and alfalfa fields. In fact, it is one of the most common species of Carabidae to be found in cultivated areas in Eastern Europe (Thiele, 1977 [167]). Its distribution extends from Europe to Central Asia and it is a very common species in Greece (Arndt *et al.*, 2011 [6]). It is a mesoxerophilous and zoophagous species (Varvara & Apostol, 2008 [184]).

This species is characteristic of organically farmed wheat cultivations. This is thought to be due to the high levels of weed cover and high field level heterogeneity seen in organic crops (Kromp, 2008 [103]). It is a species that is known to live together in large numbers and can be found under stones, logs or among the roots of grass (Fowler, 1913 [75]).

In this study, the species occurred in small numbers in the maize study field in the heterogeneous site, the olive study field in the homogeneous site and as an isolated individual in the wheat study field in the heterogeneous site. See Figure 4.23. There were no significant differences in abundance per trap between heterogeneous and homogeneous sites.

Unsurprisingly, Figure 4.56 shows that this species was found in moderately warm and dry conditions. Then, Figure 4.58 shows that it was found in sites of moderate to high percentages of fallow and wasteland. These sites also had moderate to high levels of fallow aggregation.

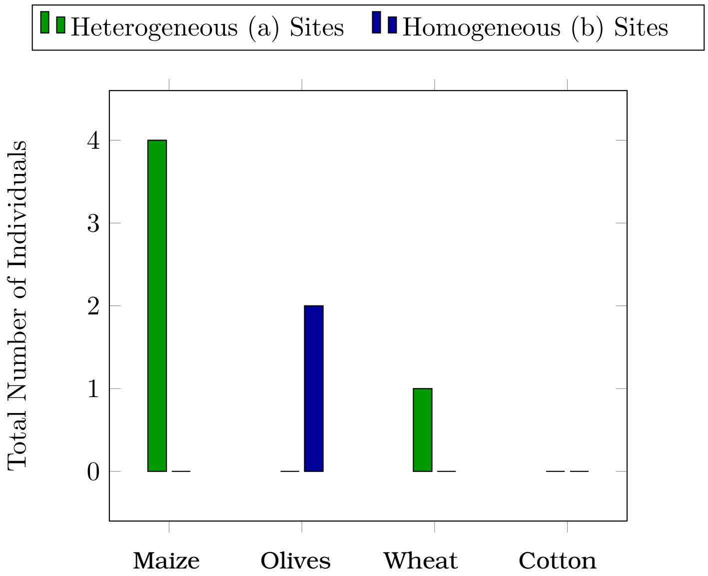


Figure 4.23: Relative abundance of *Brachinus (Brachynidius) explodens*.

4.2.8.6 *Calathus (Bedelinus) circumseptus*

Calathus (Bedelinus) circumseptus (Germar, 1824) has a distribution that covers Mediterranean Europe and parts of North Africa (Torjbio, 2006 [173]). However, it is rare in Greece (Arndt *et al.*, 2011 [6]). It can be found under stones and in plant detritus. It is mainly phytophagous but is sometimes polyphagous (Houlbert & Monnot, 1910 [94]). It has been seen to inhabit sea coasts (Champion, 1894 [26]) and the banks of large ponds (Perris, 1857 [136]).

In this study, the species was represented by only one individual trapped in the wheat study field in the homogeneous site. It was trapped in a place with a fairly high percentage of sand in the soil. See Figure 4.56. As far as landscape metrics were concerned, it was trapped in a site where there were low numbers of fallow patches in the 10 ha of land around the sampled field. See Figure 4.58.

4.2.8.7 *Calathus korax*

Calathus korax (Reitter, 1889) is endemic to Greece, but widespread within the country (Arndt *et al.*, 2011 [6]). Little seems to be known about its nutritional or habitat preferences.

In this study, it was found in high numbers in the maize study field in the heterogeneous site. Much smaller numbers of individuals were also found in the olive and wheat fields in the homogeneous sites. Finally, single individuals were found in the cotton field in the heterogeneous site and the wheat field in the heterogeneous site. See Figure 4.24. However, none of the comparisons showed significant differences in abundance per trap between heterogeneous and homogeneous sites.

The CCA plot in Figure 4.56 shows that this species generally preferred places with moderate to high plant cover and light intensity levels. As far as landscape metrics were concerned, *C. korax* was associated with moderate levels of fallow aggregation. See Figure 4.58.

4.2.8.8 *Calathus (Neocalathus) melanocephalus*

Calathus (Neocalathus) melanocephalus (Linnaeus, 1758) has a wide distribution throughout Europe, to Western Asia and North Africa (Arndt *et al.*, 2011 [6]). However, it is absent in the extreme South-West of Europe (Anderson *et al.*, 2000 [4]).

In agricultural areas, it is found primarily on arable land, although it is also found in pastureland and in alfalfa fields. It is know to be a quantitative indicator of root crops on sandy soil. It is also a species characteristic of spring planted crops and is often absent in agricultural fields where there is abundant weed cover (Holland & Luff, 2000 [90]). It likes open areas, is an autumn breeder and is thought to be capable of flight in some cases, but is usually wingless (Thiele, 1977 [167]). Although it has long been thought to be only zoophagous (Thiele, 1977 [167]), it has recently been seen to consume the seeds of the agricultural weed species *C. bursa-pastoris* (Lundgren, 2009 [117]).

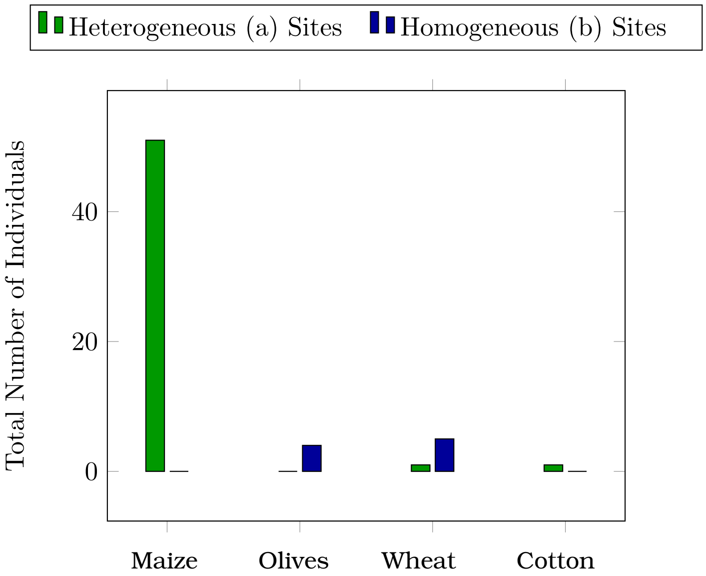


Figure 4.24: Relative abundance of *Calathus korax*.

In this study, three individuals of *C. melanocephalus* were found in the olive field in the homogeneous site. Then one individual each was found in the maize study field and the wheat study field in the homogeneous sites. See Figure 4.25.

Figure 4.56 shows that the species was found in areas of moderate temperature and moisture, on slightly sandy soil. It was also more common in places with relatively low levels of wild plant cover, as described by Holland & Luff (2000 [90]). In fact, its presence exclusively in the homogeneous sites was probably due to its dislike of thick weed cover. Weed cover was thicker in the heterogeneous sites than in the homogeneous sites. See Table 4.88.

As far as landscape metrics were concerned, this species was found in sites where there were high levels of aggregation, particularly of study crops. See Figure 4.58. This is probably due to its preference for living in arable land, which would mean it does not require a highly heterogeneous landscape.

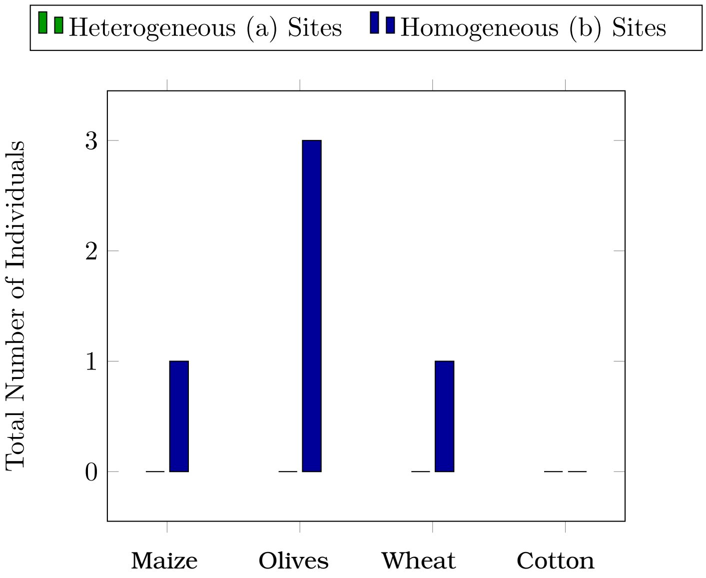


Figure 4.25: Relative abundance of *Calathus (Neocalathus) melanocephalus*.

4.2.8.9 *Carabus (Oreocarabus) preslii*

Carabus (Oreocarabus) preslii (Dejean & Boisduval, 1830) is a species that is restricted to Greece, Italy and the Balkans (Fauna Europaea, 2011 [69]), where it prefers low lying ground and low hills (Fet & Popov, 2007 [70]).

Little else appears to be known about the habitat preferences of this species, or about its nutrition. In this study, only three individuals of *C. preslii* were found in the olive study field in the homogeneous site. The field where this species was found was dry and stoney, with moderately good weed cover. See Tables 4.97 and 4.88. Within this field, it was trapped in sandy soil with moderate soil moisture and temperature. See Figure 4.56.

Figure 4.58 shows that this species was found in a site where the percentages of fallow and wasteland were very high and where the aggregation levels of fallow were also very high.

4.2.8.10 *Carabus (Pachystus) graecus*

Carabus (Pachystus) graecus (Dejean, 1826) has a distribution that covers Greece, Turkey, the Balkans and the Middle East (Fauna Europaea, 2011 [69]). Within Greece it is found on the mainland and Peloponnisos (Arndt *et al.*, 2011 [6]).

Little seems to be known about the nutritional and habitat preferences of *C. graecus*. In this study, it was found in moderate numbers in the wheat and olive study fields in the homogeneous sites. Then three individuals were found in both the wheat and olive study fields of the heterogeneous sites. See Figure 4.26. However, there were no significant differences in abundance per trap between heterogeneous and homogeneous sites. The presence of this species in the olive and wheat fields suggests that it prefers dry sandy soil with stones. In fact, the CCA plot in Figure 4.56 shows that this species was found in dry areas with high soil temperatures and sandy soil.

As far as landscape metrics were concerned, Figure 4.58 shows that this species was associated with moderate to large field sizes. This suggests that where the crop type was suitable, as wheat and olives were, it could live in large areas of unbroken cultivation.

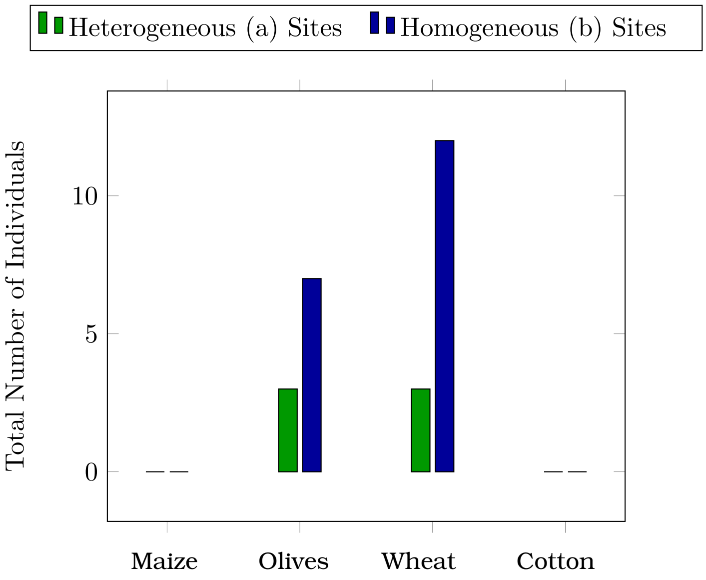


Figure 4.26: Relative abundance of *Carabus (Pachystus) graecus*.

4.2.8.11 *Carterus rotundicollis*

Carterus rotundicollis (Rambur, 1837) is macropterous and has a distribution that covers the Western Mediterranean and the Balkan Peninsula (Arndt *et al.*, 2011 [6]). It prefers open countryside (Brandmayr *et al.*, 2006 [14]) and has been found on wasteland, at the edges of fields, especially at the foot of hills, where it lives under stones (Pantel, 1888 [133]). Species of this genus are known to be phytophagous. They collect seeds, which are then stored in underground burrows (Trautner & Geigenmüller, 1987 [174]).

In this study, *C. rotundicollis* was represented by a single individual trapped in the wheat study field in the homogeneous site. It was found in sandy soil, where temperature and moisture levels were moderate. See Figure 4.56. As for landscape metrics, Figure 4.58 shows that it was found in a site of low fallow patch numbers.

4.2.8.12 *Carterus rufipes*

Carterus rufipes (Chaudoir, 1843) is macropterous and is found in Eastern Europe, the Mediterranean region, the Balkan Peninsula, the Caucasus, Asia Minor and the Near East (Arndt *et al.*, 2011 [6]). It is a phytophagous and xerophilous species (Pavlíček *et al.*, 2005 [134]).

In this study, two individuals thought to be *C. rufipes* were found in the maize study field in the homogeneous site and five in the wheat field in the heterogeneous site. Also a single individual was found in the olive field in the heterogeneous site. See Figure 4.27. There were no significant differences in abundance between heterogeneous and homogeneous sites.

This species was found most often in places that were relatively warm and dry, with a high pH. See Figure 4.56. Then, looking at Figure 4.58, it seems that this species preferred sites where fallow patch numbers were moderately high.

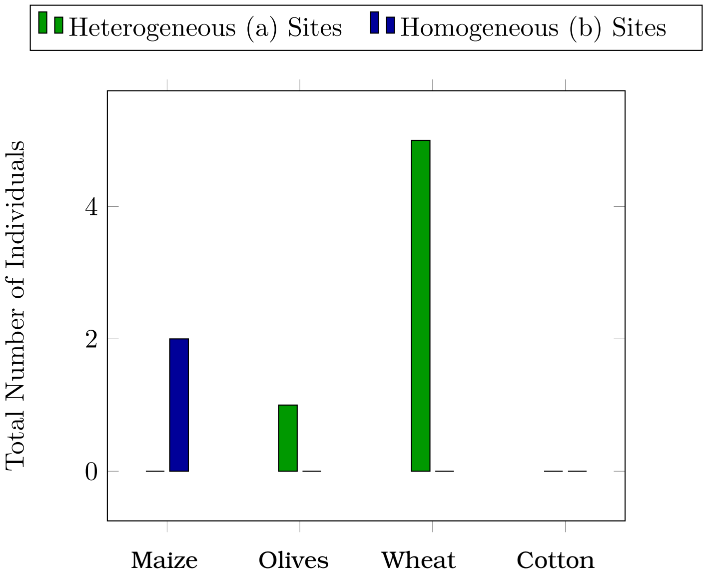


Figure 4.27: Relative abundance of *Carterus rufipes*.

4.2.8.13 *Cylindera germanica*

Cylindera germanica (Linnaeus, 1758) is found on loamy soil, often on flood plains and is present across Europe and parts of Asia (Arndt *et al.*, 2011 [6]). It is a spring breeder, mesophilous, zoophagous and prefers to live in grassland and agricultural areas (Varvara & Apostol, 2008 [184]).

In this study, *C. germanica* was found in large numbers in the maize study field in the homogeneous site, then in much smaller numbers in the maize field in the heterogeneous site and in the cotton field in the homogeneous site. See Figure 4.28. The difference in abundance per trap between the maize fields in the heterogeneous and homogeneous sites was highly significance. See Table 4.73.

Higher abundance in the homogeneous site could have be due to a number of different factors. To begin with, the maize field in the homogeneous site had the highest moisture levels of all of the study fields. See Table 4.97. Also, as maize cultivations appear to have provided *C. germanica* with suitable prey, it follows that the larger maize field in the homogeneous site would have provided more prey and so supported a greater number of individuals. Finally, this species is accustomed to living in agricultural areas (Varvara & Apostol, 2008 [184]), so a low level of landscape heterogeneity would probably not be detrimental to it.

Table 4.80 shows that there was also a highly significant difference in abundance between crop types, with the maize fields having by far the highest levels of abundance. This can also be seen in Figure 4.29.

C. germanica probably preferred the maize study fields because of their frequent high moisture levels. The CCA plot in Figure 4.56 shows that this species was found in very muddy soil.

As far as landscape metrics were concerned, this species was found in sites with low percentages of fallow and wasteland, as well as moderate levels of fallow interspersion / juxtaposition. See Figure 4.58. This may indicate that landscape heterogeneity is not very important for this species.

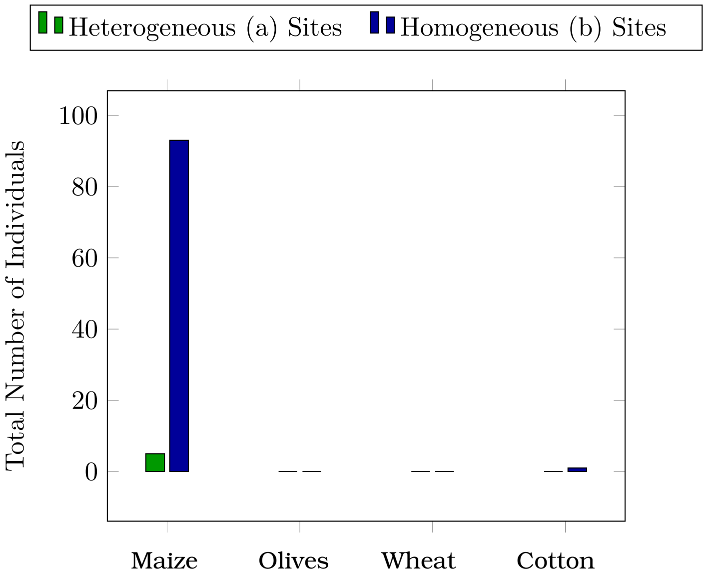


Figure 4.28: Relative abundance of *Cylindera germanica*.

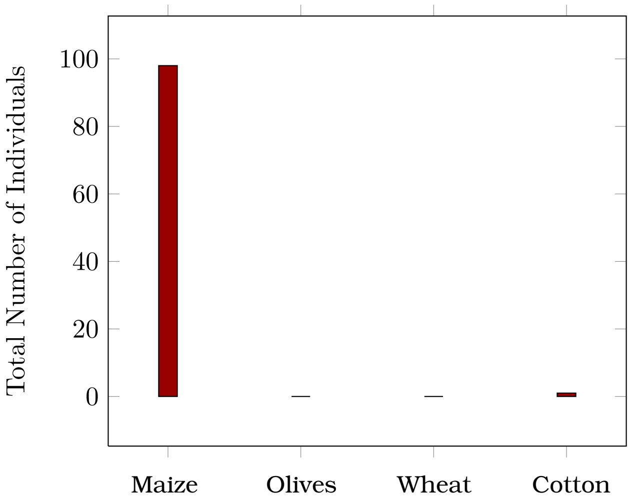


Figure 4.29: Relative abundance of *Cylindera germanica* in each crop type.

4.2.8.14 ***Dixus obscurus***

Dixus obscurus (Dejean, 1825) has a distribution that covers the Balkans, Cyprus, Asia Minor, Iran, Iraq, the Caucasus and Southern Russia (Arndt *et al.*, 2011 [6]).

In a study from Turkey, *D. obscurus* was found at the edges of forests, in areas dominated by grassland (Avgin, 2006 [7]). Other than that, little seems to be known about its habitat preferences, or about its nutrition.

The species was represented by moderate numbers trapped in the olive field in the heterogeneous site and by small numbers trapped in the wheat study fields in the heterogeneous site. See Figure 4.30. In neither of the comparisons, were there significant differences in abundance between heterogeneous and homogeneous sites.

The CCA plot in Figure 4.56 suggests that this species likes warm, dry areas in sandy soil. As far as landscape metrics were concerned, *D. obscurus* appeared to prefer sites with moderately high levels of fallow interspersion / juxtaposition. See Figure 4.58. This suggests that landscape heterogeneity was important to this species, particularly if this provided easy access to patches of fallow.

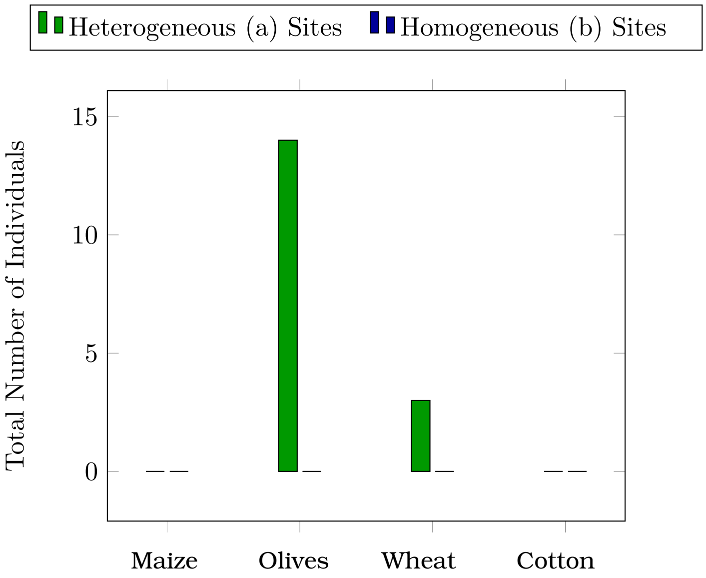


Figure 4.30: Relative abundance of *Dixus obscurus*.

4.2.8.15 *Harpalus atratus*

Harpalus atratus (Latreille, 1804) is a spring breeder. It is a mesoxerophilous and polyphagous species, which prefers to live in forested areas (Varvara, 2004 [183]). It is brachypterous or rarely macropterous and is found in Europe and the Balkans, where it prefers foothills to alpine regions (Arndt *et al.*, 2011 [6]). It has been seen to eat a mixture of seeds from agricultural crops, weeds and shrub species (Lundgren, 2009 [117]).

In this study, *H. atratus* was represented by only one individual, cautiously identified as belonging to this species. It was trapped in the wheat study field in the homogeneous site. This was the site, which according to the landscape metrics in Table 4.42, had the highest heterogeneity of the two, despite being designated homogeneous. It was found in a place with a high soil temperature, but low soil moisture. It was also found on soil with a high level of sand in it. See Figure 4.56.

As far as landscape metrics were concerned, Figure 4.58 shows that *H. atratus* was found in a site where there were very few patches of fallow in the 10 ha of land around the sampled field.

4.2.8.16 *Harpalus dimidiatus*

Harpalus dimidiatus (Rossi, 1790) is a species of dry grassland, which prefers moderate temperatures and humidity levels (Thiele, 1977 [167]). It is macropterous and has a distribution that extends from Western Europe to the Middle East (Arndt *et al.*, 2011 [6]). It is polyphagous and has been seen to consume the seeds of *Daucus* sp. (Lundgren, 2009 [117]).

In this study, *H. dimidiatus* was represented by four individuals trapped in the olive study field in the heterogeneous site. The CCA plot in Figure 4.56 shows that this species was trapped in a warm, dry place. The individuals were also found in an area with a high level of fallow interspersion / juxtaposition and low levels of aggregation. See Figure 4.58.

4.2.8.17 *Harpalus smaragdinus*

Harpalus smaragdinus (Duftschmid, 1812) is found on dry heath, in sandy areas, grassland and arable fields (Luff, 2007 [116]). It is macropterous and has a distribution that covers South and Central Europe, Asia Minor and that reaches east to Western Siberia and Western China. It prefers low lying areas to mountainous areas (Arndt *et al.*, 2011 [6]). Species of this genus are usually at least partly phytophagous (Trautner & Geigenmüller, 1987 [174]).

Single individuals, thought to belong to this species, were found in the olive study field in the homogeneous site and the wheat field in the heterogeneous site.

Figure 4.56 shows that these individuals were found in sandy soil of moderate temperature and moisture. It was also found in sites that had high levels of fallow contagion. See Figure 4.58. This may indicate that *H. smaragdinus* prefers large areas of fallow due to their resemblance to natural grassland.

4.2.8.18 ***Harpalus (Pseudoophonus) rufipes***

Harpalus (Pseudoophonus) rufipes (De Geer, 1774) is distributed from the Azores, across Europe, to North Africa and Western China (Arndt *et al.*, 2011 [6]). This is one of the most common carabid species to be found on agricultural land in Central Europe. It prefers open, dry habitats and light soils. It is most often found on arable land (Luff, 2007 [116]; Thiele, 1977 [167]), but it may also be found less abundantly on pastureland, alfalfa and in potato cultivations, where it prefers the field centers to the hedgerows or field margins (Thiele, 1977 [167]). It is common in both spring planted and autumn planted crops, as well as in ploughed fields and in those where minimum tillage has been practiced (Holland & Luff, 2000 [90]).

It is polyphagous, with its diet comprising 50 % animal matter. It has been seen to consume Arachnida, Formicidae and Hemiptera adults, as well as Lepidoptera and Silphidae larvae. On average each individual eats around 0.28 g of food a day, which is 2.31 times its own body weight. It is also known to be a pest of strawberry cultivations, where it eats the seeds, giving it the common name of the Strawberry Seed Beetle (Thiele, 1977 [167]).

H. rufipes was seen in very high abundance in the maize field in the homogeneous site, followed by the maize field in the heterogeneous site. However, it was also found in small numbers in the olive, wheat and cotton fields of the homogeneous sites. See Figure 4.31. However, no significant differences were seen in abundance per trap between heterogeneous and homogeneous sites.

The species was found most often in muddy soils of average moisture and temperature levels. See the CCA triplot in Figure 4.56. As far as landscape metrics were concerned, this species was found in sites with moderate levels of all of the most influential landscape metrics. See Figure 4.58. This indicates that none of the most influential aspects of landscape heterogeneity had a great effect on this species, possibly because it is accustomed to living in agricultural areas.

There was a highly significant difference in abundance per trap between the different crop types. See Table 4.80 and Figure 4.32. Significantly higher abundances were seen in the maize fields.

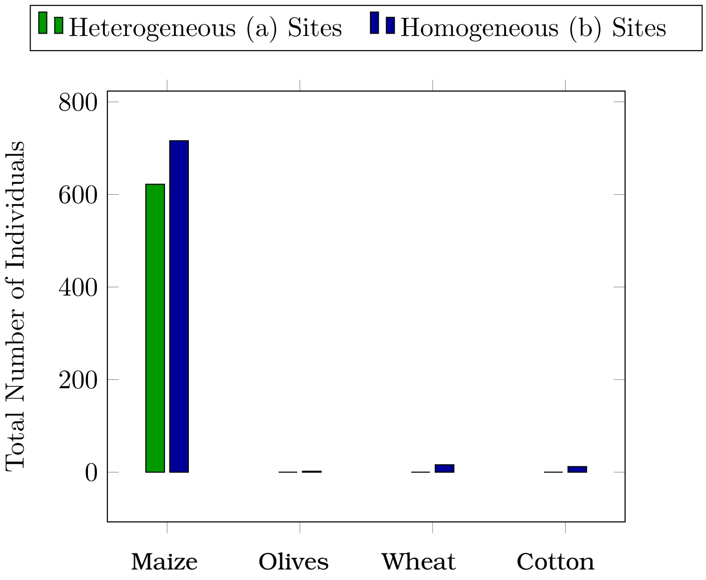


Figure 4.31: Relative abundance of *Harpalus (Pseudoophonus) rufipes*.

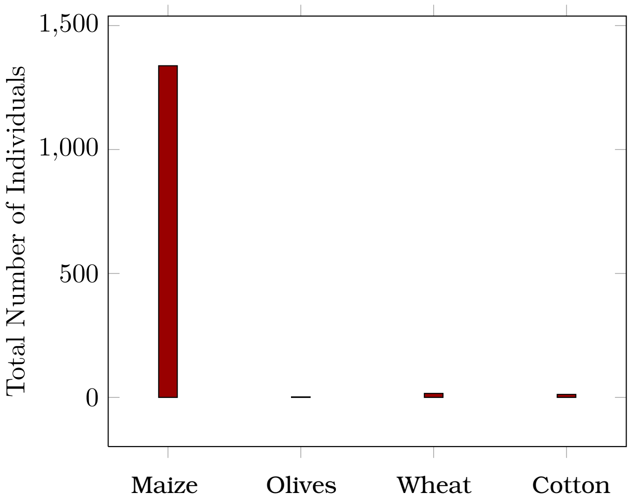


Figure 4.32: Relative abundance of *Harpalus (Pseudoophonus) rufipes* in each crop type.

4.2.8.19 *Microlestes luctuosus*

Microlestes luctuosus (Holdhaus, 1904) is widespread and common in Greece. Its distribution covers Southern Europe and Southwest Asia (Arndt *et al.*, 2011 [6]). It prefers warm, dry places (Cárdenas Talaverón & Piella, 1985 [23]), on clayey soils (Trautner & Geigenmüller, 1987 [174]) and may be found in areas of tall vegetation, those of over 20 cm in height (Fadda *et al.*, 2008 [63]). In this study, it was found on sandy soil. See Figure 4.56.

It was trapped in the olive, wheat and cotton study fields in both heterogeneous and homogeneous sites. Its highest numbers were seen in the wheat study fields. See Figure 4.33. In the olive study fields, significantly higher numbers of this species were recorded in the heterogeneous site. See Table 4.75. Then highly significant differences were also seen between the crop types. See Table 4.80 and Figure 4.34. As far as landscape metrics were concerned, Figure 4.58 shows that this species preferred sites with fairly small field sizes, indicating a preference for high heterogeneity at the landscape level.

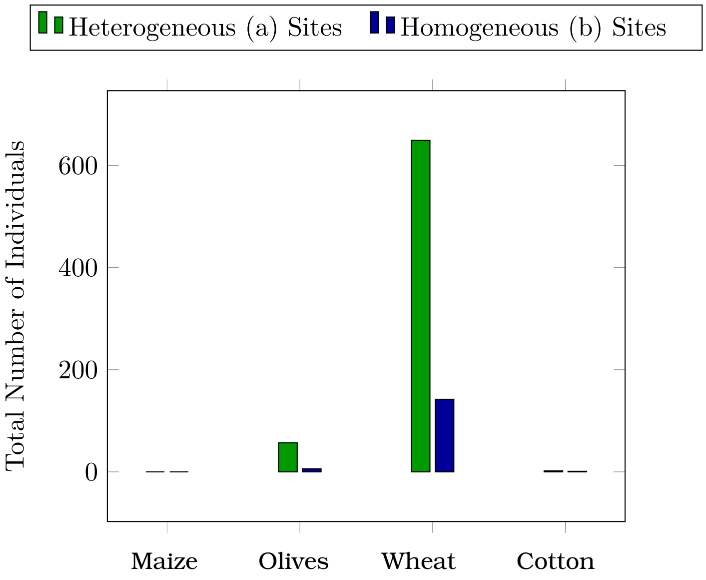


Figure 4.33: Relative abundance of *Microlestes luctuosus*.

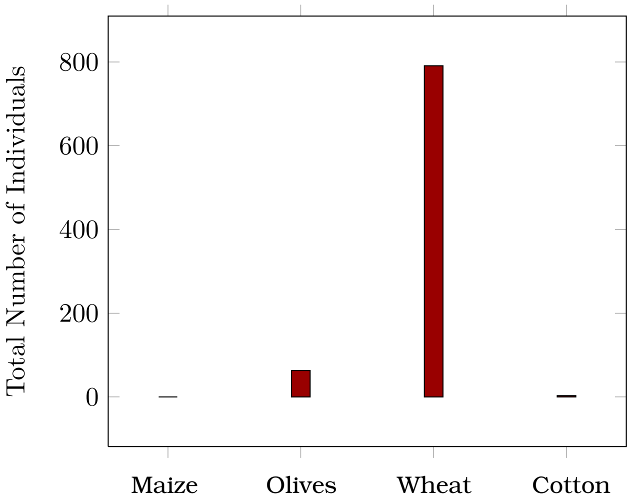


Figure 4.34: Relative abundance of *Microlestes luctuosus* in each crop type.

4.2.8.20 *Ophonus (Hesperophonus) azureus*

Ophonus (Hesperophonus) azureus (Fabricius, 1775) is a brachypterous species, with a distribution that covers Northwestern Africa, Northern, Central and Southern Europe, the Balkans, the Caucasus, Asia Minor and Northwestern China (Arndt *et al.*, 2011 [6]). Species of this genus like moist areas (Turin *et al.*, 1991 [178]), are phytophagous and eat the seeds of agricultural weeds (Honěk & Jarošík, 2000 [93]). Specifically *O. azureus* is known to consume the seeds of common agricultural weed species such as *C. bursa-pastoris*, the common dandelion (*Taraxacum officinale*) and the creeping thistle (*Cirsium arvense*) (Petit *et al.*, 2011 [137]).

In this study, *O. azureus* was represented by only one individual caught in the olive study field in the heterogeneous site. This was a field with an abundant and undisturbed weed community. See Table 4.88. Within this field it was found in a fairly warm, dry place, with moderate soil type. See Figure 4.56.

Finally, Figure 4.58 shows that this individual was found in a site of high interspersion / juxtaposition of fallow, something which may indicate a requirement for easy access to such habitat. Also, it was found in a site of low aggregation of study crops.

4.2.8.21 *Ophonus diffinis*

Ophonus diffinis (Dejean, 1829) is macropterous and has a distribution that extends from the Iberian Peninsular, through Southern and Central Europe, the Balkans, to the Near East and the Caucasus (Arndt *et al.*, 2011 [6]). It is found amongst weeds in agricultural fields and meadows, usually in damp areas (Companyo, 1901 [35]). It is polyphagous, taking insect prey, but is also known to feed on the fallen seeds of plants in the Apiaceae family (Lundgren, 2009 [117]).

In this study, *O. diffinis* was represented by just one individual trapped in the wheat study field in the homogeneous site. It was found in warm, dry, very sandy soil. See Figure 4.56. As far as landscape metrics were concerned, Figure 4.58 shows that this species was found in a site where there were few patches of fallow in the 10 ha of land around the sampled field.

4.2.8.22 *Olisthopus fuscatus*

Olisthopus fuscatus (Dejean, 1828) has a distribution that covers Southern and Western Europe, as well as the Near East (Fauna Europaea, 2011 [69]).

It is zoophagous (Vanbergen *et al.*, 2010 [182]) and in this study was represented by only two individuals, which were thought likely to belong to the species. These were trapped in the olive study field in the homogeneous site. They were found in a place of fairly low soil moisture and higher than average soil temperature. The soil was also moderately sandy. See Figure 4.56. As far as landscape metrics were concerned, this species was found in a site of high fallow aggregation, where there were high percentages of fallow and wasteland. See Figure 4.58.

4.2.8.23 *Pachycarus (Mystropterus) cyaneus*

Pachycarus (Mystropterus) cyaneus (Dejean, 1825) is found in Greece, FYROM, Bulgaria and Turkey (Arndt *et al.*, 2011 [6]). It lives in burrows that are dug underneath stones. It is phytophagous (Trautner & Geigenmüller, 1987 [174]) and xerophilous, preferring areas with sparse vegetation (Sienkiewicz, 2008 [157]).

This species was trapped in low numbers in the olive study fields in both heterogeneous and homogeneous sites. Also one individual was trapped in the maize study field in the heterogeneous site. See Figure 4.35.

It was found in warm, dry, fairly sandy places. See Figure 4.56. As far as landscape metrics were concerned, Figure 4.58 shows that this species was found in sites with moderate to high aggregation levels for study crops. This suggests that it may not require a highly heterogeneous landscape.

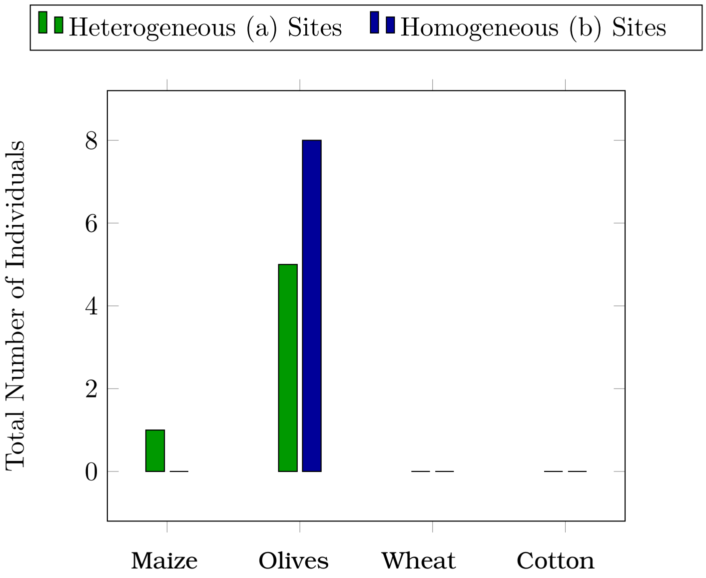


Figure 4.35: Relative abundance of *Pachycarus (Mystropterus) cyaneus*.

4.2.8.24 *Pangus scaritides*

Pangus scaritides (Sturm, 1818) is found in Southern Russia, the Caucasus, Iran, Asia Minor, the Balkans and in Southern and Central Europe (Arndt *et al.*, 2011 [6]). Little seems to be known about its habitat or dietary preferences.

In this study, *P. scaritides* was represented by a single individual trapped in the olive study field in the homogeneous site. The CCA plot in Figure 4.56 shows that it was trapped in a fairly sandy place, of moderate soil temperature and soil moisture.

Figure 4.58 shows that it was found in a site with very high percentages of fallow and wasteland, something which may indicate a requirement for this type of habitat.

4.2.8.25 *Poecilus cupreus*

Poecilus cupreus (Linnaeus, 1758) is distributed throughout Europe, Asia Minor, Central Asia and Siberia (Arndt *et al.*, 2011 [6]). It is found in mountainous beech forests, mountainous and lowland oak-hornbeam forests, as well as in ash-elm water meadows. In agricultural areas it is found in large numbers on arable land and to a lesser extent in meadows, pastures and alfalfa cultivations. In fact, it is one of the most common carabid species on agricultural land in Central Europe. The diet of this species comprises a wide variety of arthropods. It feeds on various species of Arachnida, Acari, Aphidoidea, other Hemiptera species, Staphylinidae, Thysanoptera, as well as preying on the larvae of Lepidoptera, Cantharidae, Coccinellidae and Chrysopa (Thiele, 1977 [167]).

In this study, *P. cupreus* was found as single individuals in the olive field in the heterogeneous site and in the cotton field in the homogeneous site. Small numbers were seen in the maize study field in the homogeneous site, and large numbers in the maize field in the heterogeneous site. See Figure 4.36.

There was a highly significant difference in abundance between the two maize fields. See Table 4.73. This suggests that landscape heterogeneity was also important to this species, rather than high moisture levels alone, as the field in the homogeneous site had the highest moisture levels of the pair.

Figure 4.56 shows that the species was generally found in muddy soil, where plant cover and light intensity were higher than average. When landscape metrics were considered, it was found in sites with average percentages of fallow and with average levels of fallow contagion. See Figure 4.58.

This species showed consistently higher abundances in sites that had higher heterogeneity regarding the landscape metrics identified in Table 4.42.

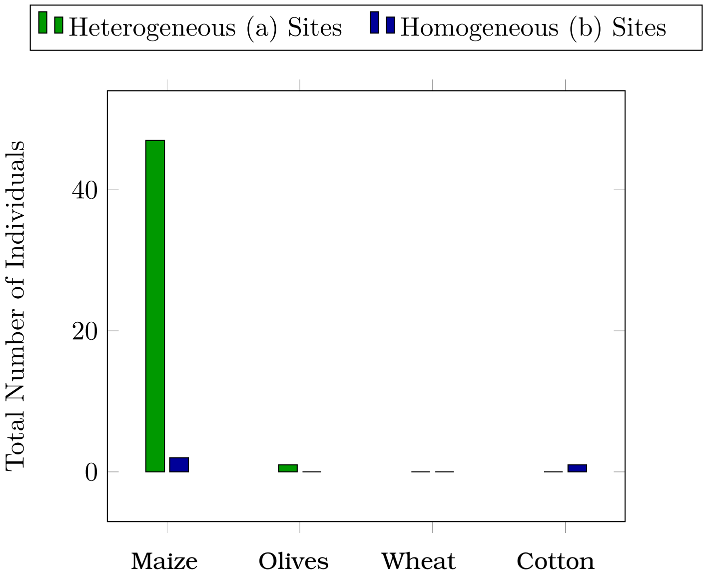


Figure 4.36: Relative abundance of *Poecilus cupreus*.

4.2.8.26 *Pterostichus (Platysma) niger*

The distribution of *Pterostichus (Platysma) niger* (Schaller, 1783) covers most of Europe, Turkey, Iran, the Caucasus, Central Asia, Mongolia, Siberia and the Far East (Arndt *et al.*, 2011 [6]).

It is found in woodland, heathland and damp grassland (Luff, 2007 [116]). It prefers beech forests, oak-hornbeam forests, oak-birch forests, as well as lowland water meadow forests of ash-elm. On agricultural land it is found in arable fields and alfalfa fields. It is also a quantitative indicator for root crops on heavy soils. It is a zoophagous species that lives close to the field margins. In fact, it cannot really survive in landscapes without hedges. It likes high temperatures, low humidity, low light levels and is an autumn breeder (Thiele, 1977 [167]). It is particularly common in spring planted crops and in those where minimum tillage has been practiced (Holland & Luff, 2000 [90]).

In this study, *P. niger* was found in order of decreasing abundance, in the maize study field in the heterogeneous site, in the maize study field in the homogeneous site, in the cotton and wheat study fields in the homogeneous site, then in the olive study field in the heterogeneous site. Then the lowest levels of abundance were seen in the cotton and wheat study fields in the heterogeneous site. It was absent from the olive study field in the homogeneous site. See Figure 4.37. In the cotton comparison, significantly higher abundance of this species was seen in the homogeneous site. See Table 4.79. However, this site was often found to be the most heterogeneous of the pair during the landscape analysis.

As far as crop type was concerned, this species was found in significantly greater numbers in the maize study fields. See Table 4.80 and Figure 4.38.

This species was found in places that had higher than average moisture levels, lower than average temperatures and that were slightly muddy. See Figure 4.56. Regarding landscape metrics, it was found in sites where the contagion of fallow was moderate to low. See Figure 4.58. It also showed consistently higher abundances in sites that had higher heterogeneity regarding the landscape metrics identified in Table 4.42.

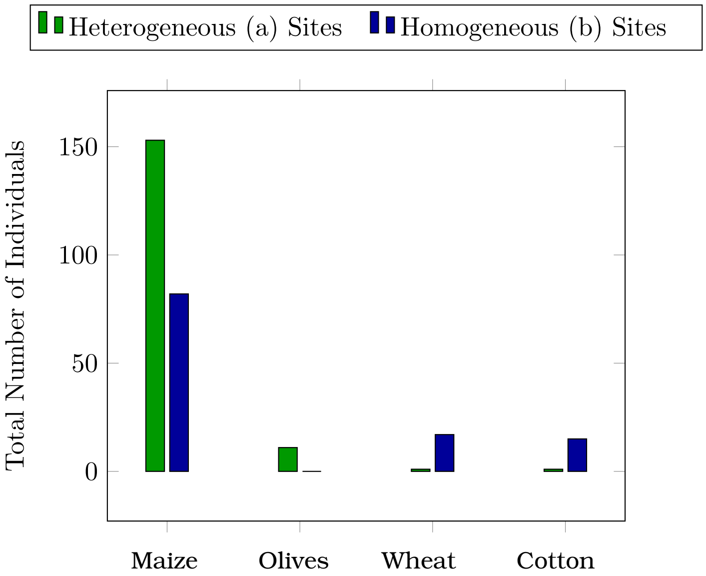


Figure 4.37: Relative abundance of *Pterostichus (Platysma) niger*.

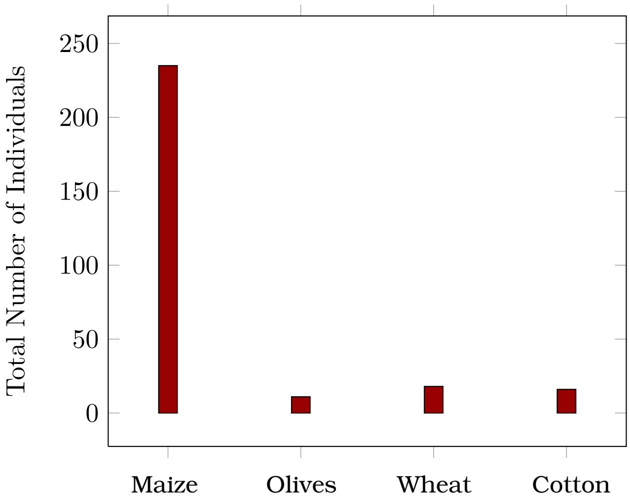


Figure 4.38: Relative abundance of *Pterostichus (Platysma) niger* in each crop type.

4.2.8.27 ***Tapinopterus taborskyi***

One individual of the species *Tapinopterus taborskyi* (Mařan, 1939) was found in the maize study field in the heterogeneous site. It was also found in small numbers in the cotton study field in the heterogeneous site, then in larger numbers in the cotton study field in the homogeneous site. See Figure 4.39. This species has only ever been found on Oiti mountain (Arndt *et al.*, 2011 [6]), which is adjacent to the study area. For the cotton comparison, significantly greater abundance of this species was seen in the homogeneous site. See Table 4.79. This site; however, was often found by the landscape analysis to be the most heterogeneous of the pair.

Little appears to be known about the habitat preferences of this species. In Figure 4.56, its distribution seemed to be determined by some variable other than those environmental variables included in the CCA. Perhaps its high abundance in site 3b was due to there being an easy migration route from Oiti in that direction, possibly due to the prevailing wind direction.

Where landscape metrics are considered, *T. taborskyi* was found in sites with moderate to low numbers of fallow patches. See Figure 4.58. This may indicate that it prefers living close to larger, non-fragmented areas of fallow. The species also showed higher abundances in sites that had higher heterogeneity regarding the landscape metrics identified in Table 4.42.

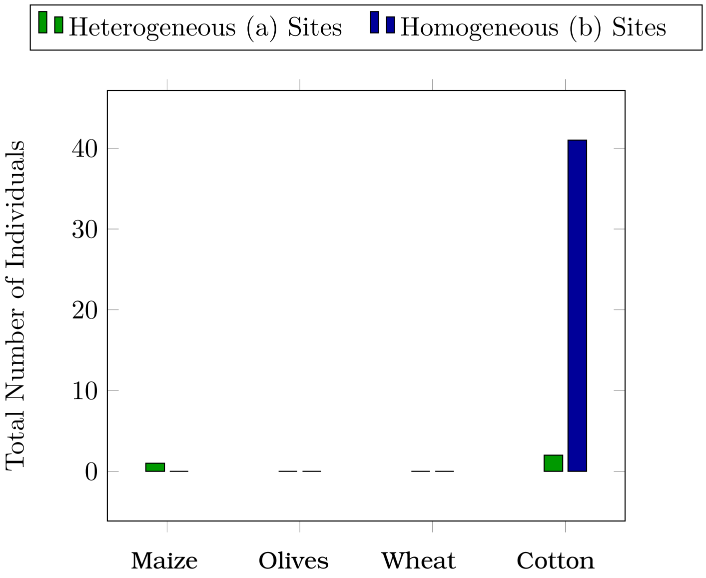


Figure 4.39: Relative abundance of *Tapinopterus taborskyi*.

4.2.8.28 *Trechus quadristriatus*

Trechus quadristriatus (Schrank, 1781) has a distribution that covers all of Europe, the Nearctic, the Near East and North Africa (Fauna Europaea, 2011 [69]). It is widespread and common in Greece (Arndt *et al.*, 2011 [6]).

This species prefers dry areas, usually disturbed habitats such as gardens and agricultural fields (Luff, 2007 [116]). However, it may also be found in beech forests, oak-hornbeam forests and in lowland water meadow forests of ash and elm. It is one of the most common carabid species found in cultivated areas in Central Europe, where it prefers arable cultivations, but may be found to a lesser extent in meadows, alfalfa fields and vegetable fields. It is also a quantitative indicator of root crops and may often be found in sandy areas. Generally, this species prefers open areas, but where there are hedgerows it will spend most of its time in close proximity to them. However, it does prefer less dense vegetation. In fact, areas which have been treated with herbicide support greater numbers of this species than those which have not (Thiele, 1977 [167]). It may be found commonly in spring planted crops and in fields that were prepared by ploughing (Holland & Luff, 2000 [90]).

T. quadristriatus is thought to be preyed on by ants, while it is itself a predator of other arthropods. It is, for example, known to prey on the eggs of the agricultural pest the cabbage root fly (*Delia radicum*) (Thiele, 1977 [167]). The species is polyphagous; however, as it has also been seen to feed on plant seeds (Lundgren, 2009 [117]). Finally, it is known to be an autumn breeder (Thiele, 1977 [167]).

In this study, *T. quadristriatus* was represented by one individual captured in the olive study field in the heterogeneous site, then by another caught in the wheat study field in the homogeneous site. Figure 4.56 shows that it was found in very sandy soil. As for landscape metrics, it was found in sites where fallow contagion was low. See Figure 4.58.

4.2.8.29 *Zabrus (Pelor) graecus*

Zabrus (Pelor) graecus (Dejean, 1828) is distributed throughout Greece, Bulgaria, FYROM, and the Near East. It is often found in Attica and on the closer islands (Arndt *et al.*, 2011 [6]). Species from this genus are phytophagous and feed on wild and cultivated grasses (Trautner & Geigenmüller, 1987 [174]).

In this study, *Z. graecus* was trapped, in order of decreasing abundance, in the wheat field in the heterogeneous site, the olive field in the heterogeneous site, the wheat field in the homogeneous site, the cotton field in the heterogeneous site, both maize fields and in the olive study field in the homogeneous site. See Figure 4.40. No significant differences were seen in abundance per trap between heterogeneous and homogeneous sites.

Figure 4.56 shows that this species was found in areas that were fairly sandy and warm. Where landscape metrics were considered, *Z. graecus* was found in sites with moderately high fallow patch numbers. See Figure 4.58.

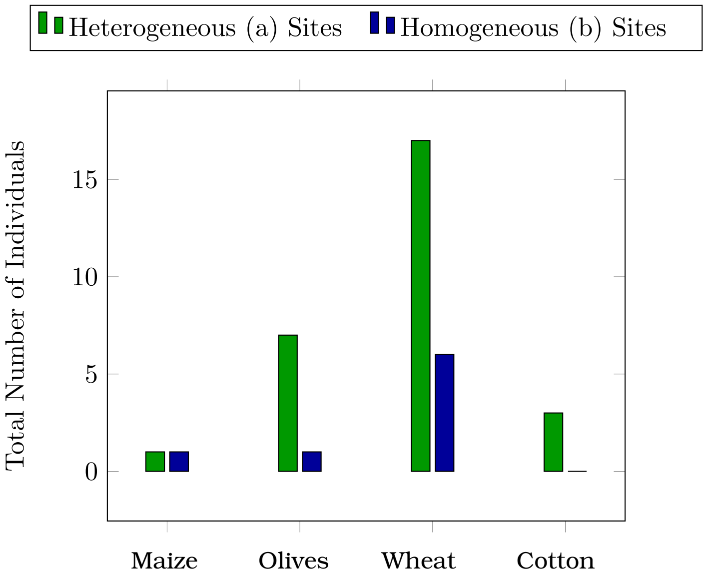
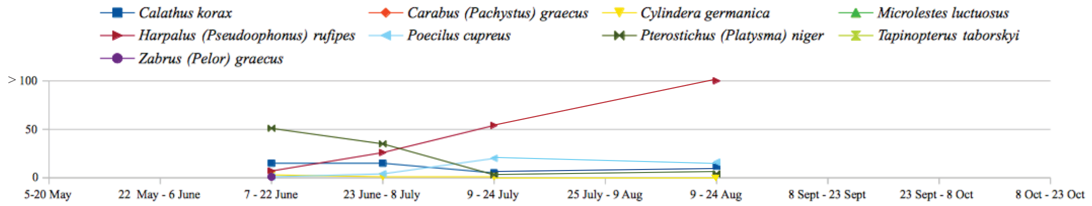
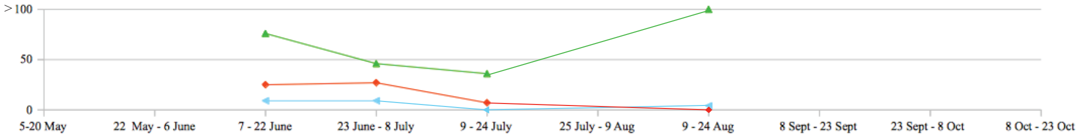


Figure 4.40: Relative abundance of *Zabrus (Pelor) graecus*.

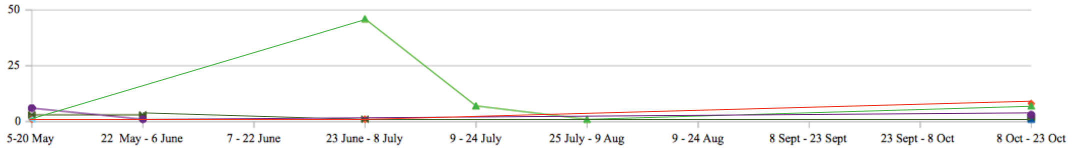
4.2.9 Temporal Variation in Carabid Abundance



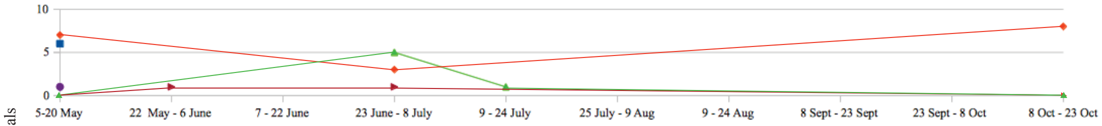
Maize Field (a) Heterogeneous Site



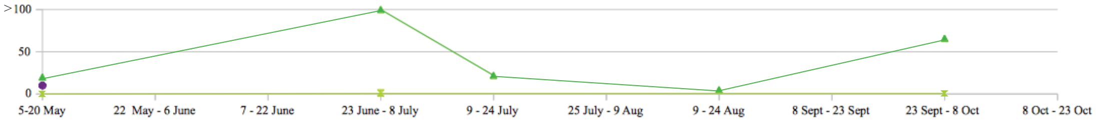
Maize Field (b) Homogeneous Site



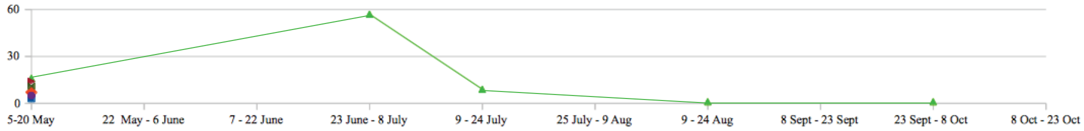
Olive Field (a) Heterogeneous Site



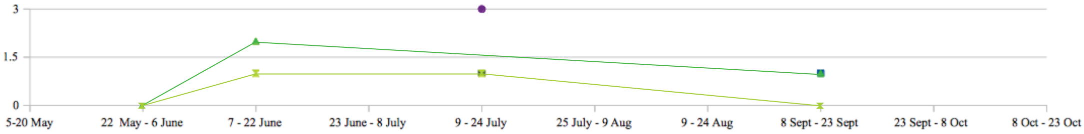
Olive Field (b) Homogeneous Site



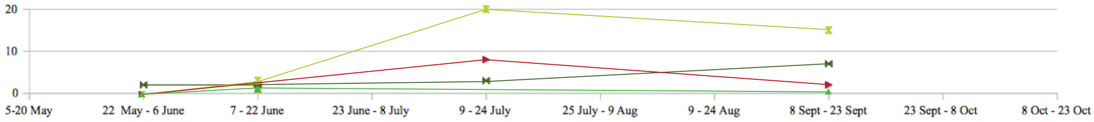
Wheat Field (a) Heterogeneous Site



Wheat Field (b) Homogeneous Site



Cotton Field (a) Heterogeneous Site



Cotton Field (b) Homogeneous Site

Figure 4.41: Temporal variation in the relative abundance of the most common carabid species.

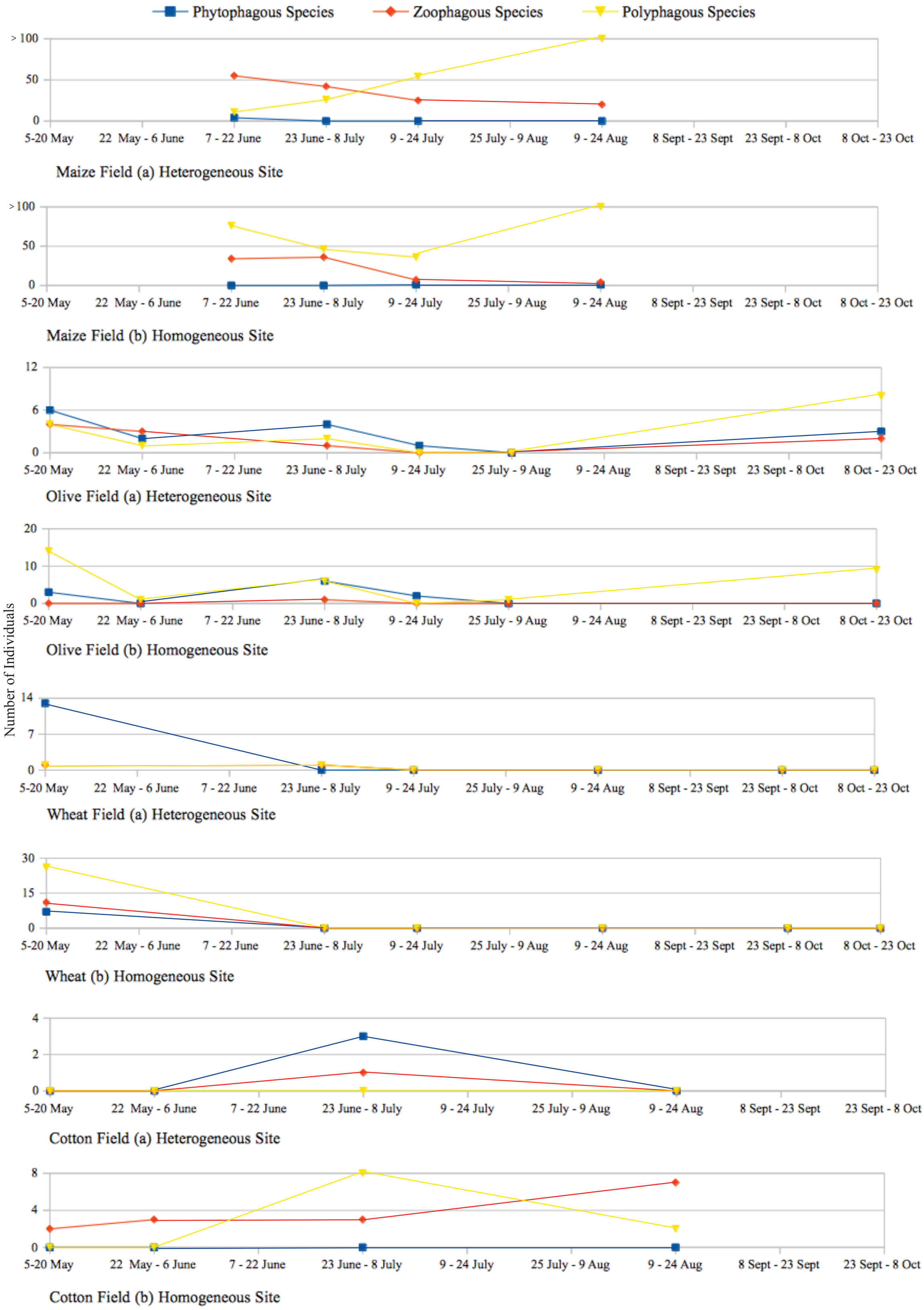


Figure 4.42: Temporal variation in phytophagous, zoophagous and polyphagous carabid species.

Figure 4.41 shows temporal variation in the abundance of the most common carabid species trapped in the different study fields. The study fields in the sites found to have higher heterogeneity according to the landscape analysis (1a, 2a, 3b) appeared to have more species present at higher abundances, for longer periods. There were similarities between fields of the same crop type in the activity patterns of *P. cupreus*, *M. luctuosus* and *C. graecus*. Fields of the same crop type showed greater similarities regarding temporal patterns of abundance, than did fields of different crops types. Again this shows the important influence of crop type in determining the distribution and abundance of carabids.

Figure 4.42 shows temporal variation in the abundance of phytophagous, polyphagous and zoophagous species. The greatest temporal variation was seen in the abundance of polyphagous species. These species appeared to dominate later in the year, while phytophagous species were at their highest abundance levels earlier on in the year. Again their were similarities in the abundances of all three groups between fields of the same crop type, indicating that crop type determined which groups would be present at certain times of the year. This was probably due to the cultivation practices taking place in the fields, which would have varied throughout the year, according to crop type.

4.2.10 Carabid Species Composition

Figure 4.43 is a CA biplot showing the carabid species and samples taken in all of the study fields. Species are represented by blue triangles and samples by black crosses. The extents of samples from different fields are shown by coloured ellipses. The eigenvalues for the first and second CA axes were 0.879 and 0.716 respectively, meaning that there was a strong correlation between the species scores and the site scores. This showed that the analysis could be considered reliable.

The use of Hill's scaling meant that samples containing a given species were scattered around that species point. It also meant that the degree of sample spread for each field indicated how similar its samples were (ter Braak *et al.*, 1995 [166]). The sample spread for each field showed that the most dissimilar samples usually came from the sites found to have the greatest heterogeneity by the landscape analysis. For the maize and olive study fields; however, differences between heterogeneous and homogeneous sites were not great.

The olive fields had by far the most dissimilar samples, echoing the results of the diversity indices calculated later in this section. The olive fields overlapped many other study fields, showing that they shared species with the other study fields.

There was also a high level of overlap between fields of the same crop type, regardless of their heterogeneity levels. This suggests that crop type was more influential that heterogeneity. If heterogeneity had been the most important factor, samples from each heterogeneity level would have been grouped together. However, this was clearly not the case. Instead there was overlap in the data from nearly all study fields, and samples from the same crop type tended to be grouped together.

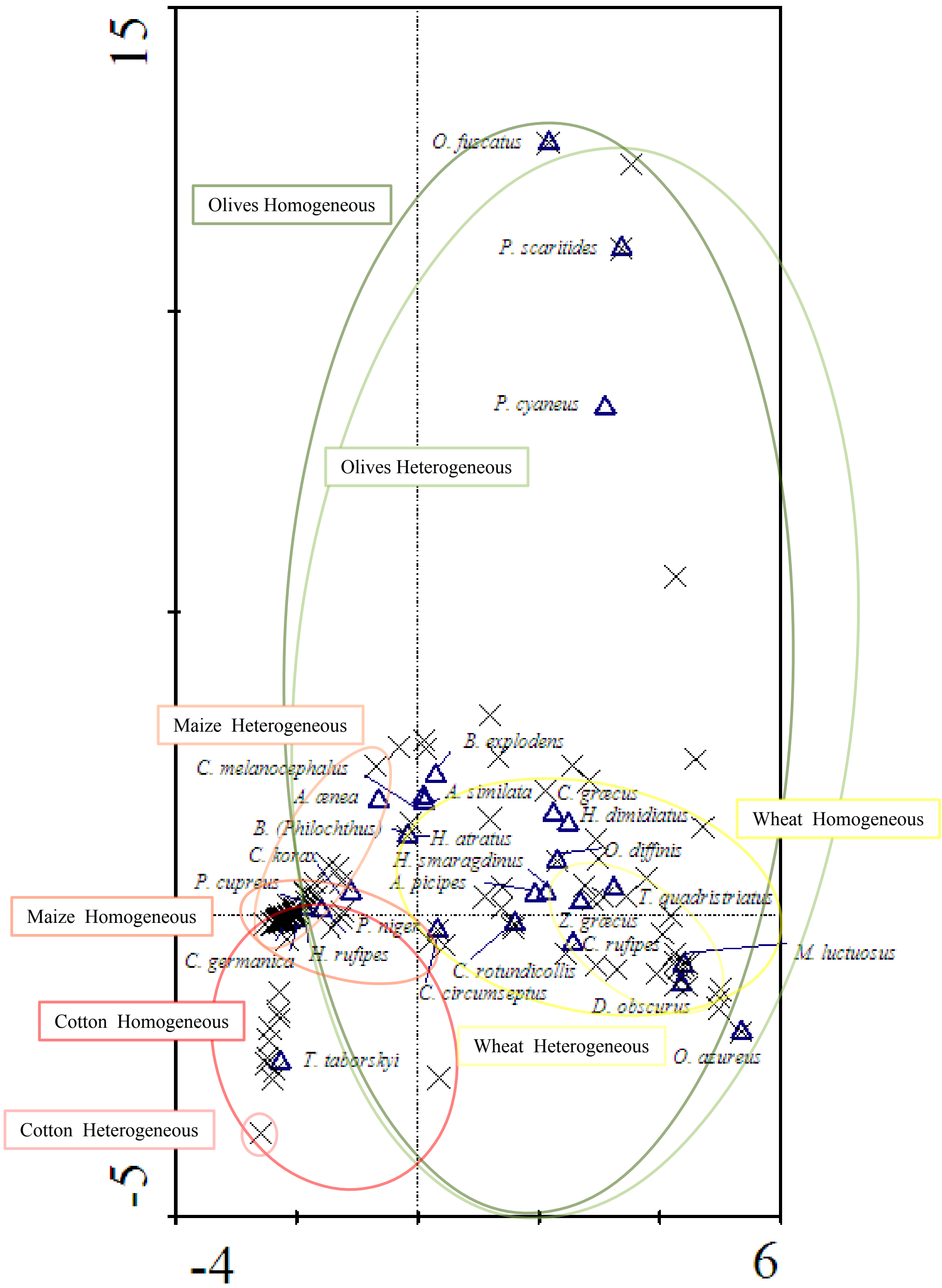


Figure 4.43: Canonical correspondence analysis biplot of carabid species and samples.

4.2.11 The Richness of Carabid Species

As the carabid data were composed mainly of species that were represented by just one or two individuals, the most appropriate estimator of species richness was the Chao 1 estimator. The results obtained by this estimator are shown in Table 4.81. However, it can be seen from the 95 % confidence intervals for this estimator that these results were not reliable. So the results of other estimators should be preferred, when trying to determine differences between heterogeneous and homogeneous sites.

Table 4.81: The mean richness of carabid species calculated using the Chao 1 estimator.

Mean Richness of Carabid Species					
Chao 1 Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**95 % Confidence Intervals**	**Homogeneous Sites (b)**	**95 % Confidence intervals**
1	Maize	11.02	0.93 - 16.96	7.33	7.02 - 12.96
2	Olives	22.50	16.32 - 57.53	18.50	16.37 - 32.98
3	Wheat	20.00	11.92 - 62.16	20.00	15.86 - 43.91
3	Cotton	5.50	5.03 - 13.26	8.5	7.15 - 22.08

The results for the Chao 2 estimator, which are shown in Table 4.82, also had wide 95 % confidence intervals, suggesting that these results were also unreliable. In addition to this, the Chao 1 and Chao 2 results showed completely different patterns regarding heterogeneous and homogeneous sites. So it appears that neither estimate is particularly suitable for these data.

Table 4.82: The mean richness of carabid species calculated using the Chao 2 estimator.

Mean Richness of Carabid Species					
Chao 2 Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**95 % Confidence Intervals**	**Homogeneous Sites (b)**	**95 % Confidence intervals**
1	Maize	11.33	11.02 - 16.86	8.47	7.15 - 21.78
2	Olives	19.91	15.85 - 43.44	20.91	16.85 - 43.39
3	Wheat	14.89	10.76 - 41.48	19.90	15.85 - 43.39
3	Cotton	5.98	5.09 - 15.47	12.87	7.94 - 43.61

Table 4.83 shows the mean richness of carabid species calculated using the Jackknife 1 estimator. Higher richness was estimated in the homogeneous sites for all comparisons except for the maize comparison. However, the standard deviations of the estimates appear to be too high to allow the differences between heterogeneous and homogeneous sites to be determined. This estimate therefore, can not be said to be reliable for these data.

Table 4.83: The mean richness of carabid species calculated using the Jackknife 1 estimator.

Mean Richness of Carabid Species					
Jackknife 1 Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	12.95	1.36	9.93	1.65
2	Olives	20.89	2.29	21.89	2.30
3	Wheat	14.89	2.08	20.88	3.02
3	Cotton	7.93	1.65	10.91	1.89

Table 4.84 shows the mean richness of carabid species calculated using the Jackknife 2 estimator. The standard deviations for each estimate are also shown. For all but one estimate the standard deviations are 0. This suggests that the results are fairly reliable. Except in the case of the cotton comparison,

they can be used to determine differences in species richness between heterogeneous and homogeneous sites. With the exception of the olive comparison, higher richness was seen in sites where the landscape analysis found higher heterogeneity. Although for the olive comparison there was not a great difference between sites.

Table 4.84: The mean richness of carabid species calculated using the Jackknife 2 estimator.

Mean Richness of Carabid Species					
Jackknife 2 Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	13.00	0.00	11.86	0.00
2	Olives	24.78	0.00	25.79	0.00
3	Wheat	18.73	0.00	24.76	0.00
3	Cotton	8.93	0.00	10.91	1.89

Table 4.85 shows the mean richness of carabid species calculated using the Bootstrap estimator. The standard deviation for each estimate is also shown. These were 0 in each case, showing that this estimator was very reliable. Generally higher richness was seen in sites found to have higher heterogeneity by the landscape analysis. In this case though, the olive study fields broke the pattern and higher richness was seen in the homogeneous site. Although the difference between the two sites was not great.

Table 4.85: The mean richness of carabid species calculated using the Bootstrap estimator.

Mean Richness of Carabid Species					
Bootstrap Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	12.09	0.00	8.22	0.00
2	Olives	17.47	0.00	18.67	0.00
3	Wheat	12.01	0.00	17.46	0.00
3	Cotton	6.36	0.00	14.73	0.00

Table 4.86 shows the mean richness of carabid species per trap calculated using rarefaction. This estimator would have been particularly appropriate for these data, as all the data obtained in the study could be used in its calculation. The standard deviation for each estimate is also shown. These are fairly low, so the results can be considered reliable. Higher species richness was estimated in the sites found to be more heterogeneous by the landscape analysis, except in the case of the olive comparison, where the estimated difference between the two sites was small anyway.

Table 4.86: The mean richness of carabid species calculated using rarefaction.

Mean Richness of Carabid Species					
Rarefaction					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	10.95	0.22	6.95	0.22
2	Olives	14.89	0.33	15.91	0.30
3	Wheat	9.89	0.33	14.88	0.34
3	Cotton	4.95	0.22	6.93	0.26

4.2.12 The Diversity and Evenness of Carabid Species

Figures 4.46 to 4.49 show the diversity of carabid species in each of the study sites, calculated using the Simpson's index (*1-D*), Whittaker's measure of β-diversity (β_W), Shannon's index (*H'*) and Margalef's index (D_{Mg}). Finally, evenness was calculated using Shannon's evenness index (*F'*). See Figure 4.50.

For all of the indices of α-diversity, the fields in heterogeneous and homogeneous sites showed the same pattern in relation to one another. This showed that these indices were reliable. However, there was no clear association between diversity and heterogeneity. For the maize and cotton study fields, all indices showed that diversity was higher in the heterogeneous sites. For the olive and wheat fields; however, diversity was always higher in the homogeneous sites.

B-diversity was highest in the cotton study field in the heterogeneous site. This was the site where the smallest number of species was sampled. Such small species numbers would have made each individual sample proportionally very different from one another.

Carabid diversity, calculated with Shannon's index, was found to be significantly correlated with only two of the landscape metrics. This was tested using the Pearson product-moment correlation. In this case, the use of parametric statistics was appropriate, as Magurran (2004, [121]) recommends their use with the Shannon index calculated for different sites. Also both data sets were found to be continuous and normally distributed, so the assumptions of the Pearson product-moment correlation were satisfied.

The strongest positive correlation was seen between carabid diversity and the percentage of the study site covered by fallow and wasteland (r = 0.924, d.f. = 5, p = 0.002). See Figure 4.44. Then another significant positive correlation was seen between carabid diversity and the percentage of each study site covered by the tree crops: olives, walnuts, almonds and plums (r = 0.783, d.f. = 5, p = 0.037). See Figure 4.45.

There were also significant positive correlations seen between carabid diversity and the percentage of land covered by olive cultivations, the percentage of land covered by fallow and the connectance level of olive cultivations. However, the data obtained from these three metrics appeared not to come from a normal distribution, so the results of the Pearson product-moment correlation may have been unreliable. When the same relationships were examined using the Spearman's rank correlation, no significant correlations were seen for these three metrics.

The fact that only a very small proportion of the calculated metrics showed significant correlations to carabid diversity may be important, as it suggest that these factors were the most influential regarding carabid diversity. Of all the land use types in the study sites, fallow, wasteland and tree crops would have resembled most closely the natural woodland and grassland preferred by many of the carabid species sampled.

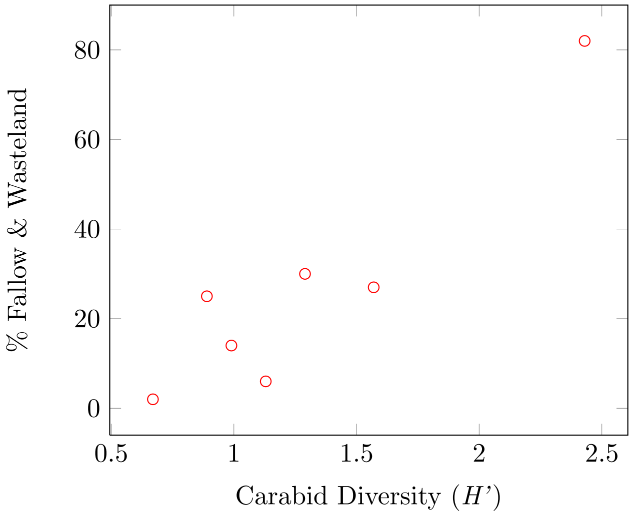


Figure 4.44: Correlation between carabid species diversity and the percentage of fallow and wasteland.

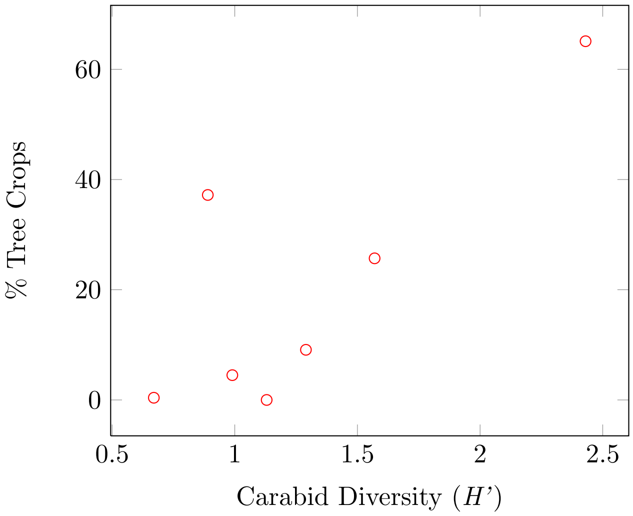


Figure 4.45: Correlation between carabid species diversity and the percentage of tree crops.

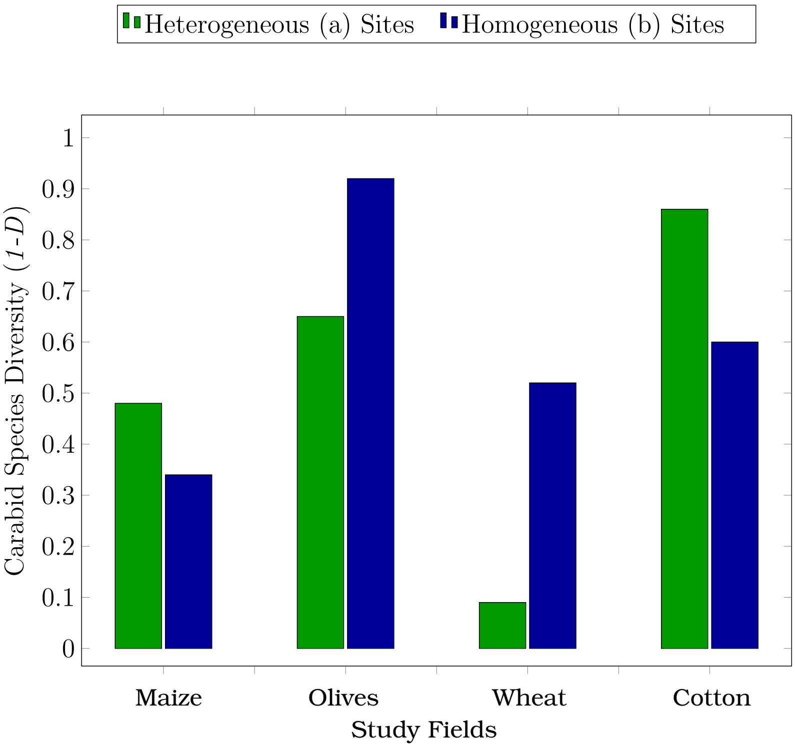


Figure 4.46: Diversity of carabid species calculated using Simpson's diversity index.

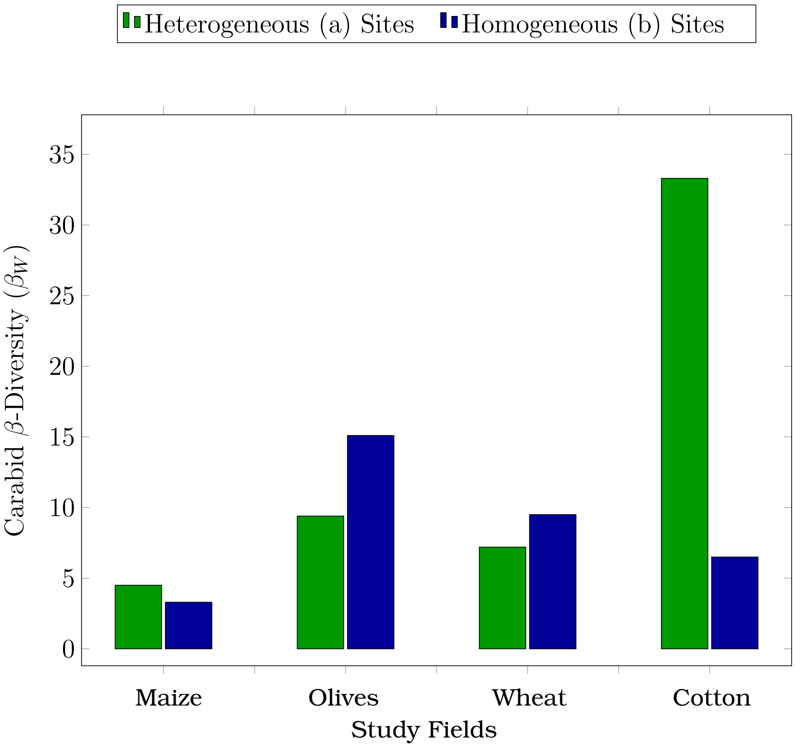


Figure 4.47: B-diversity of carabid samples calculated using Whittaker's measure.

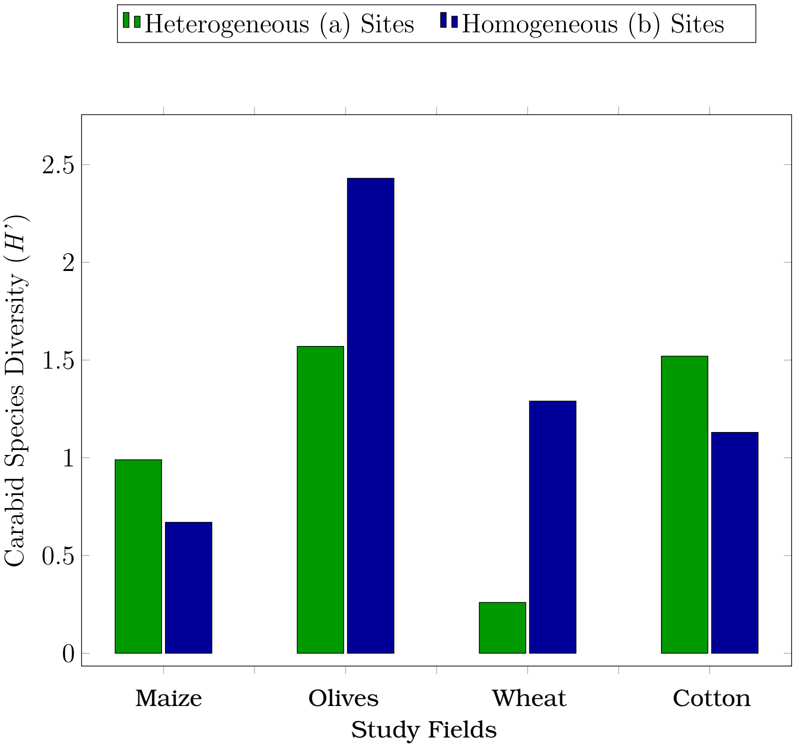


Figure 4.48: Diversity of carabid species calculated using Shannon's diversity index.

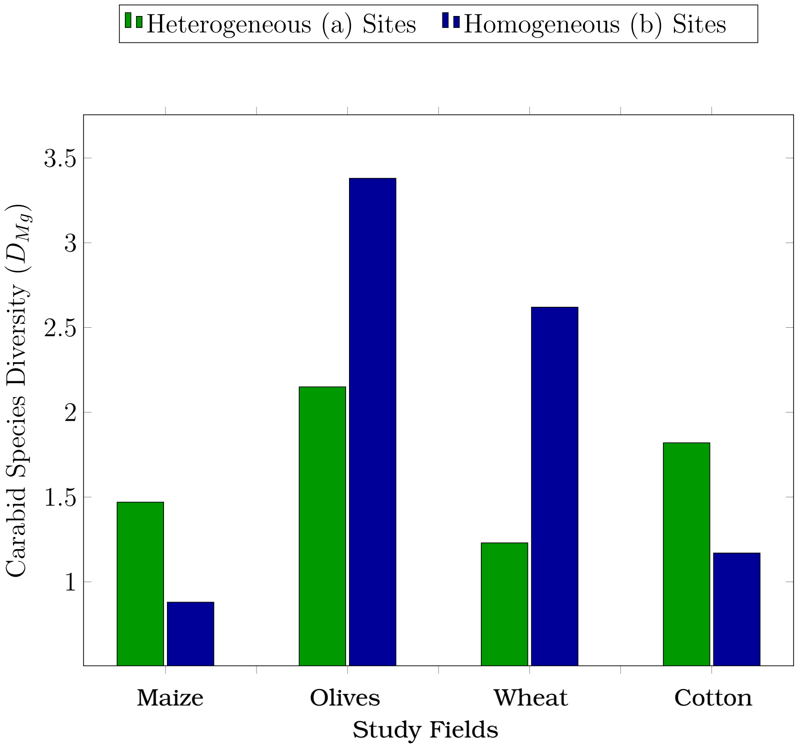


Figure 4.49: Diversity of carabid species calculated using Margalef's diversity index.

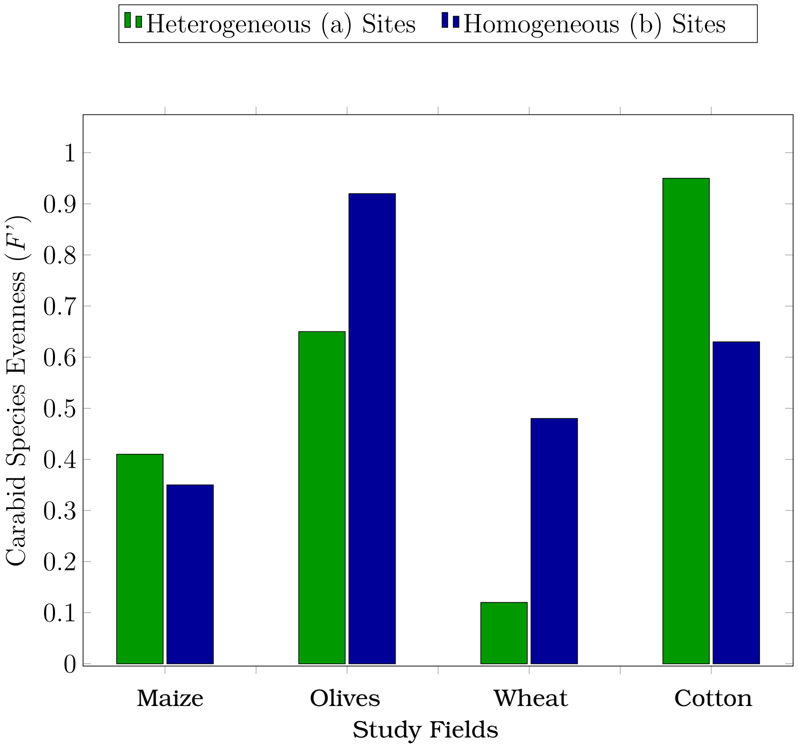


Figure 4.50: Evenness of carabid species calculated using Shannon's evenness measure.

Figures 4.51 to 4.53 show the diversity of carabid species trapped in each crop type, calculated using the Simpson's index (*1-D*), Shannon's index (*H'*) and Margalef's index (D_{Mg}). Finally evenness was calculated using Shannon's evenness index (*F'*). See Figure 4.54.

All the indices showed that the olive study fields had the greatest diversity and evenness, probably because they resembled natural woodland most closely of all the crop types. All indices except Margalef's index showed that the cotton fields had the second highest diversity and evenness levels, that the maize fields had the third highest levels and that the wheat fields had the lowest diversity and evenness levels. Using Margalef's index, the wheat study fields had the second highest diversity levels and the maize fields the lowest diversity levels.

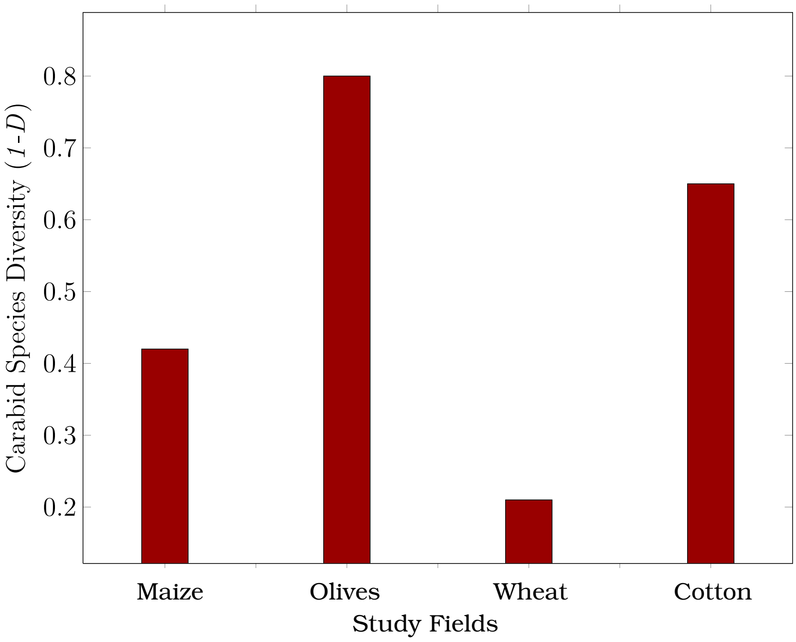


Figure 4.51: Diversity of carabid species calculated using Simpson's diversity index.

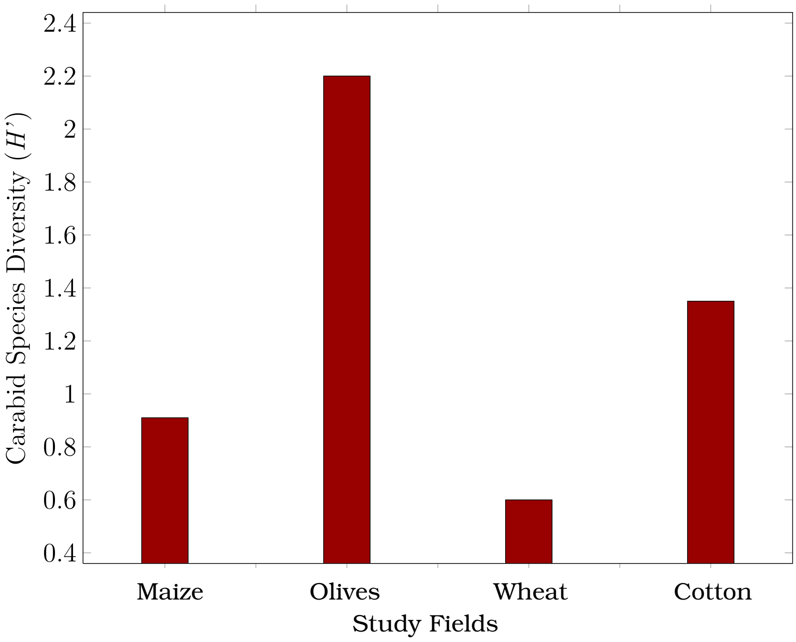


Figure 4.52: Diversity of carabid species calculated using Shannon's diversity index.

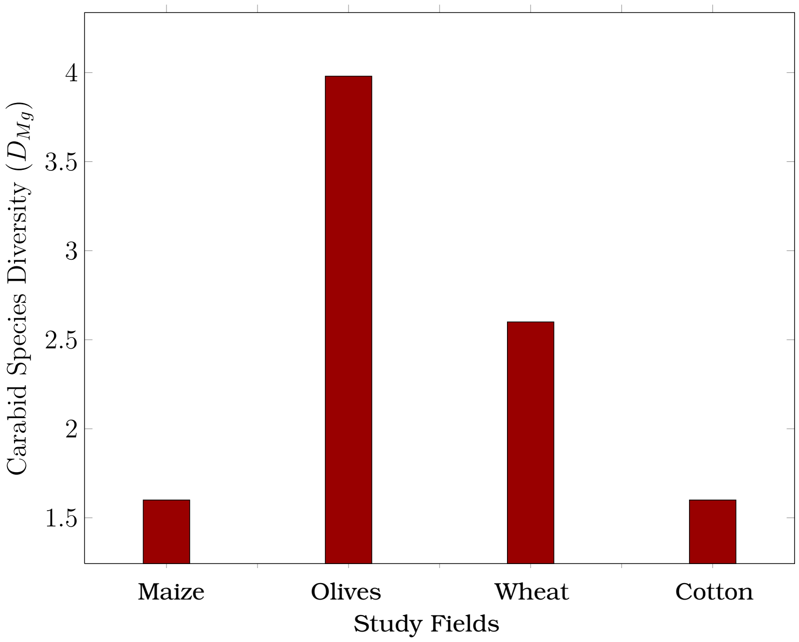


Figure 4.53: Diversity of carabid species calculated using Margalef's diversity index.

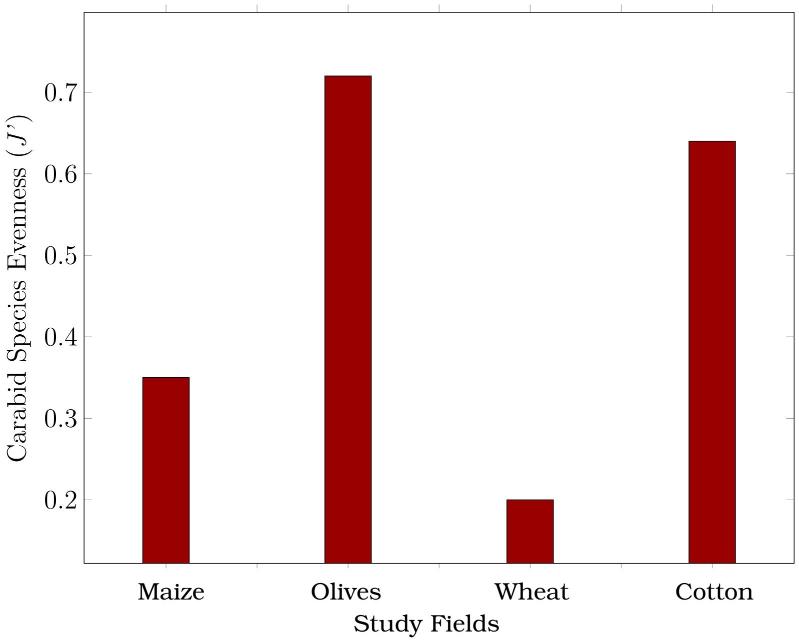


Figure 4.54: Evenness of carabid species calculated using Shannon's evenness measure.

4.2.13 The Influence of Environmental Variables on Carabid Species Composition

Figure 4.55 shows a CCA triple plot of carabid species, carabid samples and environmental variables, using data from all of the study fields. Crop type was included as an environmental variable because of its high level of influence on the local environment and so on the distribution and relative abundance of the carabid species.

The eigenvalues for the first and second axes were 0.760 and 0.442. For the first axis particularly, this showed a strong correlation between species and site scores, meaning that differentiation of the species data in relation to the variables illustrated would be possible.

The cumulative percentage variances of the species data for the first two axes were 7.9 and 12.4, meaning that the first two axes explained 20.3 % of the overall variation in the data. This is a fairly low figure and may indicate that some aspects of landscape heterogeneity also contribute to the variation in the data set.

A Monte Carlo permutation test was performed on the environmental variables, using 499 permutations. According to this, the most influential variables were crop type and soil type, followed by soil temperature and soil moisture. The least influential environmental variables were, in order of decreasing influence, soil pH, plant percentage cover, soil organic matter and light intensity.

The crop type maize explained 0.68 of the variance. The next most influential variables were those of soil type. The variance explained by the percentages of sand and mud in the soil were both 0.61. The crop types wheat and cotton explained 0.54 and 0.44 of the total variance respectively, while soil temperature and soil moisture explained 0.39 and 0.35 of the variance respectively. Finally, the crop type olives also explained 0.35 of the variance. In each case the p-values produced in the Monte Carlo permutation test were 0.002.

The strongest correlations between the variables illustrated here were seen between the percentages of sand and mud in the soil and the crop type maize. These correlations were -0.91 and 0.91 respectively, showing that the maize fields had the highest levels of mud and the lowest levels of sand in their soil.

There was also a high negative correlation between soil moisture levels and soil temperature (-0.73). This made sense, as greater irrigation levels would have caused greater evaporative cooling. Then a fairly high correlation was seen between the percentages of sand and mud in the soil and the crop type wheat (0.68 & -0.68). This meant that the wheat study fields had high levels of sand in them and low levels of mud. Also the crop types maize and wheat were negatively correlated (-0.64), meaning that they differed widely in terms of their environmental variables and their carabid species composition. Finally, soil moisture and soil pH were negatively correlated (-0.63), meaning that areas of high moisture had low pH and vice verser.

The CCA triple plot in Figure 4.56 was produced using only the environmental variables and not the crop type variables. The eigenvalues for the first two axes were 0.624 and 0.256. This meant that niche separation on the second axis was difficult to determine. This was probably because variation on the second axis was mostly determined by the crop type cotton, something which can be seen in Figure 4.55. The cumulative percentage variances of the species data on the first two axes were 6.5 and 9.1. These figures were much lower than those seen when crop type was included as an environmental variable, something which demonstrates the high level of influence of crop type.

When the influence of crop type was excluded altogether, by the using crop type data as covariables, the CCA triple plot in Figure 4.57 was produced. The eigenvalues for the first two axes were both very low (0.165 & 0.114) meaning that niche differentiation based on environmental variables alone would not be possible. The cumulative percentage variances of the species data for the first two axes were also low (2.0 and 3.4) showing that environmental variables alone did not have a great influence on carabid species composition.

To summarize then, the wheat study fields, which were unirrigated, had sandy soil, high soil temperatures, low soil moisture levels and low plant percentage cover. The maize study fields, on the other hand, were well irrigated, had high soil moisture, low temperatures and high plant percentage cover. The olive study fields were intermediately situated between the maize and wheat fields in terms of environmental variables. The cotton study fields; however, appeared to be influenced by other factors, which did not include any of the most influential environmental variables. One of these factors may have been the use of the insecticide Phosalone, which was used in both of the cotton study fields.

The influence of specific environmental variables on each of the carabid species was discussed in detail in Section 4.2.8.

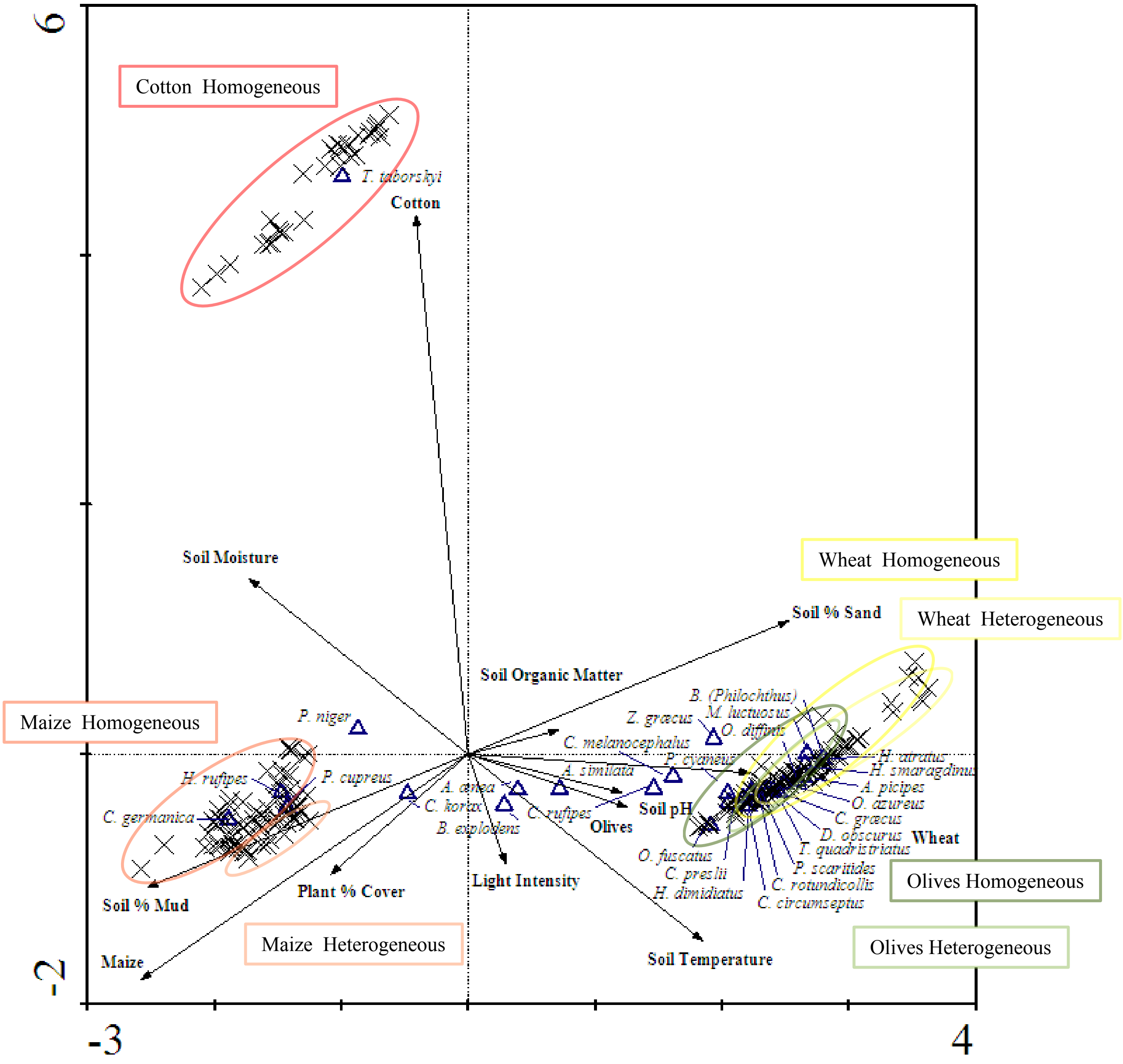


Figure 4.55: CCA triple plot of carabid species, samples and environmental variables, including crop types.

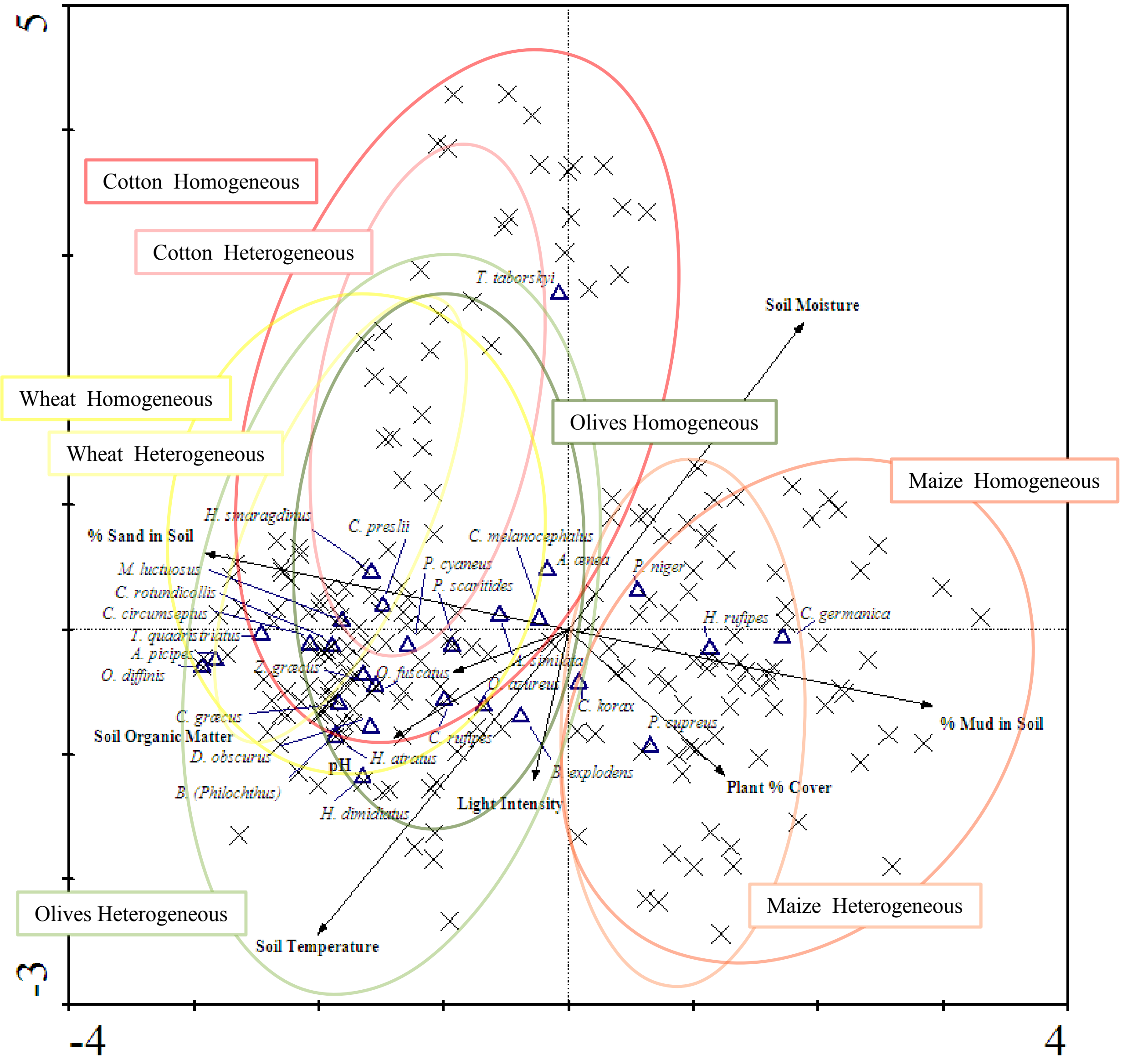


Figure 4.56: CCA triple plot of carabid species, samples and environmental variables.

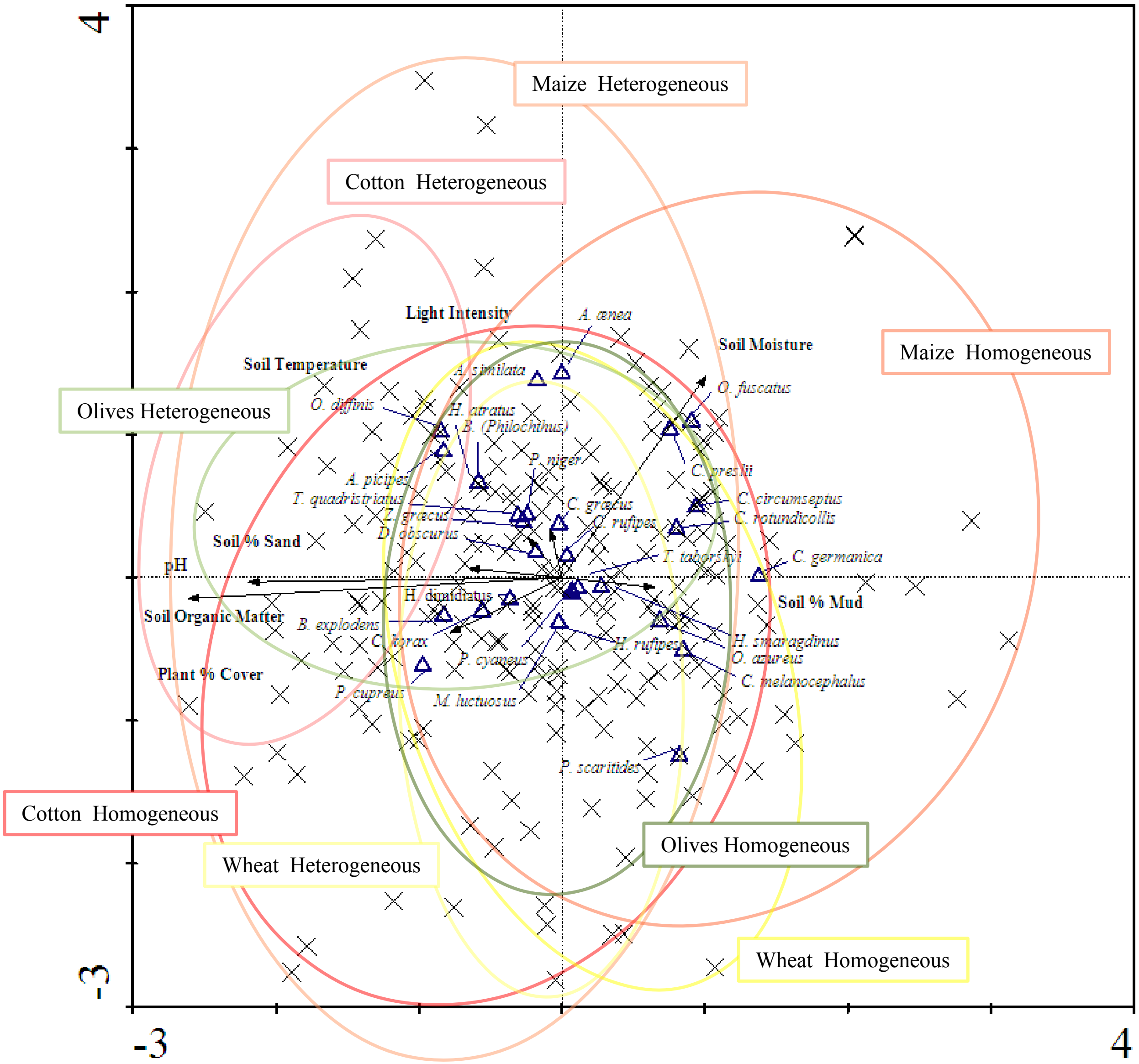


Figure 4.57: CCA triple plot of carabid species, samples and environmental variables, with crop types used as covariables.

4.2.14 The Influence of Landscape Metrics on Carabid Species Composition

Figure 4.58 shows a CCA biplot of carabid species, samples and landscape metrics. In this analysis the environmental variables and crop type variables from Figure 4.55 were used as covariables. This excluded their influence on the carabid species data. The landscape metrics were used as independent variables, so that their relative degrees of influence on the species data could be determined, without interference caused by the environmental and crop type variables.

To begin with, a preliminary CCA using a Monte Carlo permutation test was performed with 499 permutations, in order to determine which landscape metrics explained the greatest levels of variation in the species data. Of the total number of metrics calculated during the landscape analysis, many were found to be highly correlated with each other. For this reason, half of these metrics were removed from the analysis. Then after that, the most influential metrics were chosen to be included in the final analysis.

The eigenvalues for the first and second axes of this biplot were low, 0.291 and 0.116 respectively, suggesting that niche differentiation based on this plot might be difficult. Also the cumulative percentage variance of the species data for the first two axes were only 3.7 and 5.3 respectively. This meant that the first two axes explained only 9 % of the overall variation in the data. However, such a low levels were to be expected, as many landscape metrics were excluded from the analysis. Also by treating the crop type and environmental data as covariables, around 20 % of the variation in the carabid data was excluded. However, it should be remembered the the purpose of this analysis was to identify the most influential landscape metrics. These metrics actually explained a greater percentage of the variance than did the environmental variables alone.

Table 4.87 shows the five landscape metrics that were found to be most influential in determining patterns of species composition. They are ranked in order of their importance, with two pairs of metrics having equal ranks. The most influential landscape metric was the percentage of fallow and wasteland (variance explained = 0.27, p-value = 0.002). The next most influential metrics were landscape level aggregation and the percentage of fallow (variance explained = 0.26, p-value = 0.002). Then the next most influential metrics were interspersion / juxtaposition of fallow and the landscape level patch area distribution (variance explained = 0.25, p-value = 0.002). The suggested relationships between the landscape metrics and the data are also listed in Table 4.87.

Table 4.87: The five landscape metrics most influential when explaining variation in carabid species composition.

Most Influential Landscape Metrics Ranked in Order of Their Level of Influence		
Metric Rank	**Metric Type**	**Metric Name & Relationship to Data**
1	Class	% of Fallow & Wasteland Moderate-High = Many Species in High Abundance
2	Landscape	Aggregation Moderate = Many Species in High Abundance
2	Class	% of Fallow Moderate-High = Many Species in High Abundance
3	Class	Interspersion / Juxtaposition of Fallow Moderate-Low = Many Species in High Abundance
3	Landscape	Patch Area Distribution Moderate-Low = Many Species in High Abundance

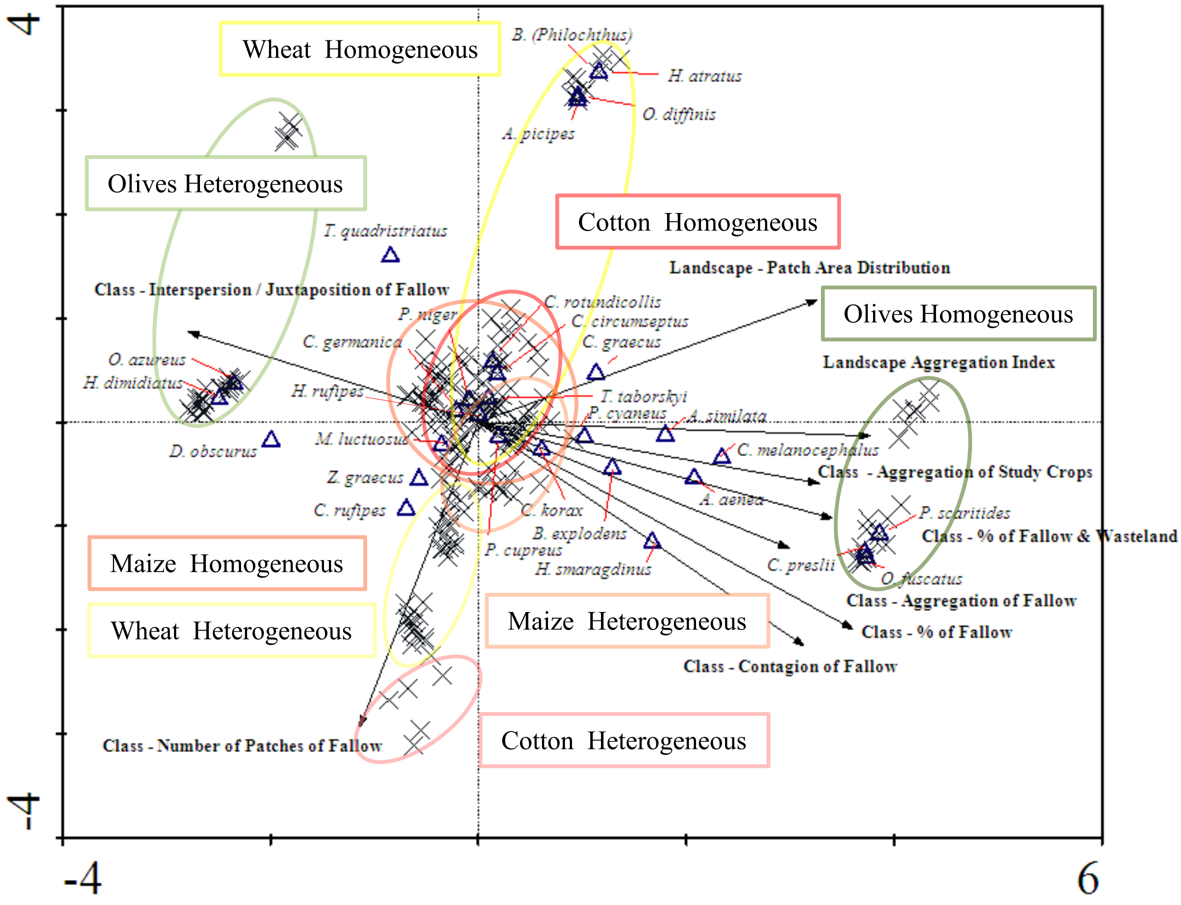


Figure 4.58: CCA triple plot of carabid species, samples and landscape metrics, with crop types and environmental variables used as covariables.

4.3 Plants

4.3.1 Plant Percentage Cover

Table 4.88 shows the mean percentage cover of plants per quadrat. The data presented were taken throughout the sampling period. A Mann-Whitney U test was used to determine the significance of the differences between heterogeneous and homogeneous sites. The U-statistics and the p-values calculated in the Mann-Whitney U tests are also shown.

These results do not show any clear influence of heterogeneity. For the maize and olive comparisons, higher levels of cover were seen in the sites found to have the highest heterogeneity. For the wheat and cotton comparisons; however, the reverse was true.

In all cases though, greater plant cover was seen in the smaller fields, so there appears to be some relationship between field size and weed cover. Possibly smaller fields were colonized more easily due to the shorter distances that seeds needed to travel from the field margins.

Table 4.88: The mean percentage cover of plants per quadrat.

Mean Percentage Cover of Plants					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**U-statistic**	**P-value**
1	Maize	46	37	1,078.5	0.2380
2	Olives	44	29	688.0	0.0001
3	Wheat	7	5	1,280.5	0.8337
3	Cotton	10	3	730.5	0.0003

4.3.2 The Number of Plant Morphospecies

Figure 4.59 shows the total number of plant morphospecies sampled in each study field throughout the sampling season. From these figures there does not appear to be a clear relationship between morphospecies numbers and heterogeneity. Higher species numbers were seen in the heterogeneous sites for the olive and wheat comparisons. For the maize comparison, more species were found in the homogeneous site, while for the cotton comparison there were equal numbers of plant morphospecies in both sites.

Table 4.89 shows the mean number of plant morphospecies per quadrat. The data presented are combined data, taken throughout the sampling period. No clear pattern was seen regarding the heterogeneity of the different study sites. Significantly higher numbers of plant morphospecies were seen in the heterogeneous sites for the olive and cotton comparisons. For the cotton comparison; however, the field with the highest number of morphospecies was actually the field that often had the lowest level of heterogeneity according to the landscape analysis.

Figure 4.60 shows the number of plant morphospecies sampled in each of the crop types. According to the results of the Kruskal-Wallis test (H = 214, p = <0.0001), there was a highly significant difference between crop types, with the olive fields having by far the greatest number of plant morphospecies.

Table 4.89: The mean number of plant morphospecies per quadrat.

Mean Number of Plant Morphospecies					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**U-statistic**	**P-value**
1	Maize	2.0	2.9	1,270.0	0.4483
2	Olives	4.2	2.7	567.0	<0.0001
3	Wheat	0.8	0.7	1,270.0	0.4483
3	Cotton	0.7	0.3	767.5	0.0005

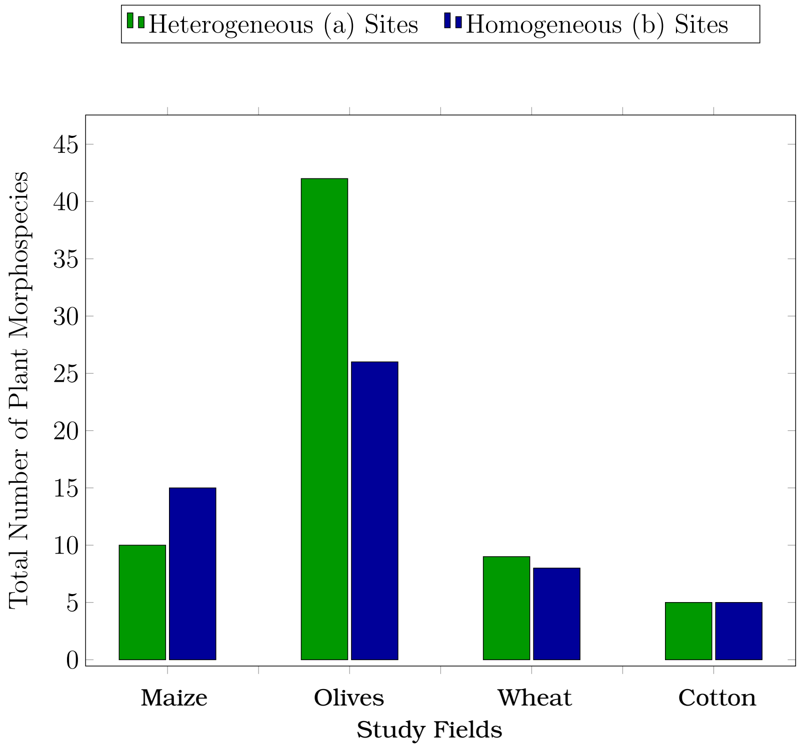


Figure 4.59: Total number of plant morphospecies in each study field.

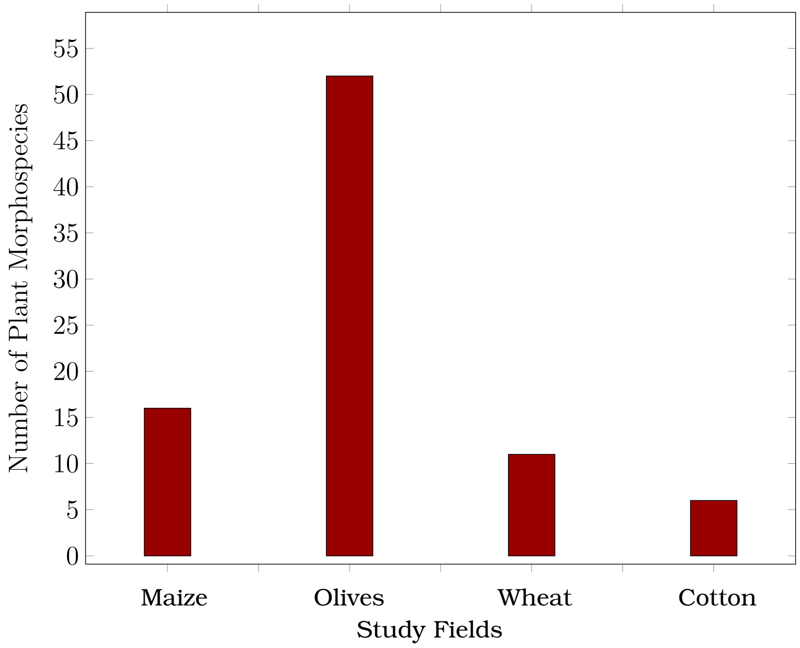


Figure 4.60: Total number of plant morphospecies in each crop type.

The dendrogram in Figure 4.61 was produced using cluster analysis of the summed plant morphospecies abundance data from 50 quadrats per field, taken throughout the sampling period. The supersamples were labelled with the crop type of the study field and the letter (a) for the heterogeneous site or the letter (b) for the homogeneous site. The analysis used the Bray-Curtis dissimilarity measure and the UPWGA algorithm. The Cophenetic correlation coefficient was 0.9318.

The data clustered clearly and consistently according to crop type. The maize, olive, wheat and cotton fields all formed separate groups. This shows clearly that crop type had a much greater influence on the plant communities of a field than did the level of landscape heterogeneity.

It also shows that the crop types wheat and cotton were the most similar in terms of their plant communities. The next most similar crop type was maize, while the olive fields were the most distinctive, probably due to their high diversity and richness levels.

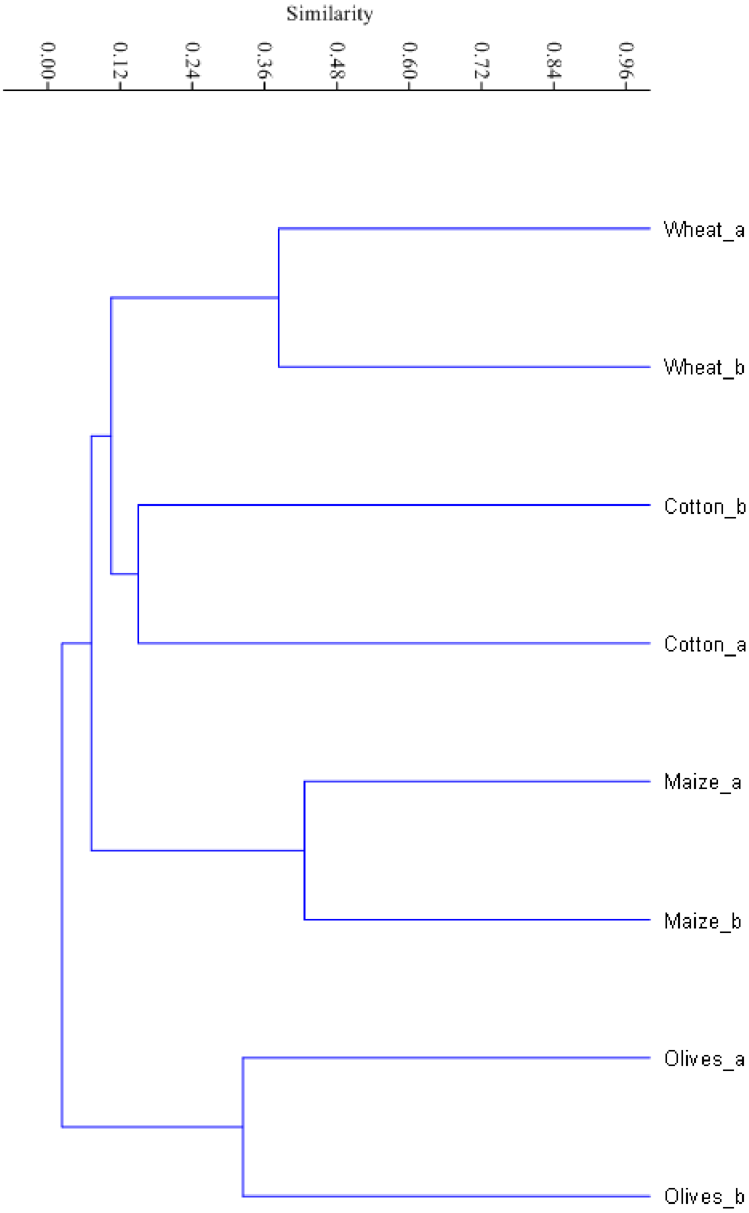


Figure 4.61: Cluster analysis of plant morphospecies abundance data. Data taken from entire sampling period.

4.3.3 The Richness of Plant Morphospecies

Table 4.90 shows the mean richness of plant morphospecies calculated using the ACE estimator. This was the most appropriate richness estimator for these data. It also produced very reliable estimates, as the standard deviation for each estimate was 0. For the olive, wheat and cotton comparisons, richness was higher in sites where the landscape metrics in Table 4.42 indicated higher landscape heterogeneity. For the maize comparison; however, the reverse was true, although this was probably due to the high soil moisture levels seen in the maize field in the homogeneous site.

Table 4.90: The mean richness of plant morphospecies calculated using the ACE estimator.

Mean Richness of Plant Morphospecies					
ACE Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	10	0	16	0
2	Olives	44	0	26	0
3	Wheat	10	0	12	0
3	Cotton	5	0	6	0

Table 4.91 shows the mean richness of plant morphospecies estimated using the ICE estimator. The standard deviations were also low for this estimate, indicating that it too was reliable. The results of this estimate showed the same pattern as for the ACE estimator. Plant richness was estimated to be higher in sites of high heterogeneity, except in the maize comparison, where moisture levels were highest in the homogeneous site.

Table 4.91: The mean richness of plant morphospecies calculated using the ICE estimator.

Mean Richness of Plant Morphospecies					
ICE Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	12	0.01	17	0.00
2	Olives	45	0.00	31	0.00
3	Wheat	10	0.00	11	0.01
3	Cotton	5	0.00	6	0.00

Table 4.92 shows the mean richness of plant morphospecies calculated using the Jackknife 1 estimator. The standard deviations for this estimator are slightly higher, but still low enough to be able to distinguish differences between heterogeneous and homogeneous sites. For this estimator, the heterogeneous and homogeneous sites 3 were estimated to have equal plant richness, something which was not seen using any of the previous estimators.

Table 4.92: The mean richness of plant morphospecies calculated using the Jackknife 1 estimator.

Mean Richness of Plant Morphospecies					
Jackknife 1 Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	13	1.66	18	1.66
2	Olives	49	2.80	33	3.13
3	Wheat	11	1.37	11	1.66
3	Cotton	6	0.98	6	0.98

Table 4.93 shows the mean richness of plant morphospecies calculated using the Jackknife 2 estimator. The standard deviation for each estimate is also shown in Table 4.93. These were zero for each estimate, meaning that the Jackknife 2 was more reliable than the Jackknife 1. In this case, the pattern seen regarding heterogeneous and homogeneous sites was similar to that seem for the ACE estimator, which is probably the most reliable estimator.

Table 4.93: The mean richness of plant morphospecies calculated using the Jackknife 2 estimator.

Mean Richness of Plant Morphospecies					
Jackknife 2 Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	16	0	20	0
2	Olives	47	0	36	0
3	Wheat	12	0	13	0
3	Cotton	6	0	5	0

Table 4.94 shows the mean richness of plant morphospecies calculated using the Bootstrap estimator. The standard deviations for each estimate are also shown. As these too were all 0, this estimator can also be considered reliable. However, the results of these estimates do not show any clear pattern regarding the heterogeneity levels in each site.

Table 4.94: The mean richness of plant morphospecies calculated using the Bootstrap estimator.

Mean Richness of Plant Morphospecies					
Bootstrap Estimator					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Standard Deviation**	**Homogeneous Sites (b)**	**Standard Deviation**
1	Maize	11	0	16	0
2	Olives	46	0	29	0
3	Wheat	12	0	9	0
3	Cotton	6	0	6	0

4.3.4 The Diversity and Evenness of Plant Morphospecies

Figures 4.63 to 4.66 show the diversity and evenness of plant morphospecies in each of the study sites, calculated using the Simpson's index (*1-D*), Shannon's index (*H'*), Margalef's index (D_{Mg}) and Shannon's evenness index (*F'*).

For all of the indices, the fields in heterogeneous and homogeneous sites showed the same pattern in relation to one another. This shows that the indices were reliable. However, there was no clear relationship between diversity and heterogeneity. For the maize and cotton study fields, all indices showed that diversity was higher in the homogeneous sites. For the olive and wheat fields; however, diversity was always higher in the heterogeneous sites.

There was a significant negative correlation between plant diversity and the number of patches of cotton in the study site (r = -0.733, d.f. = 6, p = 0.039). See figure 4.62. This was probably because cotton cultivation requires the use of a lot of fertilizers and pesticides, which are known to decrease wild plant diversity (De Snoo *et al.*, 1999 [45]; Kleijn *et al.*, 2009 [99]).

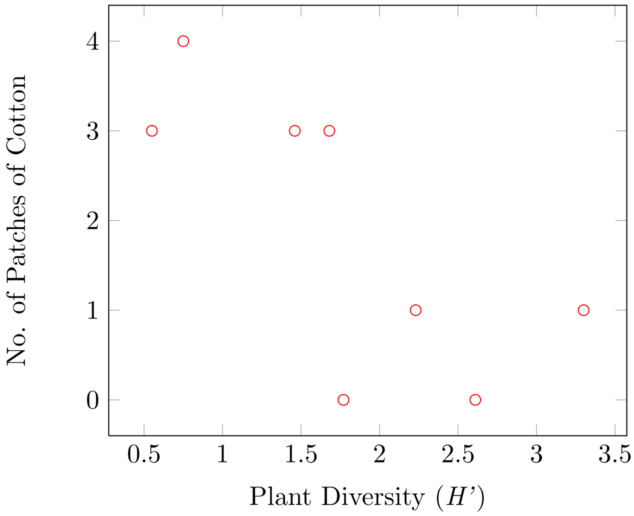


Figure 4.62: Correlation between plant morphospecies diversity and the number of patches of cotton.

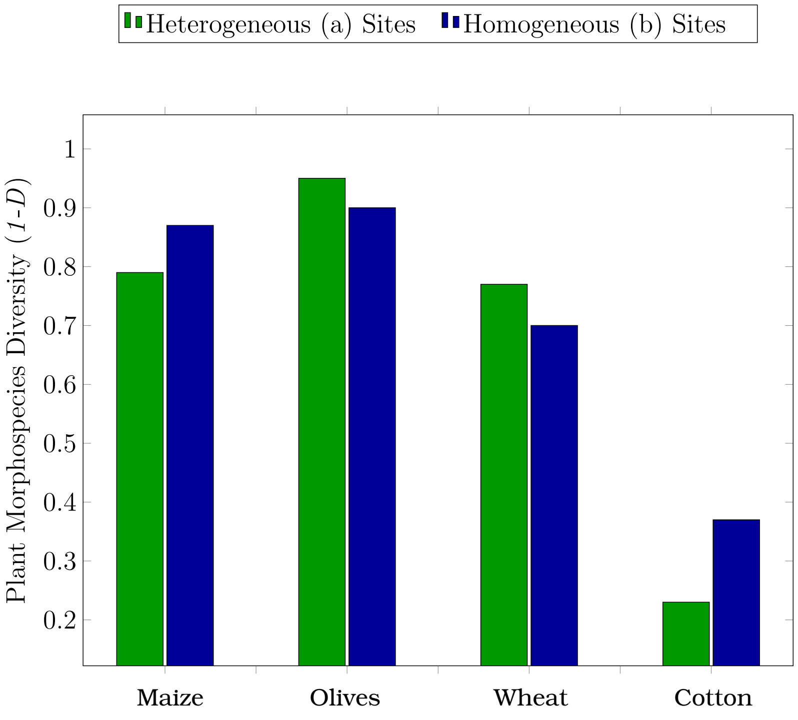


Figure 4.63: Diversity of plant morphospecies calculated using Simpson's diversity index.

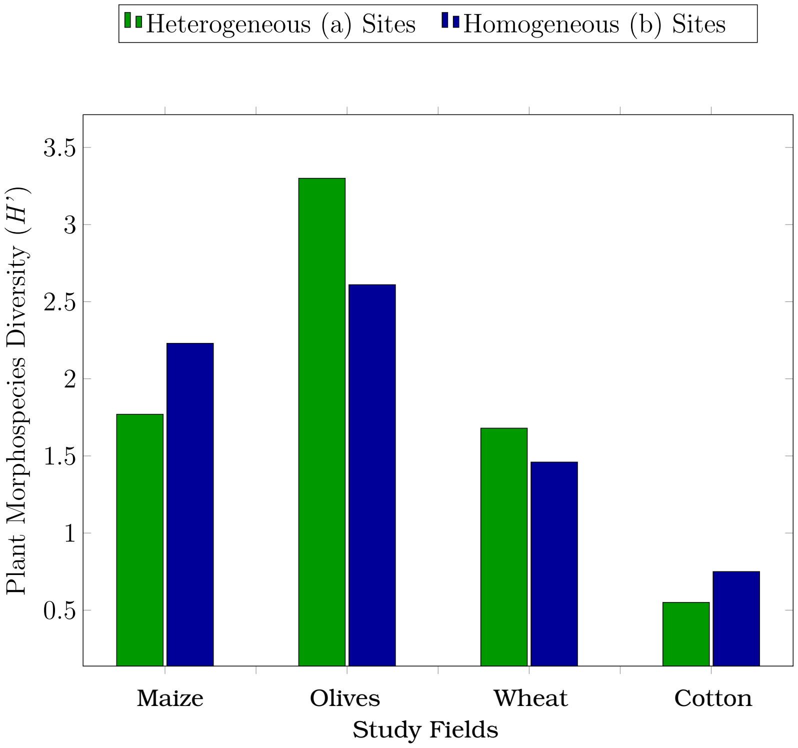


Figure 4.64: Diversity of plant morphospecies calculated using Shannon's diversity Index.

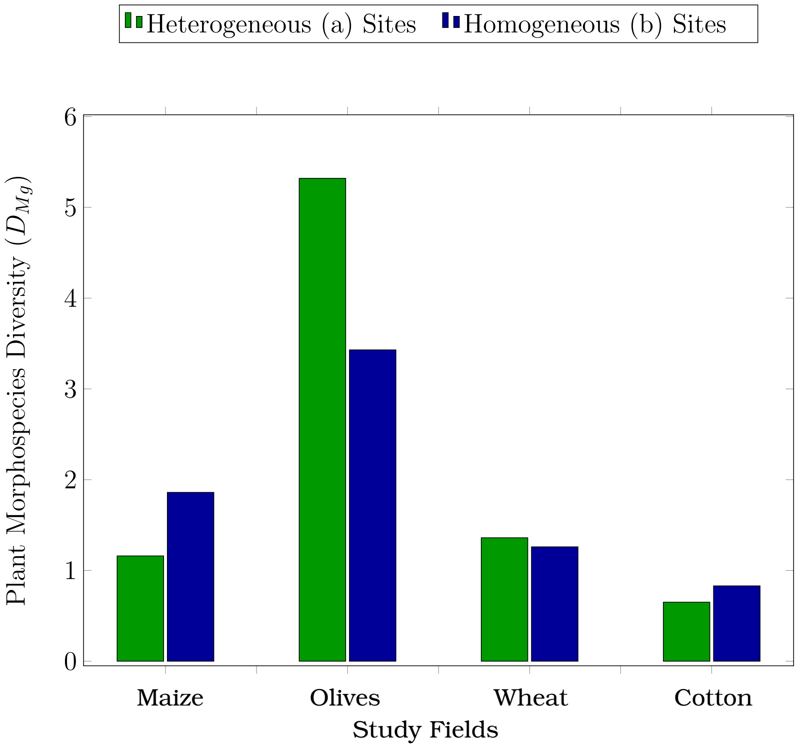


Figure 4.65: Diversity of plant morphospecies calculated using Margalef's Diversity Index.

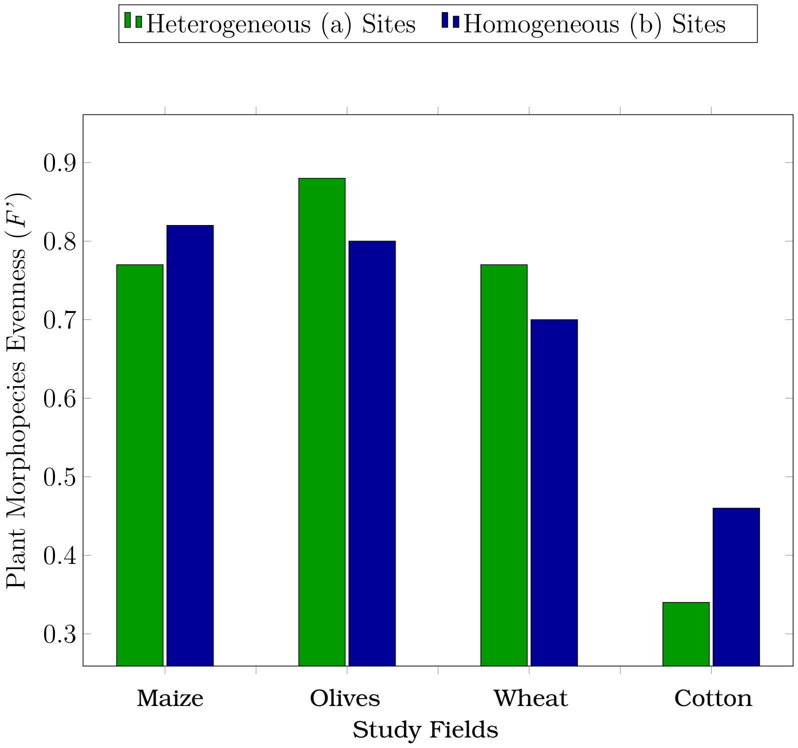


Figure 4.66: Evenness of plant morphospecies calculated using Shannon's evenness measure.

Figures 4.67 to 4.70 show the diversity and evenness of plant morphospecies in each of the crop types, calculated using the Simpson's index (*1-D*), Shannon's index (*H'*), Margalef's index (D_{Mg}) and Shannon's evenness index (*F'*). All indices showed that the olive study fields had the greatest diversity, followed by the maize study fields, the wheat and then the cotton. A similar pattern was seen for evenness, except that the wheat fields had higher evenness than the maize fields.

The olive fields would have had the greatest plant diversity because, of all the different crop types, the soil in these fields was the least disturbed. These fields were never ploughed, sprayed, or even irrigated, so the wild plant communities here were fairly well established.

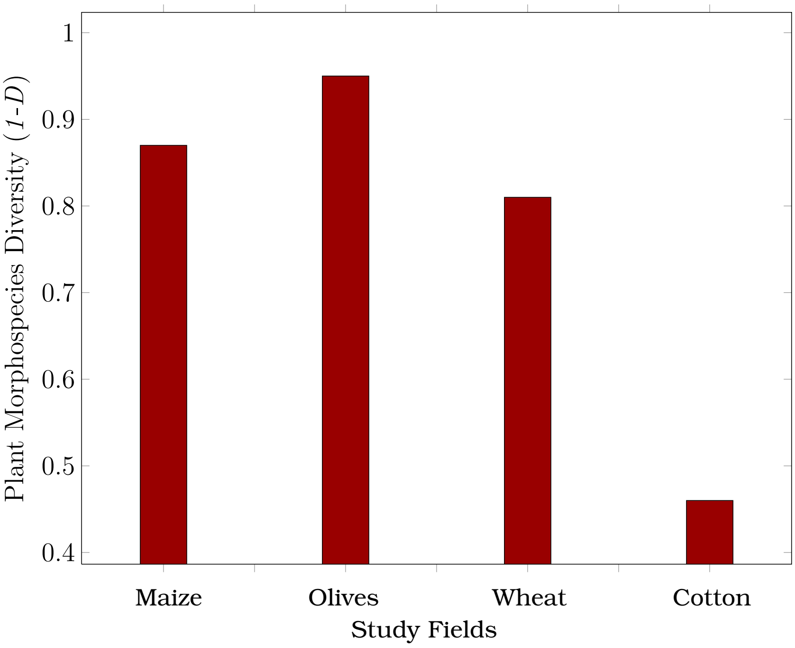


Figure 4.67: Diversity of plant morphospecies calculated using Simpson's diversity index.

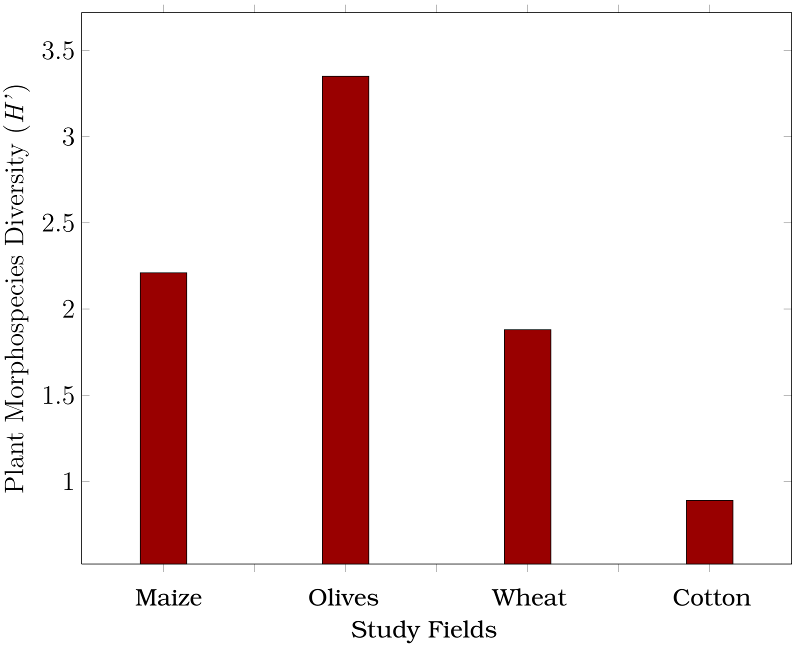


Figure 4.68: Diversity of plant morphospecies calculated using Shannon's diversity index.

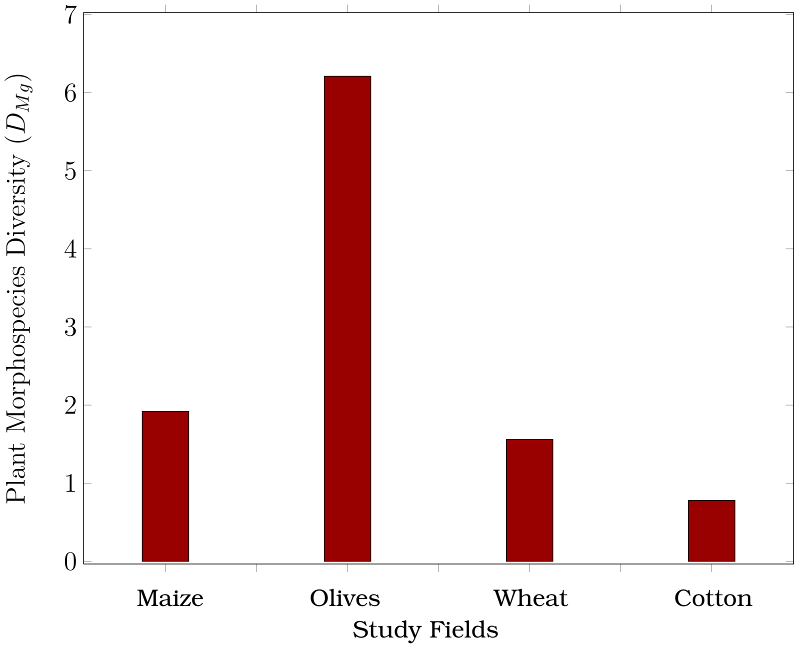


Figure 4.69: Diversity of plant morphospecies calculated using Margalef's Diversity Index.

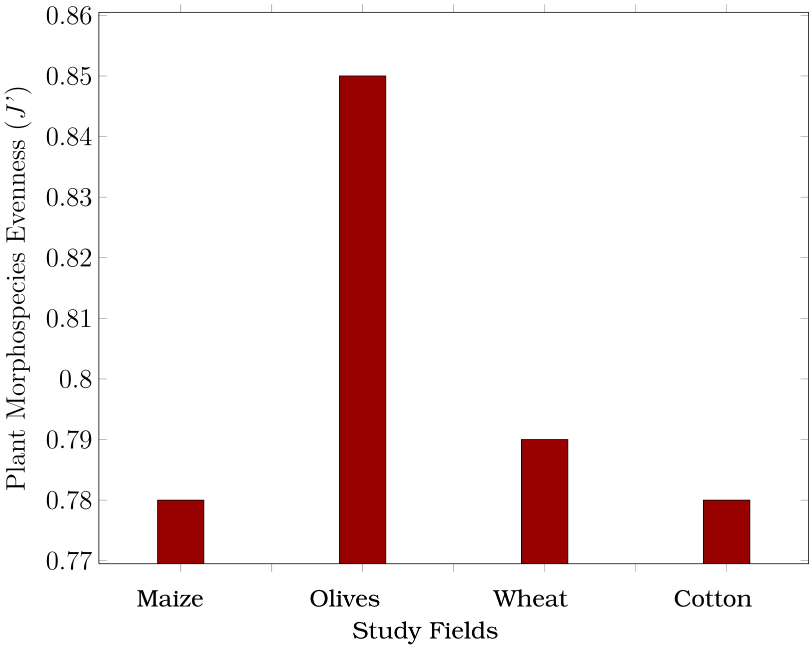


Figure 4.70: Evenness of plant morphospecies calculated using Shannon's evenness measure.

4.4 Environmental Data

4.4.1 Soil Temperature

Table 4.95 shows the mean soil temperature per sampling point. The data presented are combined data, taken throughout the sampling period. A Mann-Whitney U test was used to determine the significance of the differences between heterogeneous and homogeneous sites. The U-statistics and the p-values calculated in the Mann-Whitney U tests are also provided. In all comparisons, soil temperature was higher in the heterogeneous sites than in the homogeneous site, although no significant differences were seen between sites.

Table 4.95: The mean soil temperature per sampling point.

Mean Soil Temperature (°C)					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**U-statistic**	**P-value**
1	Maize	24.0	23.8	1,233.0	0.9124
2	Olives	29.5	28.2	1,161.0	0.5419
3	Wheat	30.4	29.4	1,073.5	0.2263
3	Cotton	28.1	26.3	1,012.0	0.1010

4.4.2 Light Intensity at Ground Level

Table 4.96 shows the mean light intensity per sampling point. The data presented are combined data, taken throughout the sampling period. There was no consistent pattern to be seen regarding heterogeneous and homogeneous sites. No significant differences between heterogeneous and homogeneous sites were seen for these data.

Table 4.96: The mean light intensity per sampling point.

Mean Light Intensity at Ground Level (ph)					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**U-statistic**	**P-value**
1	Maize	4.19	4.53	1,434.5	0.2041
2	Olives	4.86	4.80	1,115.5	0.3576
3	Wheat	4.44	3.83	1,016.5	0.1074
3	Cotton	4.31	4.46	1,196.0	0.7114

4.4.3 Soil Moisture

Table 4.97 shows the mean soil moisture per sampling point, using data taken throughout the sampling period. Moisture levels were higher in homogeneous sites than in heterogeneous sites. A significant difference between the heterogeneous and homogeneous site was seen for the maize comparison. This must have been due to differences in irrigation levels between the two fields.

Table 4.97: The mean soil moisture per sampling point.

Mean Soil Moisture (θ)					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**U-statistic**	**P-value**
1	Maize	0.42	0.59	1,645.0	0.0065
2	Olives	0.12	0.12	1,23.5	0.9840
3	Wheat	0.12	0.18	1,355.5	0.4715
3	Cotton	0.39	0.39	1,361.5	0.4413

4.4.4 Soil pH

Table 4.98 shows the mean soil pH per sampling point. The data presented are combined data, taken throughout the sampling period. There was no consistent pattern to be seen regarding the pH of heterogeneous and homogeneous sites. However, there were significantly higher pH levels in the heterogeneous sites for the maize and cotton comparisons. The difference between the two maize fields was the largest. This is unsurprising, as these fields had very different soil moisture levels, something that would have influenced the soil pH. The highest pH levels were seen in the driest fields, the lowest pH levels in the dampest fields.

Table 4.98: The mean soil pH per sampling point.

Mean Soil pH					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**U-statistic**	**P-value**
1	Maize	7.71	7.44	649.5	<0.0001
2	Olives	7.73	7.78	1,430.0	0.2150
3	Wheat	7.79	7.79	1,271.0	0.8887
3	Cotton	7.73	7.60	325.0	0.0034

4.4.5 Soil Organic Matter

Table 4.99 shows the mean soil organic matter per sampling point. A t-test was used to determine the significance of the differences between heterogeneous and homogeneous sites. A t-test was used for these comparisons only, as these were the only data that conformed to the assumptions of parametric statistics. Higher organic matter levels were seen in the heterogeneous sites, for all comparisons. The organic matter levels were significantly higher in these sites for the maize and cotton comparisons. It is likely that the small-scale farmers in the sites that were initially chosen as heterogeneous removed less weeds and crop residue than their more large-scale counterparts.

Table 4.99: The mean soil organic matter per sampling point.

Mean Organic Matter Content - LOI ($g\ kg^{-1}$)					
Study Site	**Study Field**	**Heterogeneous Sites (a)**	**Homogeneous Sites (b)**	**t-statistic**	**P-value**
1	Maize	64	36	11.5	0.0010
2	Olives	61	39	1.7	0.1850
3	Wheat	64	44	1.4	0.2940
3	Cotton	62	46	3.5	0.0410

4.4.6 Soil Type

Figures 4.71 and 4.72 show the soil types of ten soil samples taken from each of the maize study fields. Some samples from the homogeneous site were slightly muddier than those from the heterogeneous site, although the difference between fields was not great.

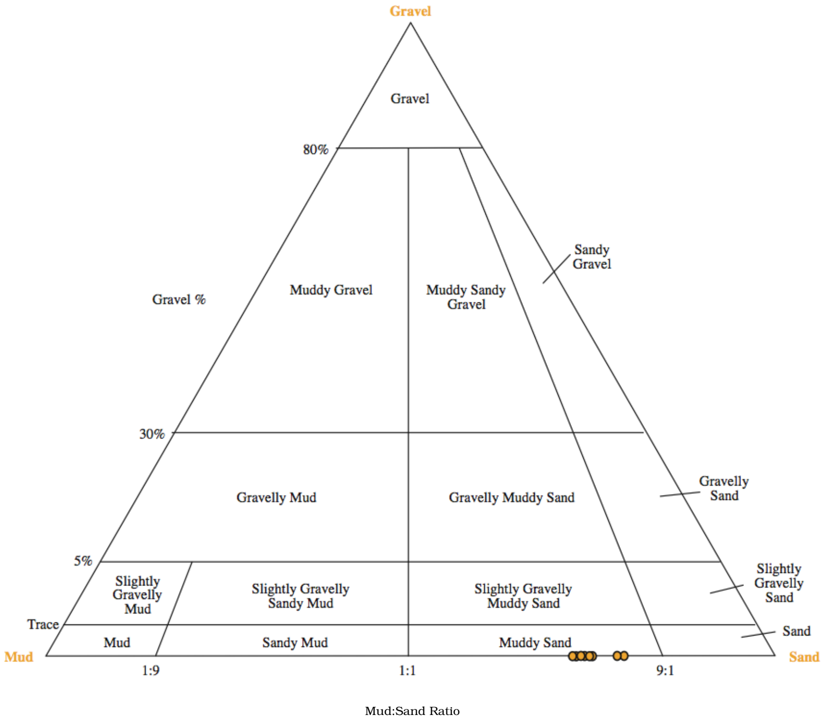


Figure 4.71: Soil type in the maize study field in heterogeneous site 1a.

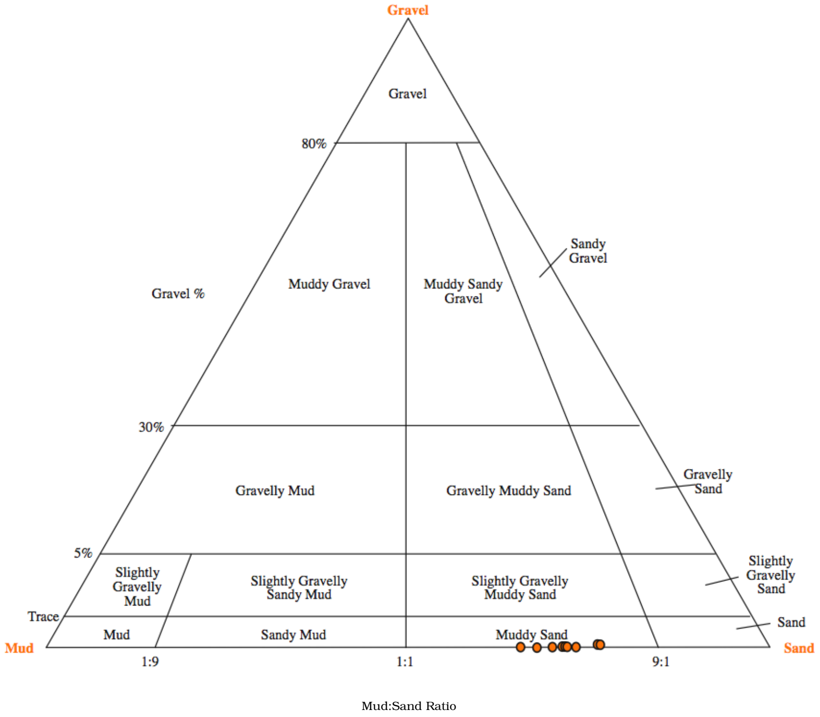


Figure 4.72: Soil type in the maize study field in homogeneous site 1b.

Figures 4.73 and 4.74 show the soil types of ten soil samples taken from each of the olive study fields. Some samples from the heterogeneous site were sandier than those from the homogeneous site.

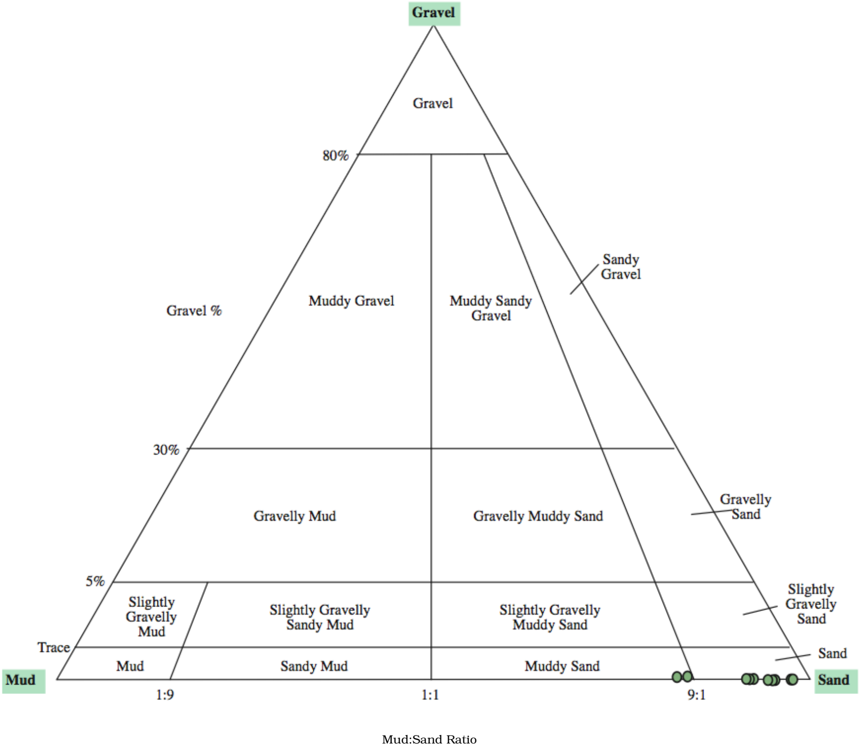


Figure 4.73: Soil type in the olive study field in heterogeneous site 2a.

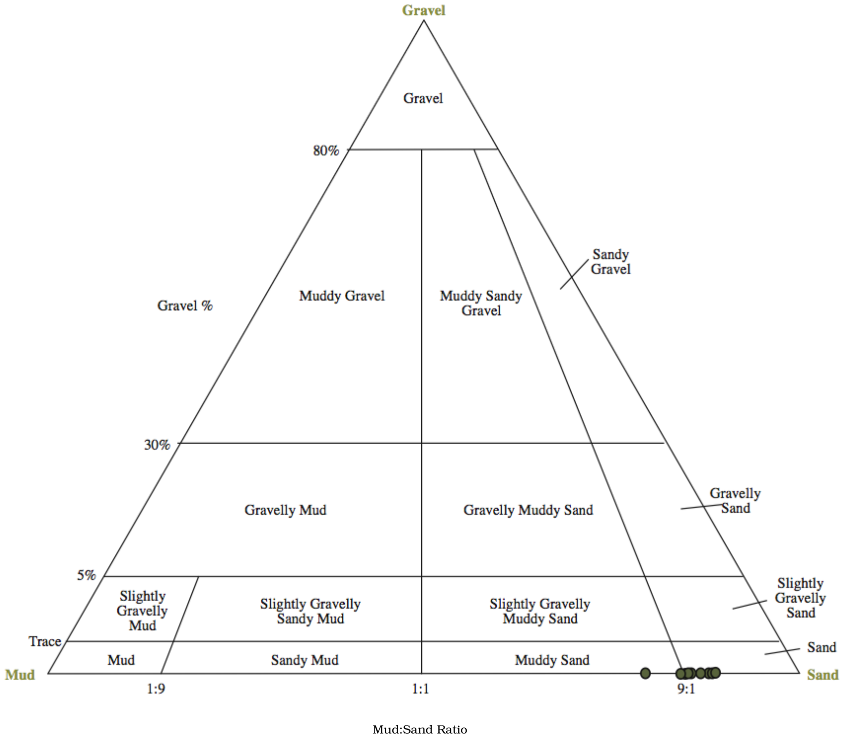


Figure 4.74: Soil type in the olive study field in homogeneous site 2b.

Figures 4.75 and 4.76 show the soil types of ten soil samples taken from each of the wheat study fields. Some samples from the homogeneous site were slightly sandier than those from the heterogeneous site.

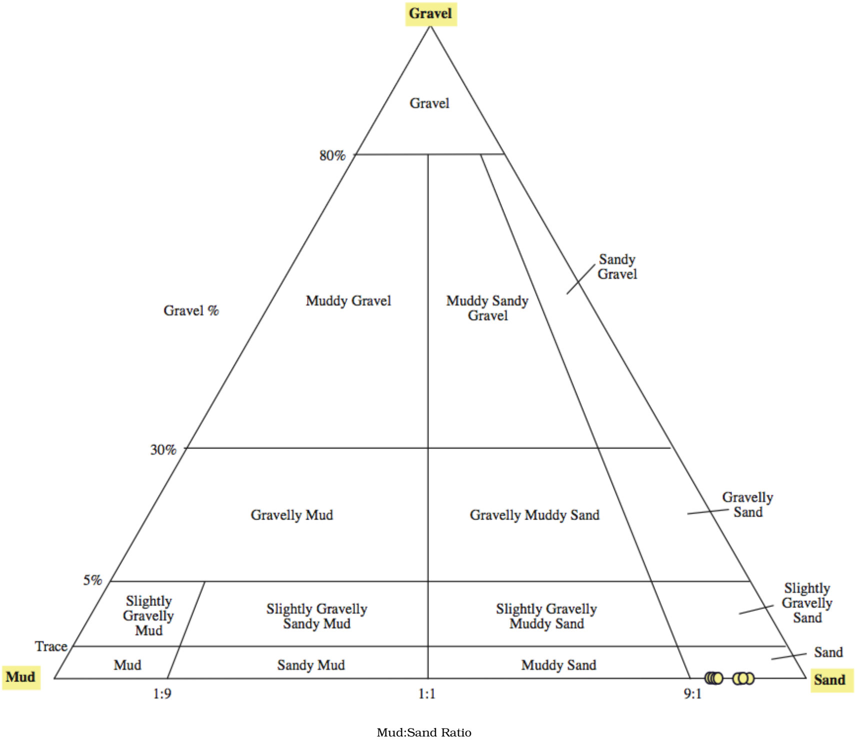


Figure 4.75: Soil type in the wheat study field in heterogeneous site 3a.

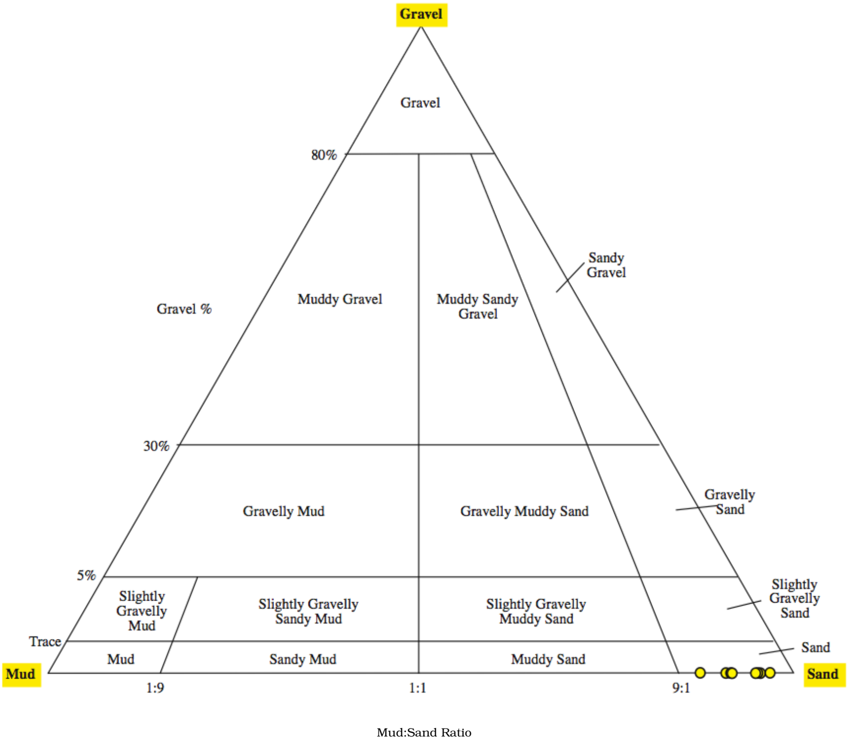


Figure 4.76: Soil type in the wheat study field in homogeneous site 3bi.

Figures 4.77 and 4.78 show the soil types of ten soil samples taken from each of the cotton study fields. Some samples from the homogeneous site were slightly muddier than those from the heterogeneous site. Overall though, while there were difference in soil type between crop types, there did not appear to be much difference between heterogeneous and homogeneous sites.

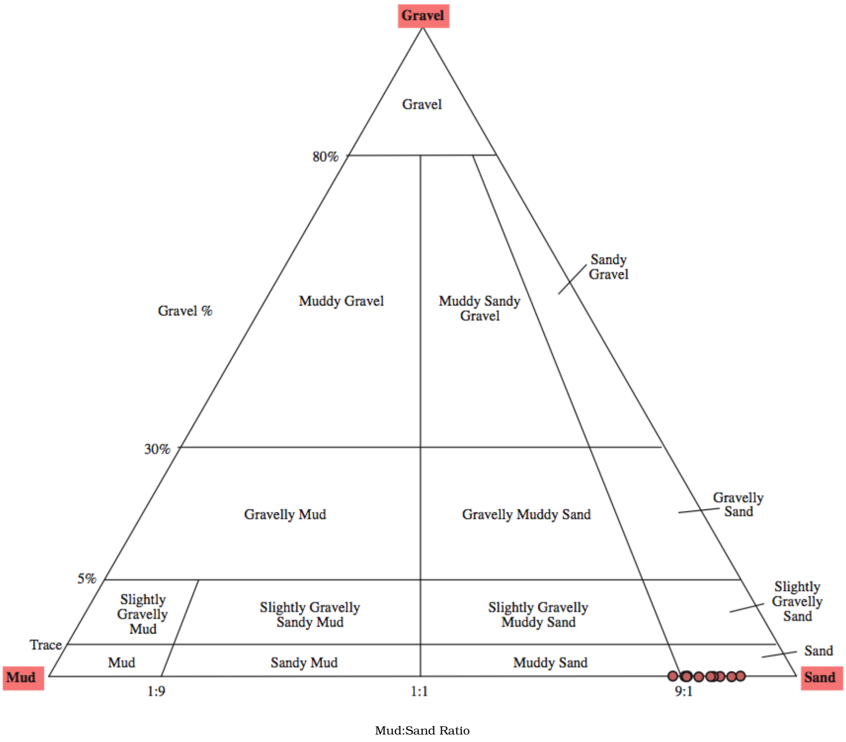


Figure 4.77: Soil type in the cotton study field in heterogeneous site 3a.

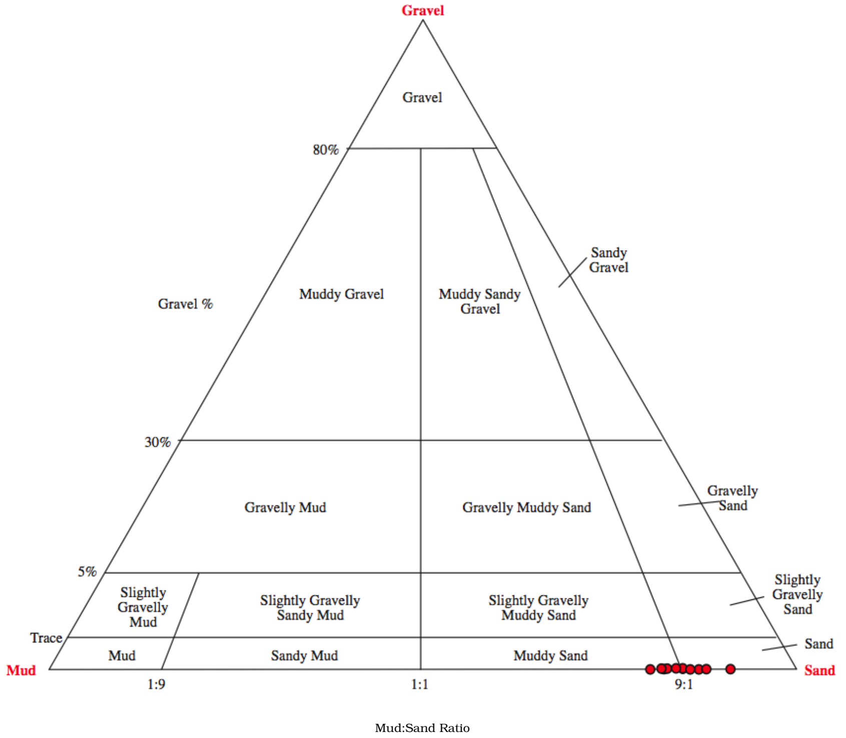


Figure 4.78: Soil type in the cotton study field in homogeneous site 3bii.

Chapter 5

Conclusions

5.1 The Influence of Heterogeneity

The results obtained in this study show that the different aspects of heterogeneity do exert some influence on the invertebrate communities within individual fields. Their influence; however, appeared to be secondary to other influences, particularly those of crop type.

From the landscape analysis results, it can be seen that the distinction between heterogeneous and homogeneous sites 3, was less clear than for sites 1 and 2. This means that for many metrics, the heterogeneity classifications of sites 3a and 3b could have been reversed. If this is taken into account and the metrics listed in Table 4.42 are recognized as important constituents of heterogeneity, then it may be concluded that where heterogeneity is high, so is the number of higher invertebrate taxa, as well as the relative abundance of certain carabid species, Coleoptera families and higher invertebrate taxa.

Additionally, a significant, positive correlation was found between the percentage of non-cropped, non-forested habitat and the diversity of carabid species. Then a slightly weaker, positive correlation was seen between the percentage of tree crops in a site and carabid diversity. These findings demonstrate the particular importance of these types of habitat for the Carabidae.

A positive influence of heterogeneity was also found by authors such as Benton *et al.*, (2003 [11]), Tscharntke *et al.*, (2005 [177]), Ostman *et al.*, (2001 [130]), Kromp, (1999 [102]), Sunderland & Samu, (2000 [164]) and Weibull *et al.*, (2000 [187]).

However, despite the presence of discernible patterns regarding heterogeneity, in many of the comparisons made in this study, differences between heterogeneous and homogeneous sites were not found to be statistically significant. This may have been due to the fact that the relationship between heterogeneity and biodiversity is believed to be nonlinear (Fahrig *et al.*, 2011 [64]), suggesting that sampling may not have detected differences in the invertebrate communities that were due to heterogeneity alone.

Fahrig *et al.*, (2011 [64]) recommend that when examining the influence of landscape heterogeneity, a large range of study sites should be chosen that form a gradient in terms of their heterogeneity. In this study though, a paired design was used and different crop types were sampled in the different site pairs. They also recommend sampling a much larger number of sites (between 40 and 60). Here though, only six sites were sampled, so replication occurred within the sampled fields, rather than at the landscape level. While this produced data at a local level, concerning the sampled fields themselves, it would not have provided information at the site level. So it is likely, that if a larger number of sites had been sampled, the independent influence of landscape heterogeneity would have been seen more clearly.

A related issue may have been that too few land use types were sampled in this study. One particular way in which heterogeneity is thought to enhance biodiversity is through different species being associated with different land use types, at different times in their lives (Dunning *et al.*, 1992 [53]; Pollard, 1968 [140]; Sotherton, 1985 [161]; Desender & Turin, 1989 [44]). This suggests that if more land use types had been sampled, a more consistent pattern may have been seen in the results of this study.

Additionally, as heterogeneous and homogeneous sites were closely matched in order to control for other factors apart from their heterogeneity, this may have meant that the chosen sites did not differ greatly enough in all aspects of their heterogeneity. This can be seen particularly in study site 3, whose heterogeneous and homogeneous sites turned out to be similar regarding some of the landscape metrics. For example, although land use diversity was high and land use similarity was low in all of the heterogeneous sites, land use richness did not always follow this pattern. For the wheat comparison, land use richness was slightly higher in the homogeneous site, while for the cotton comparison land use richness was the same in both sites. This suggests that heterogeneous and homogeneous sites may not have been different enough to greatly influence the invertebrates present within them. Having said that though, highly homogeneous farmland was not present in the Spercheios Valley, so comparing widely different heterogeneity levels would have meant comparing sites from different regions.

It is also possible, as mentioned by Fahrig *et al.*, (2011 [64]), that while appearing to be heterogeneous in satellite photographs and in the landscape analysis, heterogeneous sites in this study were not in fact functionally heterogeneous from the perspective of the invertebrates. The different land use types in the heterogeneous sites may have actually provided similar resources for invertebrates. Woodland and tree crops, such as olives, walnuts, almonds and plums, for example, may have formed large areas of functionally similar land use types, due to their low disturbance levels and their rich wild plant communities. So a site like heterogeneous site 3a may have actually been less heterogeneous than it appeared, both in satellite pictures and in the landscape analysis.

Despite these issue however, results such as these, which suggest that heterogeneity is beneficial, are nevertheless important. This is particularly true, as small-scale farming, with its high heterogeneity levels, is usually found in areas that are in danger of being abandoned due to low productivity and high production costs. It is important then, that despite these economic pressures, such extensively farmed areas are maintained.

5.1.1 The Influence of Crop Type

Crop type was found to be the most influential variable of all. This was probably due to the specific microclimate created by each crop, the differences in husbandry each crop required and the different habitats each crop provided for wild plants and invertebrates.

The wheat study fields had the highest invertebrate abundance levels, probably because the stubble was left intact for a long period over the summer and autumn. Also though, these fields were not irrigated and had no pesticide or herbicide input. The olive study fields had the highest diversity and richness levels for both the carabid and plant data sets. This was probably because these fields were organically farmed, not irrigated, and were left relatively undisturbed for most of the year, allowing a natural, wild plant community to develop. Olive cultivations would also have resembled the natural forest habitat preferred by many of the carabid species trapped in this study.

Plant percentage cover was highest in the maize study fields. This was probably due to the application of fertilizers and the high irrigation levels required by this crop type, as well as to the method of irrigation, which used pipes and flooding. The cotton fields, which were also fertilized and regularly irrigated, had much poorer plant communities, possibly because a hose reel irrigator was regularly wheeled between the rows.

5.1.2 The Most Important Aspects of Heterogeneity

An important point raised in this study is that it is not easy to predict which areas of farmland have the highest heterogeneity, simply by observing them from the ground, or by viewing them using satellite pictures. Heterogeneity comprises many different factors, most of which have complicated and variable influences on carabid communities.

The following paragraphs discuss the aspects of heterogeneity that were found to have the greatest influence on carabid species composition, once the more apparent influences of crop type and environmental variables were excluded using CCA. Determining the exact natures of these influences was beyond the scope of this study, but the most likely possibilities are discussed below.

5.1.2.1 Wasteland and Fallow

Metrics concerning wasteland and fallow were found to have the greatest influence on carabid species composition and carabid diversity. The summed percentage of fallow and wasteland was ranked first in the list of most influential landscape metrics. Then the percentage of fallow on its own was ranked joint second, while the interspersion / juxtaposition of fallow was ranked joint third. There was also found to be a significant positive correlation between carabid diversity and the most influential metric, the percentage of fallow and wasteland.

These metrics were found to be more important than those concerning non-cropped habitat, which comprised wasteland, fallow, woodland, hedgerows and field margin habitat altogether. They were also more important than those concerning only woodland and hedgerows. This implies that there was something special about wasteland and fallow, rather than about non-cropped habitat in general. This makes sense, as the reduction of non-forested, semi-natural habitat has long been known to cause reductions in carabid diversity (Desender & Turin, 1989 [44]), while set-aside land has been seen to provide benefits for many groups of invertebrates (Desender & Bosmans 1998 [43]; Huusela-Veistola & Hyvanen 2006 [82]; Moreby & Aebischer 1992 [126]).

In this study, fields that had been left uncultivated for one or two years were classed as fallow. Fields that had not been cultivated for longer periods and were identified by the growth of coarser, woody plants were classed as wasteland.

Moderate to high percentages of wasteland and fallow were found to be most beneficial for the Carabidae. At these levels, more carabid species were trapped in greater numbers. It also appears that fairly low levels of fallow interspersion / juxtaposition were beneficial to the Carabidae. Interspersion / juxtaposition was negatively correlated with contagion and connectivity. So sites with low wasteland and fallow interspersion / juxtaposition also had high levels of contagion and connectivity.

High contagion and connectivity levels, for this type of habitat, would have created dispersal opportunities within the landscape, as discussed by Burel (1996 [17]), Petit & Usher (1998 [138]) and den Boer (1990b [41]), especially when the wasteland and fallow formed nodes, creating larger interconnected areas (Holland & Luff, 2000 [90]). Such habitat would have acted as arteries, penetrating cultivated land, aiding dispersal in and out of it and providing refuges during times of disturbance. These areas are probably also used as overwintering sites by the Carabidae and in addition to this, increase their foraging opportunities. See discussion by Frank (1997 [76]) and Lys & Nentwig (1994 [118]).

The fact that wasteland and fallow were found to be particularly influential is important. It suggests that the decision of the CAP, in 2008, to abandon set-aside schemes may have been detrimental to farmland carabids. In the most recent CAP reforms; however, measures have been brought in that could rectify this. For example, as part of the new Greening Measures, farmers will have to turn 5 % of their land into permanent grassland. Also some farmers will be required to set up Ecological Focus Areas, which may include some areas of fallow (DEFRA, 2014 [39]; Pe'er *et al.,* 2014). The results found here, indicating the importance of fallow and wasteland, suggest that the new measures of the CAP may provide benefits for the Carabidae, if they are implemented wildly enough.

5.1.2.2 Aggregation

Aggregation at the landscape level was also found to be an important factor regarding carabid species composition. This metric was ranked joint second in the list of most influential landscape metrics. Many carabid species were associated with moderate levels of this metric. This suggests that having the same land use type covering very large areas has a negative impact on carabid communities.

This implies that, where possible, farmers should avoid planting the same crop in areas of over about 7 ha. The reasons for this relationship are probably similar to those discussed below, regarding field size. Having many fields of the same crop type in an area would appear to be just as detrimental as having just one large field, although there must be benefits created by keeping hedgerows and field margins intact.

High levels of aggregation also increase the overall similarity of the landscape. In their review paper, Benton *et al.* (2003 [11]) identified the reduction in the number of land use types as a major factor in the loss of heterogeneity and thence biodiversity from agricultural landscapes. So it seems that increasing the number of different crop types in farmland would be a good way of benefitting carabid communities. However, farming a wide range of crop types in a given area is not very cost effective, so any biodiversity benefits would come with an economic cost to the farmer.

This is especially important when the policies of the CAP are considered, where market forces drive farmers to produce the most competitive products, or those most easy to cultivate in particular areas. A good example involves EU sugar production. Until 2005, Greece was producing nearly two hundred and sixty thousand tons of sugar. Then cultivation in the country was cut by the CAP, so that its production could be concentrated in the areas of Europe where both farming and processing could be done on a larger scale. This meant that two sugar processing factories in Greece were closed, while the efficiency of production in Germany, France, Poland and the UK was increased (EBZ, 2011 [55]). Such a situation must have led to increases in crop similarity in all the areas affected by the change.

The CAP's new 3-Crop Rule, which will be implemented in 2015 on farms over 30 ha (DEFRA, 2014 [39]) may prevent further increases in crop similarity on the largest farms. However, as 3 crops per 30 ha is lower than the current EU average for crop diversity, it is likely that this measure will not go far enough (Pe'er *et al.,* 2014 [135]).

5.1.2.3 Field or Patch Size

The patch area distribution, or the average field size in each area was also found to be an important factor influencing carabid species composition. This metric was ranked joint third in the list of most influential metrics. Where field sizes were moderate to small, around half a hectare, many carabid species were recorded in high numbers.

So it seems that small that moderate field sizes are generally beneficial to Carabidae communities. This was something identified by Kromp in 1999 ([102]). Smaller fields, meant that the distances carabids needed to travel after periods of disturbance were far shorter, so recolonization could happen more rapidly and easily.

Also Holland *et al.*, (1999 [91]) found that Carabidae usually lived within 60 m of field margins. It follows therefore, that landscapes with smaller fields, where proportionally more land is within 60 m of a field margin would be very suitable for carabids.

Again though, this is a situation that is not cost effective for farmers, as smaller, more fragmented fields are much more difficult and time consuming to cultivate. Economies of scale mean that farms with large fields and larger continuous areas of the same crop type will always be at a competitive advantage.

5.2 Relative Abundance

The overall abundance of invertebrates was always higher in the larger members of the study field pairs, suggesting an area relationship. The level of heterogeneity, as determined by the landscape analysis, did not appear to have much influence. As crop type can determine which invertebrates are found in a field, large fields would have supported higher abundances of species that preferred the conditions created by that crop type. The wheat fields supported by far the highest numbers of invertebrates. This may have been due to the favorable conditions created by the long term presence of wheat stubble (Evans *et al.*, 2002 [62]).

The Diptera, Hymenoptera, Isopoda, Chilopoda and Orthoptera only showed significantly higher abundances in heterogeneous sites. The Diplura alone showed significantly higher abundances only in the homogeneous sites. Cluster analysis of the higher taxa abundance data also seemed to point to there being some influence of heterogeneity, although crop type was slightly more influential.

Heterogeneity did not appear to have a great influence on the relative abundance of Coleoptera families. For these data, cluster analysis showed that crop type had a slightly greater influence than heterogeneity. However, the Staphylinidae, Carabidae and Elateridae only had significantly higher abundances in heterogenous sites. While the Tenebrionidae only had significantly higher abundance in homogeneous sites.

The cluster analysis of the carabid species data showed that heterogeneity had some influence on species relative abundance, but crop type was more influential than both heterogeneity and the date of sampling. Significantly higher abundances of the species *Pterostichus (Platysma) niger*, *Poecilus cupreus*, *Microlestes luctuosus* and *Tapinopterus taborskyi* were seen in the sites that had the highest heterogeneity, according to the landscape analysis. That *P. niger* was found in greater abundance in heterogeneous sites is unsurprising, as it is known to favour meadows over cultivations and to depend on the presence of hedgerows in a landscape. It also seems to like areas that are less frequently disturbed, as it has shown a preference for minimum tillage over conventional cultivation techniques (Thiele, 1977 [167]; Holland & Luff, 2000 [90]).

P. cupreus, on the other hand, is a species that is very common in farmland. Its preference for heterogeneous sites in this study may be due to the fact that it also often inhabits forested areas (Thiele, 1977 [167]), which were more common in the heterogeneous sites. *M. luctuosus* is known to prefer areas of tall vegetation (Fadda *et al.*, 2008 [63]), which it would have found to a greater degree in heterogeneous sites, due to greater percentages of fallow, wasteland, woodland and hedgerows.

Not much is known about the habitat preferences of *T. taborskyi*, except that it has only ever been found in a mountainous area close to the study site (Arndt *et al.*, 2011 [6]). As mountainous areas resemble heterogeneous agricultural areas much more than homogeneous sites, this may explain its preference for high levels of heterogeneity.

The species *Cylindera germanica* was found in significantly greater abundance in homogeneous sites. This is probably because the species is accustomed to living in agricultural areas, (Varvara & Apostol, 2008 [184]), so a low level of heterogeneity and high disturbance levels would not be detrimental to it.

5.3 Species Richness

When estimating carabid species richness, the Chao 1 estimator would have been most appropriate. This is because it uses the species present in the samples that are only represented by one or two individuals to produce the estimates, while low abundances of species per sample were characteristic of the data obtained in this study. However, the 95 % confidence intervals of these estimates were wide, indicating that it would have been difficult to determine differences between the study fields using these estimates.

The Jackknife 2 and Bootstrap estimators were probably the most reliable for the carabid data, as their standard deviations were either very low, or in most cases zero. These estimators both showed that species richness was higher in the sites found to have high heterogeneity by the landscape analysis, except for the olive field comparisons. Here estimates were slightly higher in the olive field in the homogeneous site. The difference in species richness between these two fields; however, was a lot smaller than between the other field pairs being compared. For this reason then, it is possible that the level of heterogeneity did have some influence on species richness.

Overall, the morphospecies richness estimates for the plants appeared to be more reliable than those for the species richness of the Carabidae. For the ACE estimator, the most appropriate for use on the plant data, the standard deviations were all 0, indicating that the estimates were very reliable. Except for the maize comparison, higher morphospecies richness was estimated in sites, which according to the landscape analysis, had higher heterogeneity. Higher species richness in the maize field in the homogeneous site was probably due to the high soil moisture levels seen in that field.

5.4 Diversity and Evenness

The results of the diversity and evenness indices did not show any clear influence of heterogeneity, either for the carabid data or for the plant data. However, crop type did appear to influence both diversity and evenness. The olive study fields had the highest levels of both carabid and plant diversity and evenness, probably because they were the least disturbed study fields, which of all the crop types most resembled natural woodland.

There was a significant, positive correlation between carabid species diversity and the percentage of land covered by tree crops. These were olives, walnuts, almonds and plums. Again these crop types tended to be less disturbed than annual crops, so they would have resembled natural woodland most closely of all the crop types.

The percentage of non-forrested, non-cropped habitat showed an even stronger correlation with carabid diversity. This correlation was also significant. Such a result suggests that the amount of wasteland and fallow was probably the most important factor in determining carabid diversity.

There was no clear influence of heterogeneity on plant morphospecies diversity. However, there was a significant negative correlation between plant diversity and the number of fields of cotton in an area. This suggests that cotton fields were particularly depauperate in wild plants, probably because of the way they were irrigated and the high levels of agrochemical use these cultivations required.

5.5 Environmental Factors

Most of the study fields could be distinguished by their local environmental conditions, something which appeared to influence the carabid communities present within them. The wheat study fields were dry, warm, sunny and sandy, while the maize fields were damp, cool, shady and more muddy, with the olive fields falling somewhere in-between these two extremes. The cotton study fields; however, were more difficult to categorize according to their environmental variables. They were fairly sandy and had low plant cover, but the carabid communities in these fields seemed to be influenced by some other factor apart from environmental variables.

The most influential environmental variable, in terms of carabid species composition, was soil type or soil grain size. This was followed by soil temperature, soil moisture, soil pH, plant percentage cover, soil organic matter and the light intensity at ground level.

However, significant differences between heterogeneous and homogeneous sites were only seen in a small number of fields regarding soil moisture, pH and organic matter.

5.6 Overview

To conclude, this study found some differences in invertebrate communities, which were associated with the level of heterogeneity. High levels of relative abundance and high numbers of certain taxa were found where there were high levels of farmland heterogeneity. The influence of heterogeneity; however, was relatively weak and was secondary to those influences exerted by crop type and by some environmental variables.

This study also identified which, of the many aspects of heterogeneity, exerted the most influence on carabid species composition. In order of their level of influence, these aspects were the percentage of fallow and wasteland in a site. This was followed by the aggregation of land use types at the landscape level and the percentage of fallow in a site. Then came the interspersion / juxtaposition of fallow and the average field size.

High percentages of fallow and wasteland, as well as high percentages of tree crops in the study areas were associated with high carabid diversity levels. This was probably because these land use types most resembled the original habitat of many of the carabid species.

More work would be needed to find out the exact natures of the relationships identified in this study, but it is nonetheless useful to have an idea of which aspects of heterogeneity are the most beneficial to carabid communities. Extensive, small-scale farming is not a profitable form of agriculture. So by identifying which aspects of heterogeneity are the most important for wildlife, it may be possible to make biodiversity conservation more cost effective for the farmer.

From this study, it appears that the best ways to benefit farmland invertebrates would be, in order of their level of importance, to create interconnected areas of fallow and wasteland, to make sure that one crop type is not planted in adjacent fields during the same season, to promote the creation of small fields of around half a hectare and to increase the percentage of land devoted to tree crops.

Then, as knock-on effects have been seen to extend from one group of species to another (Smart *et al.*, 2000 [160]; Benton *et al.*, 2002 [10]), the measures listed above may, in turn, create benefits for other groups, such as birds and mammals.

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Chapter 6

Appendices

Appendix 1 - Landscape Data Used to Match Sites

Table 1: Data used to match the heterogeneous (a) and homogeneous (b) sites.

Study Site	**1a**	**1b**	**2a**	**2b**	**3a**	**3b**
Average elevation (m)	157.40	155.60	78.40	72.50	52.80	45.00
Distance to village (km)	0.99	0.84	0.42	0.52	0.99	1.20
Distance to road (km)	0.36	0.67	0.95	0.95	0.37	0.51
Distance to river (km)	1.81	1.70	0.97	0.85	2.18	1.21
Distance to stream (km)	0.40	0.43	0.19	0.16	0.27	0.26
Distance to woodland (km)	0.79	0.65	0.53	0.54	0.82	0.72
Distance to wasteland (km)	0.38	0.30	0.05	0.11	0.10	0.10

Appendix 2 - Site Maps

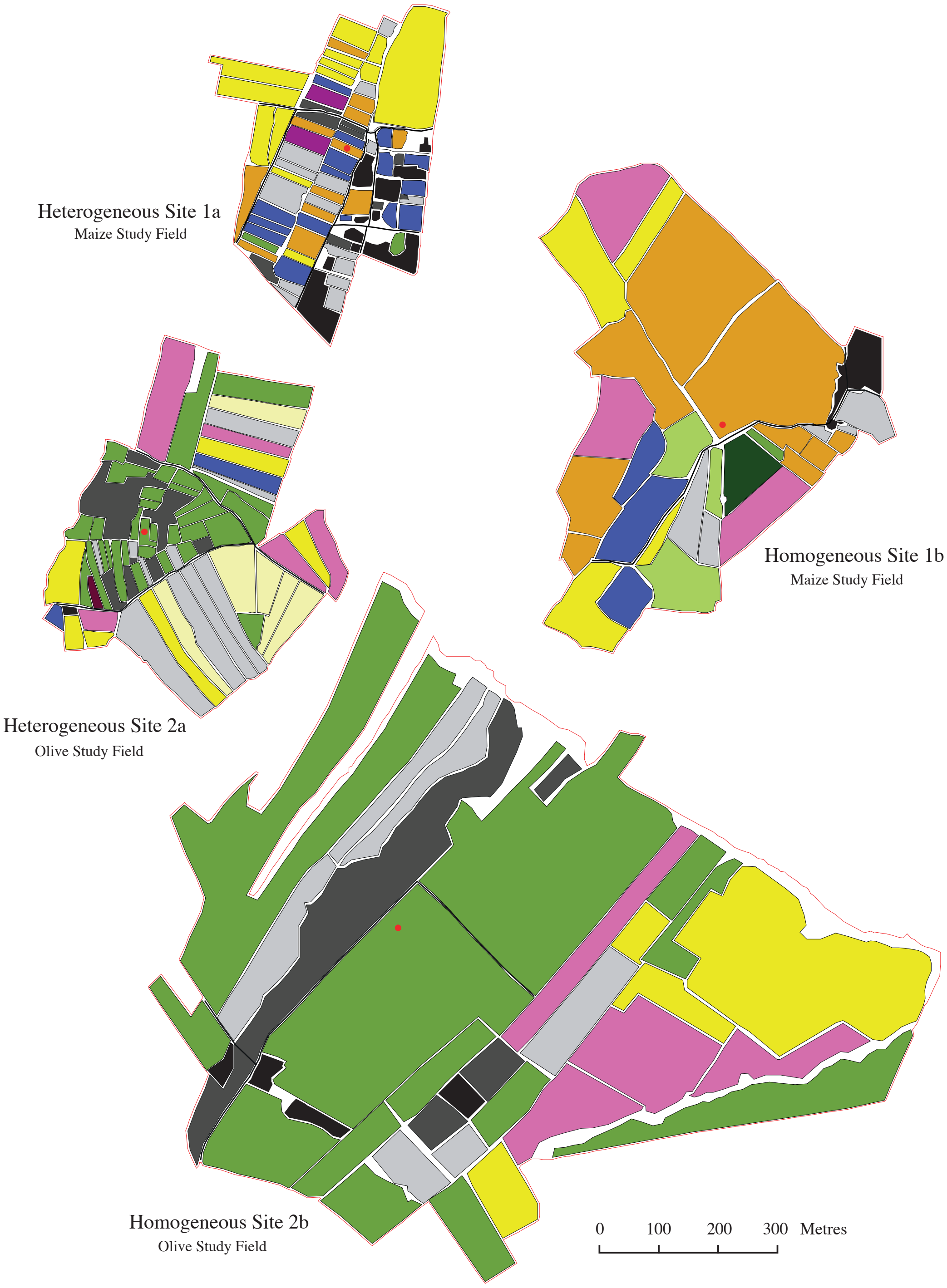

Figure 1: Land use maps of heterogeneous site 1a, homogeneous site 1b, heterogeneous site 2a and homogeneous site 2b.

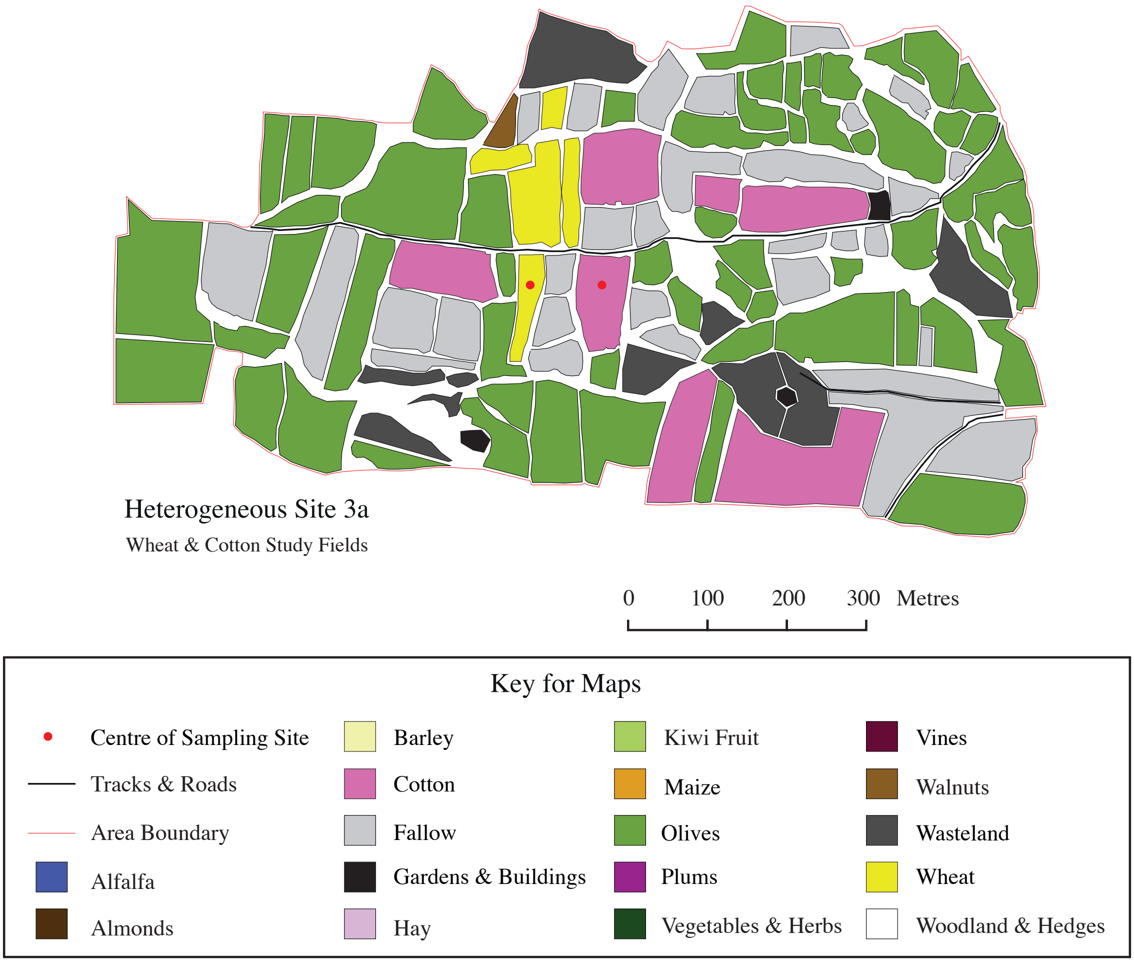

Figure 2: Land use map of heterogeneous site 3a. Also the key for the land use maps.

Figure 3: Land use maps of homogeneous sites 3bi and 3bii.

Appendix 3 - Landscape Analysis Algorithms

Algorithms for Patch Level Metrics

Metric = Site

$$AREA = a_{ij} \left(\frac{1}{10,000} \right)$$

Where:

- a_{ij} = area (m^2) of habitat patch ij.
- $i = 1, \ldots, m$ or m' habitat classes.
- $j = 1, \ldots, n$ habitat patches.
- n = number of habitat patches.
- m = number of habitat classes present in the landscape, excluding the landscape border if present.
- m' = number of habitat classes present in the landscape, including the landscape border if present.

Metric = Proximity Index

$$PROX = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}{}^{2}}$$

Where:

- a_{ijs} = area (m^2) of habitat patch ijs within specified neighborhood (m) of habitat patch ij.
- $s = 1, \ldots, n$ habitat patches, within specified neighborhood.
- h_{ijs} = distance (m) between habitat patch ijs and habitat patch ij.

Metric = Similarity Index

$$SIMI = \sum_{s=1}^{n} \frac{a_{ijs} \; . \; d_{ik}}{h_{ijs}^{2}}$$

Where:

- d_{ik} = similarity between habitat classes i and k (Values of d obtained from similarity weightings given to each habitat pair).

Algorithms for Class Level Metrics

Metric = Percentage of Landscape

$$PLAND = P_i = \frac{\sum_{j=1}^{n} a_{ij}}{A}(100)$$

Where:

- Pi = proportion of the landscape occupied by patch type (class) i.
- A = total landscape area (m^2).

Metric = Number of Patches

$$NP = n_i$$

Where:

- n_i = number of habitat patches of habitat patch type (class) i.

Metric = Contagion Index

$$Mean = \frac{\sum_{j=1}^{n} x_{ij}}{n_i} \ of \ CONTIG = \frac{\left(\frac{\sum_{r=1}^{n} c_{ijr}}{a_{ij}}\right) - 1}{v - 1}$$

Where:

- c_{ijr} = contagion value for pixel r in patch ij.
- x_{ij} = any given habitat patch ij.
- v = sum of the values in a 3-by-3 cell template (13 in this case).

Metric = Aggregation Index

$$AI = \left[\frac{g_{ii}}{max \rightarrow g_{ii}}\right](100)$$

Where:

- g_{ii} = number of like adjacencies between pixels of habitat patch type (class) i.
- $max \rightarrow g_{ii}$ = maximum number of like adjacencies between pixels of patch type (class) i.

Metric = Interspersion / Juxtaposition Index

$$IJI = \frac{-\sum_{k=1}^{m}\left[\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right) ln \left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right)\right]}{ln(m-1)}(100)$$

Where:

- e_{ik} = total length (m) of edge in landscape between habitat patch types (classes) i and k.

Metric = Connectance Index

$$CONNECT = \left[\frac{\sum_{j=k}^{n} c_{ijk}}{\frac{n_i \quad (n_i - 1)}{2}}\right](100)$$

Where:

- c_{ijk} = joining between patch j and k (0 = unjoined, 1 = joined) of the corresponding patch type i.

Algorithms for Landscape Level Metrics

Metric = Number of Patches

$$NP = N$$

Where:

- N = total number of patches in the landscape, excluding any background patches.

Metric = Largest Patch Index

$$LPI = \frac{max(a_{ij})}{A}(100)$$

Metric = Patch Area Distribution

$$Mean = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} x_{ij}}{N} \; of \; AREA = a_{ij}\left(\frac{1}{10,000}\right)$$

Metric = Proximity Index Distribution

$$Mean = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} x_{ij}}{N} \; of \; PROX = \sum_{s=1}^{n}\frac{a_{ijs}}{h_{ijs}^{2}}$$

Metric = Similarity Index Distribution

$$Mean = \frac{\sum_{i=1}^{m}\sum_{j=1}^{n} x_{ij}}{N} \; of \; SIMI = \sum_{s=1}^{n}\frac{a_{ijs} \; . \; d_{ik}}{h_{ijs}^{2}}$$

Metric = Contagion Index

$$CONTAG = \left[1 + \frac{\sum_{i=1}^{m}\sum_{k=1}^{m}\left[(P_i)\left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}}\right)\right] \; . \; \left[ln(P_i)\left(\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}}\right)\right]}{2ln(m)}\right](100)$$

Where:

- g_{ik} = number of adjacencies between pixels of habitat patch types (classes) i and k.

Metric = Aggregation Index

$$AI = \left[\sum_{i=1}^{m}\left(\frac{g_{ii}}{max \rightarrow g_{ii}}\right) Pi\right](100)$$

Metric = Interspersion / Juxtaposition Index

$$IJI = \frac{-\sum_{k=i}^{m}\left[\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right)\ ln\left(\frac{e_{ik}}{\sum_{k=1}^{m} e_{ik}}\right)\right]}{ln(m-1)} \quad (100)$$

Metric = Land Use Richness

$$PR = m$$

Metric = Simpson's Diversity Index

$$SIEI = \frac{1-\sum_{i=1}^{m} P_i^2}{1-\left(\frac{1}{m}\right)}$$

Appendix 4 - Class Level Metrics

Table 2: Class level metrics: the percentage of landscape, the number of patches and the contagion index.

Land Use - Study Site	% of Landscape	No. of Patches	Contagion
Alfalfa - 1a	9.1	9	0.69
Fallow - 1a	10.7	8	0.76
Gardens & Buildings 1a	10.8	6	0.75
Maize - 1a	12.1	11	0.68
Non-Cropped - 1a	27.3	34	-
Olives - 1a	1.4	1	0.76
Plums - 1a	3.2	2	0.84
Tracks & Roads - 1a	4.1	3	0.32
Wasteland - 1a	3.5	6	0.62
Wheat - 1a	31.9	3	0.75
Woods & Hedges - 1a	13.1	20	0.26
Cotton - 1b	14.9	1	0.93
Fallow - 1b	2.2	1	0.87
Gardens & Buildings - 1b	0.6	1	0.73
Maize - 1b	49.0	2	0.93
Non-Cropped - 1b	7.1	7	-
Olives - 1b	0.4	1	0.68
Tracks & Roads - 1b	1.1	1	0.26
Vegetables & Herbs - 1b	2.2	0	0.87
Wheat - 1b	9.2	1	0.63
Woods & Hedges - 1b	4.9	6	0.18
Alfalfa - 2a	2.1	2	0.23
Barley - 2a	13.4	3	0.32
Cotton - 2a	13.3	1	0.31
Fallow - 2a	17.5	5	0.24
Non-Cropped - 2a	31.5	50	-
Olives - 2a	25.7	8	0.31
Wasteland - 2a	9.2	8	0.29
Wheat - 2a	11.2	3	0.30
Woods & Hedges - 2a	4.8	37	0.08
Tracks & Roads - 2a	2.4	1	0.14
Cotton - 2b	1.9	0	0.80
Fallow - 2b	7.8	0	0.88
Gardens & Buildings - 2b	2.5	0	0.86
Non-Cropped - 2b	29.4	3	-
Olives - 2b	65.1	1	0.94
Tracks & Roads - 2b	16.5	0	0.88
Woods & Hedges - 2b	5.1	3	0.16

Table 3: Class level metrics: the percentage of landscape, the number of patches and the contagion index.

Land Use - Study Site	**% of Landscape**	**No. of Patches**	**Contagion**
Cotton - 3a	11.9	3	0.91
Fallow - 3a	19.1	8	0.83
Gardens & Buildings - 3a	0.5	0	0.75
Non-Cropped - 3a	45.2	19	-
Olives - 3a	36.8	9	0.78
Tracks & Roads - 3a	1.5	2	0.26
Walnuts - 3a	0.4	0	0.81
Wasteland - 3a	5.6	4	0.74
Wheat - 3a	3.7	2	0.84
Woods & Hedges - 3a	20.6	7	0.21
Alfalfa - 3bi	6.2	4	0.57
Almonds - 3bi	2.5	0	0.72
Cotton - 3bi	20.0	3	0.64
Gardens & Buildings - 3bi	0.7	1	0.58
Fallow - 3bi	11.6	1	0.62
Hay - 3bi	2.6	1	0.90
Non-Cropped - 3bi	41.9	19	-
Olives - 3bi	6.6	0	0.75
Tracks & Roads - 3bi	1.5	2	0.15
Wasteland - 3bi	17.4	3	0.92
Wheat - 3bi	18.0	3	0.67
Woods & Hedges - 3bi	13.0	15	0.14
Alfalfa - 3bii	18.7	3	0.88
Cotton - 3bii	46.3	4	0.92
Fallow - 3bii	6.2	2	0.89
Maize - 3bii	8.9	1	0.83
Non-Cropped - 3bii	16.5	8	-
Tracks & Roads - 3bii	2.6	2	0.32
Vegetables & Herbs - 3bii	4.0	1	0.64
Wheat - 3bii	3.3	0	0.91
Woods & Hedges - 3bii	10.3	6	0.41

Table 4: Class level metrics: the interspersion / juxtaposition index, the aggregation index and the connectance index.

Land Use - Study Site	**Interspersion / Juxtaposition**	**Aggregation**	**Connectance**
Alfalfa - 1a	63.6	86.8	4.4
Fallow - 1a	70.9	89.3	10.7
Gardens & Buildings 1a	48.4	87.8	19.0
Maize - 1a	72.9	86.6	6.1
Olives - 1a	66.4	91.0	0.0
Plums - 1a	65.8	95.0	0.0
Tracks & Roads - 1a	87.9	48.0	0.0
Wasteland - 1a	61.9	80.5	80.5
Wheat - 1a	36.5	94.7	20.0
Woods & Hedges - 1a	91.3	63.6	4.3
Cotton - 1b	35.5	96.4	0.0
Fallow - 1b	64.2	95.2	0.0
Gardens & Buildings - 1b	25.0	88.4	0.0
Maize - 1b	38.1	97.1	0.0
Olives - 1b	18.7	81.2	0.0
Tracks & Roads - 1b	66.4	29.5	0.0
Vegetables & Herbs - 1b	64.2	95.2	0.0
Wheat - 1b	37.3	97.1	33.3
Woods & Hedges - 1b	84.3	33.1	5.1
Alfalfa - 2a	67.0	65.6	2.6
Barley - 2a	66.1	71.3	0.8
Cotton - 2a	60.5	60.3	3.4
Fallow - 2a	81.6	69.6	0.8
Olives - 2a	84.7	63.8	1.5
Tracks & Roads - 2a	84.5	25.4	0.1
Wasteland - 2a	53.1	60.7	2.6
Wheat - 2a	78.6	71.3	0.8
Woods & Hedges - 2a	81.1	23.0	0.3
Cotton - 2b	3.1	89.3	0.0
Fallow - 2b	2.6	92.9	0.0
Gardens & Buildings - 2b	66.1	91.8	0.0
Olives - 2b	41.3	97.8	30.0
Tracks & Roads - 2b	55.1	47.9	100.0
Woods & Hedges - 2b	38.6	95.8	0.0

Table 5: Class level metrics: the interspersion / juxtaposition index, the aggregation index and the connectance index.

Land Use - Study Site	Interspersion / Juxtaposition	Aggregation	Connectance
Cotton - 3a	15.1	95.1	4.8
Fallow - 3a	18.4	90.1	4.0
Gardens & Buildings - 3a	68.2	89.4	0.0
Olives - 3a	14.9	90.8	5.7
Tracks & Roads - 3a	53.2	37.0	33.3
Wasteland - 3a	15.7	90.3	8.3
Wheat - 3a	16.8	92.2	50.0
Woods & Hedges - 3a	74.1	64.7	11.4
Walnuts - 3a	64.6	95.0	0.0
Alfalfa - 3bi	17.2	90.9	6.6
Almonds - 3bi	38.4	93.3	0.0
Cotton - 3bi	27.2	91.5	2.2
Fallow - 3bi	24.0	86.3	3.9
Gardens & Buildings - 3bi	72.6	75.0	0.0
Hay - 3bi	35.5	96.4	0.0
Olives - 3bi	32.7	86.7	5.5
Tracks & Roads - 3bi	45.2	38.3	3.2
Wasteland - 3bi	36.3	96.6	0.0
Wheat - 3bi	31.7	91.6	4.4
Woods & Hedges - 3bi	85.6	43.1	1.3
Alfalfa - 3bii	25.7	95.7	4.4
Cotton - 3bii	21.2	96.9	13.2
Fallow - 3bii	6.5	93.4	0.0
Maize - 3bii	14.7	96.9	16.7
Tracks & Roads - 3bii	59.9	48.4	10.0
Vegetables - 3bii	23.7	97.8	100.0
Wheat - 3bii	6.5	94.4	0.0
Woods & Hedges - 3bii	87.9	61.7	16.7