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CARBON AND NITROGEN STABLE ISOTOPES IN FRUITS AND ARTHROPODS THAT ARE EATEN BY SONGBIRDS DURING MIGRATION

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ABSTRACT- Stable isotope analysis is becoming increasingly common in studies of foraging ecology. In this study, we investigated whether significant differences exist between the stable carbon and nitrogen isotope values of fruits and arthropods that are used by migratory songbirds on Block Island, Rhode Island. Eight species of fruits and nine orders of arthropods were collected from Block Island, Rhode Island in Fall 2010 and analyzed for their isotopic compositions at the University of Rhode Island in Spring 2011. Overall, there were isotopic differences between fruits and arthropods in general as well as between the specific fruit species and arthropod orders. These isotopic differences are ecologically important as the general resource use of migratory songbirds on Block Island can potentially be examined by comparing the isotopic composition of their tissues and these resources.

Key Words: stable isotopes, fruits, arthropods, migratory birds, Rhode Island

Isotopes are forms of the same element that differ only in the number of neutrons found in their nucleus. “Stable isotopes” are simply isotopes that do not noticeably decay or break down over time, in contrast to radioactive isotopes. Neutron differences generally cause only subtle chemical differences, and hence isotopes of the same element tend to behave similarly. However, isotopes with extra neutrons are more massive, or heavier, than their light isotope counterpart, and thus slightly slower to react in certain reactions. This separation of lighter and

heavier isotopes during a reaction is called isotopic fractionation, and several resulting patterns in nature are very useful to animal ecologists.

The use of stable isotope analysis is becoming more common in all areas of animal ecology (Wolf et al. 2009). In particular, natural variation in the abundance of stable isotopes makes them useful in studies of foraging ecology. For example, stable nitrogen isotopes tend to accumulate with increasing trophic level, and stable carbon isotopes tend to trace the original source of carbon in a system [e.g., photosynthetic pathway, terrestrial vs. marine] (Bennett and Hobson 2009). This natural variation in stable isotopes is potentially useful for quantifying resource use because the isotopic composition of an animal's diet is assimilated somewhat predictably into the animal's tissues (Martinez del Rio and Anderson-Sprecher 2008). In fact, the ratio of naturally-occurring isotopes in consumer tissues can be more dependable in dietary assessment than other methods such as stomach, pellet, and fecal analyses (Sydeman et al. 1997) and can provide valuable information on the diets of both individuals and populations (Hobson 1995).

In this study I examined the carbon and nitrogen isotope composition of arthropods and fruits eaten by migratory songbirds on Block Island, Rhode Island. My objective was to quantify isotopic differences between fruits and arthropods in general, between various arthropod orders and fruit species in particular, and to evaluate potential explanations for any observed differences. Determining the extent to which these possible dietary resources differ isotopically is an important first step in evaluating resource use of migratory birds using stable isotopes.

We hypothesize that there will be significant differences in the general stable nitrogen isotope composition of fruits and arthropods as well as among different taxa of arthropods and, to a lesser extent, fruits. Because nitrogen increases with trophic level, we expect carnivorous

arthropods such as Araneae and Acari to have higher levels of nitrogen than herbivorous arthropods such as Heteroptera and Isopoda. We predict orders such as Coleoptera and Formicidae to have intermediate nitrogen levels due to their more generalist feeding habitats. The only difference in nitrogen composition that we expect in fruits is with northern bayberry (*Morella pensylvanica)*. Northern bayberry is the only species examined in this study that uses nitrogen fixation, or obtains some of its nitrogen from the atmosphere, and thus may have a different nitrogen isotope composition than the other species. Because all arthropod and fruit samples were collected from a predominantly terrestrial C_3 photosynthesis environment, we do not expect much variation in stable carbon isotope composition among arthropods or fruits.

METHODS

Field Methods

From 16 September - 12 November 2010 on the northern end of Block Island (Bayrose and Clayhead properties), we collected fruits and foliar- and ground-dwelling arthropods expected to be relevant food resources for migrating songbirds (Figure 1).

Fruit specimens were collected from eight of the most important species to migratory songbirds (northern and southern arrowwood, *Viburnum recognitum* and *Viburnum dentatum*, respectively*;* northern bayberry; Virginia creeper, *Parthenocissus quinquefolia*; multiflora rose, *Rosa multiflora*; pokeweed, *Phytolacca americana*; Japanese barberry, *Berberis thunbergii*; and Asiatic bittersweet, *Celastrus orbiculatus*). For all species except the arrowwoods, we collected fruits from one or two individual plants at four distinct locations on the northern end of Block Island. It was not possible to collect all species at a given location, which complicates isotopic comparisons among species. For the arrowwood species, arguably the most preferred fruit on the

island (Smith et al. 2007; Bolser 2010), we collected samples more widely from six (southern arrowwood) or five (northern arrowwood) locations throughout the island. Fruits were collected as close to peak ripeness as possible. They were transferred to Ziploc® bags and kept frozen until processing.

We collected ground-dwelling and foliar arthropod specimens on days with no precipitation, and usually under light to moderate winds. Ground-dwelling arthropods were collected weekly through leaf litter sampling. Sampling was conducted around mid-day at six locations representing three habitats (goldenrod fields, upland maritime shrubland, and wetland maritime shrubland). There were two collection sites per habitat. Litter samples consisted of approximately 3 - 4 liters of litter material (avoiding collection of subsoil) collected in 3 - 6 separate subsamples within an approximately 25 m^2 area. After collection, litter samples were aggressively agitated using a manual Berlese apparatus (Ward's Natural Science) for 1 minute. Filtered arthropods and litter were transferred to Ziploc® bags and then frozen for 48 - 72 h to kill the arthropods prior to sorting and identification. Foliar arthropods were also collected weekly around mid-day. As with leaf litter, sampling occurred at two sites in each habitat type. Foliar samples were collected via sweep netting in which representative foliage was aggressively swept for two minutes with a 0.3 m diameter canvas insect net. Collected arthropods were transferred to Ziploc® bags and then frozen for 48 - 72 h to kill the arthropods prior to sorting and identification. Arthropods were then sorted and identified to taxonomic order, with two exceptions: I distinguished (1) between the suborders Heteroptera (true bugs) and Auchenorrhyncha (primarily hoppers) within the order Hemiptera, and (2) between ants (family Formicidae) and non-ants in the order Hymenoptera. The final sample comprised nine orders of arthropods (Phylum Arthropoda) of potential relevance as food resources for migratory

songbirds: two within the Class Arachnida (orders Acari and Araneae), one within the Class Crustacea (order Isopoda), and the balance within the Class Insecta (orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera), with further divisions as noted above. Arthropods were stored in glass scintillation vials by taxon, collection date, and habitat and kept frozen until processing. Insect taxonomy follows Triplehorn and Johnson (2004).

Laboratory methods

Arthropod and fruit samples were prepared for stable isotopic analysis in a University of Rhode Island laboratory. Fruit samples were first deseeded by hand and the pulps stored in glass scintillation vials. They were then placed in a -80˚ C freezer for at least 24 hours, and then lyophilized for 4-7 days. After sufficient drying, the fruit pulps were powdered using a mortar and pestle and then weighted (5 - 9 mg depending on species) into tin capsules; we analyzed up to six replicates of each fruit species at each location. These capsules stored in well trays and kept frozen until isotopic analysis. Individual arthropods (weighing between 0.8 - 1.5 mg) were placed in tin capsules; we analyzed up to ten separate individuals of each order on each sample collection date. The capsules were also stored in well trays and kept frozen until stable isotopic analysis.

Carbon and nitrogen isotopic analyses were performed at the U.S. Environmental Protection Agency Atlantic Ecology Division laboratory. Arthropod samples were analyzed using a Carlo-Erba NA 1500 Series II Elemental Analyzer interfaced with an Elementar Optima isotope ratio mass spectrometer. Samples were first combusted (1020˚C, chromic oxide catalyst) and then reduced (650˚C, copper) sending CO_2 and N_2 to the mass spectrometer for the measurement of carbon and nitrogen isotope ratios, respectively. Fruit samples were analyzed using an Elementar Vario Micro Cube elemental analyzer interfaced with an Isoprime 100

isotope ratio mass spectrometer. Samples were first combusted (950˚C, chromic oxide catalyst) and then reduced (650˚C, copper) sending CO_2 and N_2 to the mass spectrometer for the measurement carbon and nitrogen isotope ratios, respectively. Stable-carbon and nitrogen isotope ratios are expressed in δ notation as parts per thousand (‰) deviation from the international reference standards Vienna Pee Dee Belemnite and AIR, respectively. We analyzed two internal laboratory standards (blue mussel [*Mytilus edulis*] for arthropods, NIST 1547 peach leaves for fruits) after every 12 samples in sequence. $\delta^{13}C$ and $\delta^{15}N$ values for internal standards were calibrated against sucrose ANU (NIST RM8542) and ammonium sulfate (IAEA-N-1). Our blue mussel internal standard has a running average $\delta^{13}C$ and $\delta^{15}N$ measurement precision (standard deviation) of ±0.15‰ and ±0.06‰, respectively. Our NIST peach leaves internal standard has a running average $\delta^{13}C$ and $\delta^{15}N$ measurement precision (standard deviation) of ±0.18‰ and ±0.10‰, respectively. Propagating measurement uncertainty in our reference and internal standards with that in repeated fruit and arthropod measurements, reported $\delta^{13}C$ and $\delta^{15}N$ measurements have estimated measurement precisions (standard deviations) of ± 0.22‰ and ± 0.22‰ for fruit and ± 0.22‰ and ± 0.15‰ for arthropods, respectively.

Statistical Methods

I used multivariate analysis of variance (MANOVA) and, if warranted, protected analyses of variance (ANOVA) to compare $\delta^{13}C$ and $\delta^{15}N$ between fruits and arthropods in general, without regard to fruit or arthropod taxonomy. I used PROC GLM in SAS 9.2 (SAS Institute 2007) to evaluate the MANOVA and ANOVA models. Subsequently, I compared $\delta^{13}C$ and $\delta^{15}N$ among fruit and arthropod taxa using linear mixed effects models. Specifically, for isotopic comparisons among fruits, replicate measurements from the same plant were not

independent; thus, I considered plant as a random effect and the species of fruit as the fixed effect of interest. For arthropods, I considered sampling occasion during the fall as a random effect and order as the fixed effect of interest. Although isotopic differences in arthropods among habitats, as well as between specific locations of arthropod within a habitat (i.e., foliage [sweep netting] or ground [leaf litter]), may be of potential interest, I do not evaluate them here for two primary reasons: (1) arthropod orders were not well-represented in all habitats or collection methods (i.e., data was very unbalanced); and (2) inferring isotopic differences related to habitat *per se* would require comparisons among arthropods with identical ecologies (i.e., comparisons of the same species among habitats). The three primary habitats used by migrating songbirds were sampled with the intention to quantify the full range of isotopic variation in food resources, and to explore taxonomic isotopic differences in spite of this variation. I used PROC MIXED in SAS 9.2 to evaluate the mixed effects models. Denominator degrees of freedom in the global tests for $\delta^{13}C$ and $\delta^{15}N$ differences among fruit species and arthropod orders were adjusted using Kenward and Roger's (1997) approximation, as recommended by Schaalje et al. (2002). I calculated simultaneous confidence intervals to evaluate contrasts of $\delta^{13}C$ and $\delta^{15}N$ values among fruit species and arthropod orders (ADJUST = SIMULATE option in the LSMEANS statement of PROC MIXED) with a familywise $\alpha = 0.05$ (Westfall et al. 1999). I report least squares means ± standard error for the isotopic compositions of fruit and arthropods unless noted otherwise.

RESULTS

Block Island arthropods and fruits differed in $\delta^{15}N$ and $\delta^{13}C$ (MANOVA: Wilk's $\lambda = 0.80$, $F_{2,509} = 55.97$, $P < 0.0001$), and protected ANOVAs indicated differences between fruits and arthropods in $\delta^{15}N$ (ANOVA: $F_{1,510} = 118.78$, $P < 0.0001$) and $\delta^{13}C$ (ANOVA: $F_{1,510} = 14.25$, P

= 0.0002). Although the differences in stable-nitrogen and carbon isotope signatures of fruits and arthropods are highly significant, Block Island fruits and arthropods do not occupy exclusive isotopic space, and the difference in occupied isotopic space relates particularly to $\delta^{15}N$ (Figure 2).

Fruits

Significant variation existed in $\delta^{15}N$ ($F_{7,26.9} = 4.76$, $P < 0.002$) and $\delta^{13}C$ ($F_{7,27} = 12.33$, $P < 0.0001$) among fruits commonly consumed by songbirds on Block Island (Figures 3 and 4). Most fruits did not differ significantly in their $\delta^{15}N$ compositions; pokeweed was the exception with significantly higher $\delta^{15}N$ values than all other fruits except multiflora rose and Asiatic bittersweet (Figure 3). However, multiflora rose, northern arrowwood, and southern arrowwood possessed more positive $\delta^{13}C$ values than Japanese barberry, Asiatic bittersweet, northern bayberry, and Virginia creeper; pokeweed possessed intermediate $\delta^{13}C$ values (Figure 4).

Arthropods

Significant variation existed in $\delta^{15}N$ ($F_{10,485} = 22.06$, $P < 0.0001$) and $\delta^{13}C$ ($F_{10,470} = 11.90$, $P < 0.0001$) among arthropod taxa sampled on Block Island (Figures 5 and 6). Arthropod $\delta^{15}N$ values showed considerable variation among taxa (Figure 5). For example, several taxa possessed relatively low $\delta^{15}N$ values, including the Coleoptera (beetles), Heteroptera, non-formicid Hymenoptera, and Isopoda (woodlice). Conversely, several taxa were characterized by relatively high $\delta^{15}N$ values, including the Acari (ticks, mites), Araneae (spiders), Diptera (flies), and Auchenorrhyncha. The remaining taxa, including the Formicidae, Lepidoptera (caterpillars), and Orthoptera (crickets, grasshoppers), exhibited somewhat intermediate average $\delta^{15}N$ values. For carbon isotopes in general, most arthropod orders exhibited relatively similar $\delta^{13}C$ values,

although the Lepidoptera possessed significantly lower $\delta^{13}C$ values than all other orders expect the Coleoptera (Figure 6).

DISCUSSION

In this study, we found that fruits and arthropods occupy a different, but not entirely exclusive, isotopic space. As expected, there was a distinct difference between fruits and arthropods in their nitrogen stable isotope values, which is in agreement with the different trophic positions occupied by these two groups. The fruits are a result of primary production while the arthropods are consumers and thus the nitrogen in their tissues has been through a process (i.e.-, protein catabolism) that apparently results in the heavier nitrogen isotopes being differentially retained in their tissues (Gannes et al. 1998). The difference we found in carbon isotopes between fruits and arthropods is more difficult to explain, and there is clearly a lot of overlap in the carbon isotope compositions of fruits and arthropods. In any case, the general differences in stable isotope compositions of fruits and arthropods is our most important results because it potentially allows the examination of general resource use by migratory birds on Block Island.

Fruits

Contrary to expectation, northern bayberry did not exhibit distinct $\delta^{15}N$ values relative to the other species. Unexpectedly, pokeweed, multiflora rose, and Asiatic bittersweet had higher $\delta^{15}N$ values than the other species. Interestingly, these three species possess the highest protein levels of the species sampled in this study (Smith et al. 2007), which points to a possible correlation between protein and nitrogen isotope levels. Additionally, nitrogen stable isotopes are known to vary greatly among different soil types (Herlihy 1979), so the result may relate to

growing location rather than an ecological process. However, we sampled from several widespread locations, so we expect this to be a less viable explanation.

There was more variation among fruit species in their stable carbon isotope values than originally expected. Multiflora rose, northern arrowwood, and southern arrowwood all had significantly higher $\delta^{13}C$ values compared to some other species. This variation is unexpected because all the species use C_3 photosynthesis and were collected from a terrestrial environment. At this time, these results remain inexplicable except for the possibility that the species may vary subtly in the specifics of their photosynthesis; more study is warranted.

Arthropods

Arthropod orders separated in their stable nitrogen isotope values in general accordance to trophic level. Generally, carnivorous orders (e.g., Acari, Araneae, Diptera) possessed the highest, herbivores (e.g., non-formicid Hymenoptera, Isopoda [detritivores], Heteroptera, Coleoptera) the lowest, and more omnivorous orders (e.g., Formicidae, Orthoptera) more intermediate $\delta^{15}N$ values. Bennett and Hobson (2009) found similar relationships among arthropod orders. The pattern was not without exception, however. For example, the orders Auchenorrhyncha and Lepidoptera exhibited higher $\delta^{15}N$ values than expected, given their relatively strict mucivory (sap-eating) and herbivory, respectively. Regarding the Auchenorrhyncha, however, there are good physiological reasons to expect plant sap to be more $\delta^{15}N$-enriched relative to the plant material (Handley and Raven 1992). High $\delta^{15}N$ values in Lepidoptera are more puzzling, but considering that Lepidopteran larvae are known to be very host-specific, our results may simply represent sampling bias (all Lepidopteran samples were collected in goldenrod prairies).

In general, the results for stable carbon isotope values in arthropods showed relatively consistent signatures. The only possible exceptions were Lepidoptera, which possessed significantly lower $\delta^{13}C$ values than every other order except Coleoptera, and Orthoptera, which possessed higher $\delta^{13}C$ values than several other orders. As mentioned above, Lepidopteran larvae tend to be very host-specific, and thus may sample a narrower range of the plant community and thus a narrower and potentially distinct carbon isotope range. The slightly higher $\delta^{13}C$ values in Orthoptera seems to results from the incorporation of C_4 photosynthetic plant material (e.g., grasses) into their diet in individuals sampled in the goldenrod prairies; C_4 photosynthesis results in plant tissues with distinctly higher $\delta^{13}C$ values than C_3 photosynthesis (Gannes et al. 1998)

SUMMARY

Given the extent of isotopic variation among fruit and arthropod taxa, it is likely not possible to use stable isotopes for examining specific resource use on Block Island (e.g., what types of fruits or arthropods). However, because the fruits and arthropods available to migratory songbirds on Block Island occupy relatively distinct isotopic space, the potential of inferring general resource use by songbirds during stopover on Block Island is worth exploring. Additionally, it will be necessary to consider the role of animal physiology in the incorporation of dietary isotopic compositions (e.g.; exploring resource use using the stable isotope composition of bird tissues indicative of recent diet, such as plasma).

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FIGURE LEGENDS

FIGURE 1. Study area (red polygon on inset) for field collections of fruits and arthropods consumed by migratory songbirds on Block Island, Rhode Island during the 2010 fall migration (September - November).

FIGURE 2. Carbon and nitrogen stable isotope values of fruits and arthropods collected on Block Island, Rhode Island during the 2010 fall migration (September - November).

FIGURE 3. Nitrogen stable isotope values of eight fruit species collected on Block Island, Rhode Island during the 2010 fall migration (September - November). Species abbreviations:

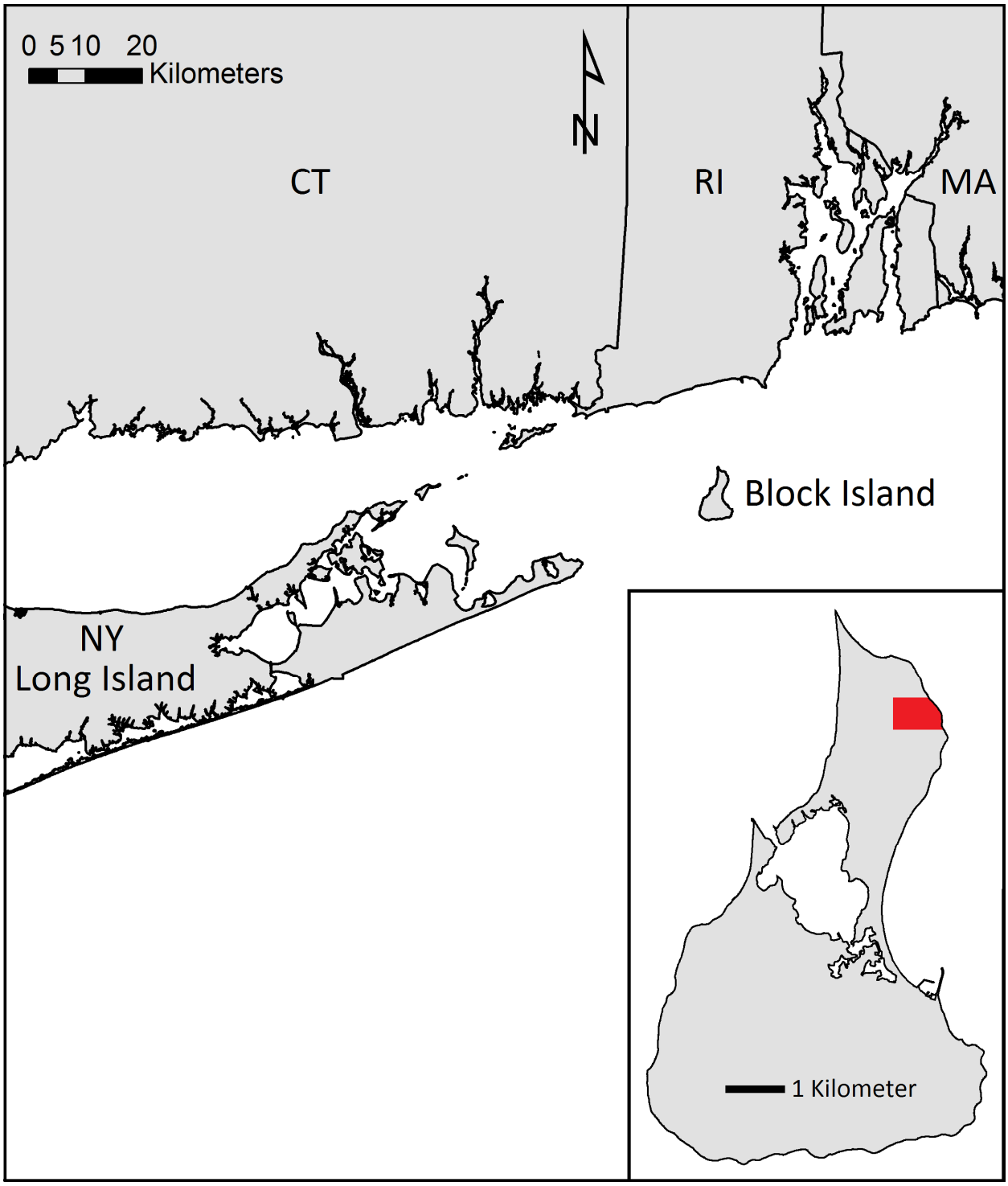
VIDE (southern arrowwood), MOPE (northern bayberry), VIRE (northern arrowwood), PAQU (Virginia creeper); BETH (Japanese barberry), CEOR (Asiatic bittersweet), ROMU (multiflora rose), and PHAM (pokeweed). Number of samples analyzed indicated in parentheses. Species with different letters are significantly different at $P < 0.05$ based on multiple comparisons tests (see text). Boxplots indicate median (dark line), interquartile range (box) and 10^{th} and 90^{th} percentiles (whiskers); outliers are excluded for clarity.

FIGURE 4. Carbon stable isotope values of eight fruit species collected on Block Island, Rhode Island during the 2010 fall migration (September - November). Species abbreviations: VIDE (southern arrowwood), MOPE (northern bayberry), VIRE (northern arrowwood), PAQU (Virginia creeper); BETH (Japanese barberry), CEOR (Asiatic bittersweet), ROMU (multiflora rose), and PHAM (pokeweed). Number of samples analyzed indicated in parentheses. Species with different letters are significantly different at $P < 0.05$ based on multiple comparisons tests (see text). Boxplots indicate median (dark line), interquartile range (box) and 10^{th} and 90^{th} percentiles (whiskers); outliers are excluded for clarity.

FIGURE 5. Nitrogen stable isotope values of eleven arthropod taxa (see text) collected on Block Island, Rhode Island during the 2010 fall migration (September - November). Number of samples analyzed indicated in parentheses. Species with different letters are significantly different at $P < 0.05$ based on multiple comparisons tests (see text). Boxplots indicate median (dark line), interquartile range (box) and 10^{th} and 90^{th} percentiles (whiskers); outliers are excluded for clarity.

FIGURE 6. Carbon stable isotope values of eleven arthropod taxa (see text) collected on Block Island, Rhode Island during the 2010 fall migration (September - November). Number of samples analyzed indicated in parentheses. Species with different letters are significantly different at $P < 0.05$ based on multiple comparisons tests (see text). Boxplots indicate median (dark line), interquartile range (box) and 10^{th} and 90^{th} percentiles (whiskers); outliers are excluded for clarity.

FIGURE 1.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N
CT
RI
MA
Block Island
NY
Long Island
1 Kilometer

FIGURE 2.

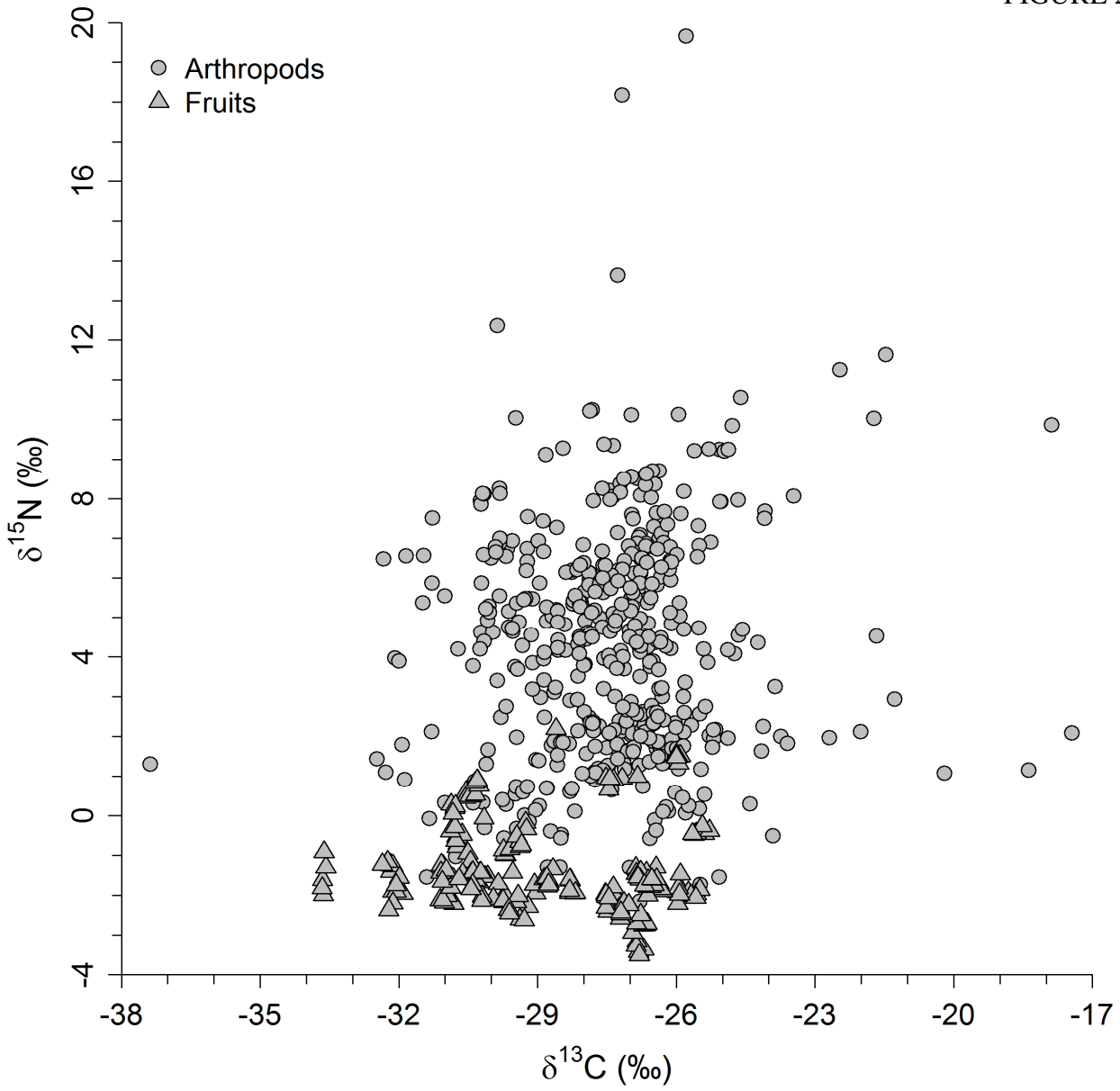

Arthropods
Fruits
20
16
12
8
4
0
-4
δ15N (‰)
-38
-35
-32
-29
-26
-23
-20
-17
δ13C (‰)

FIGURE 3.

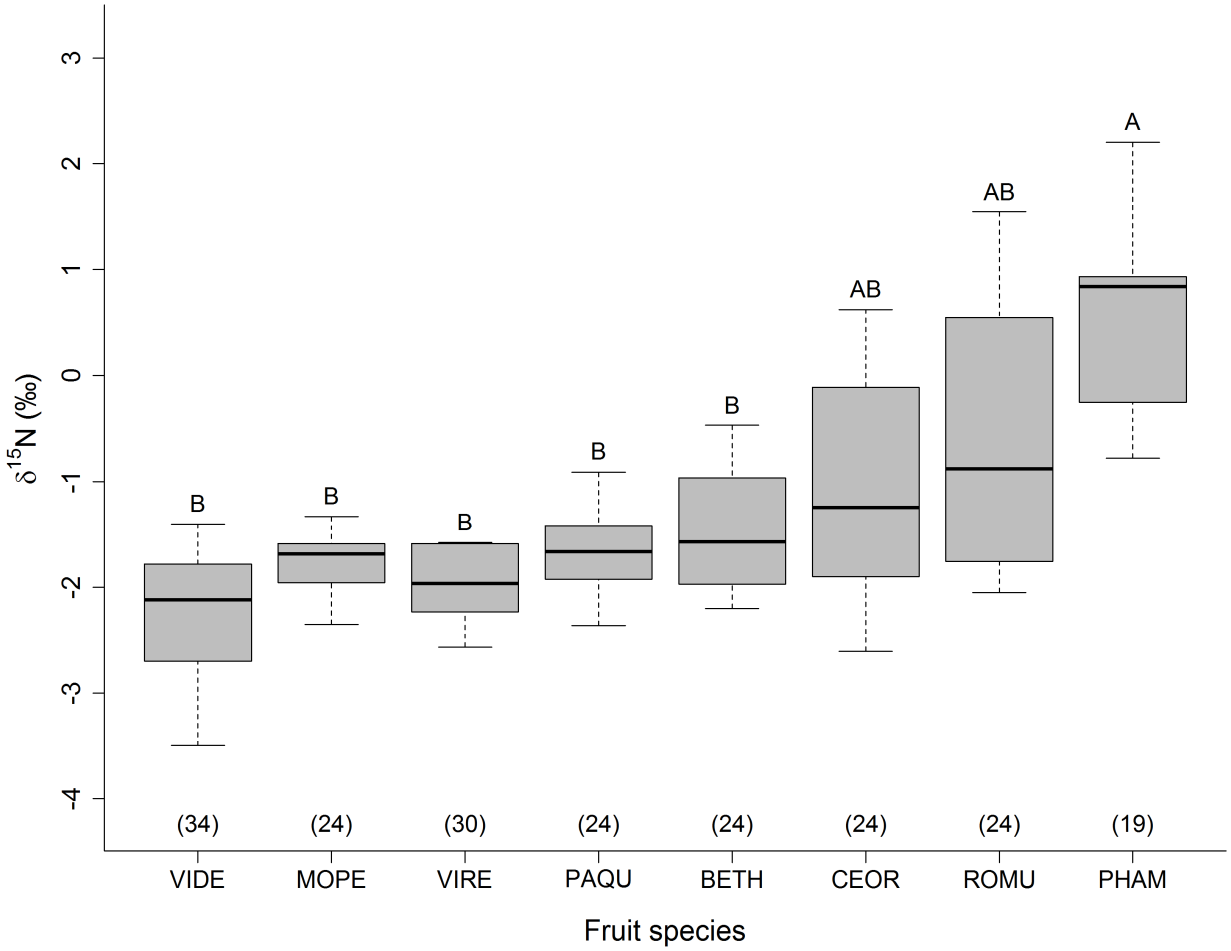
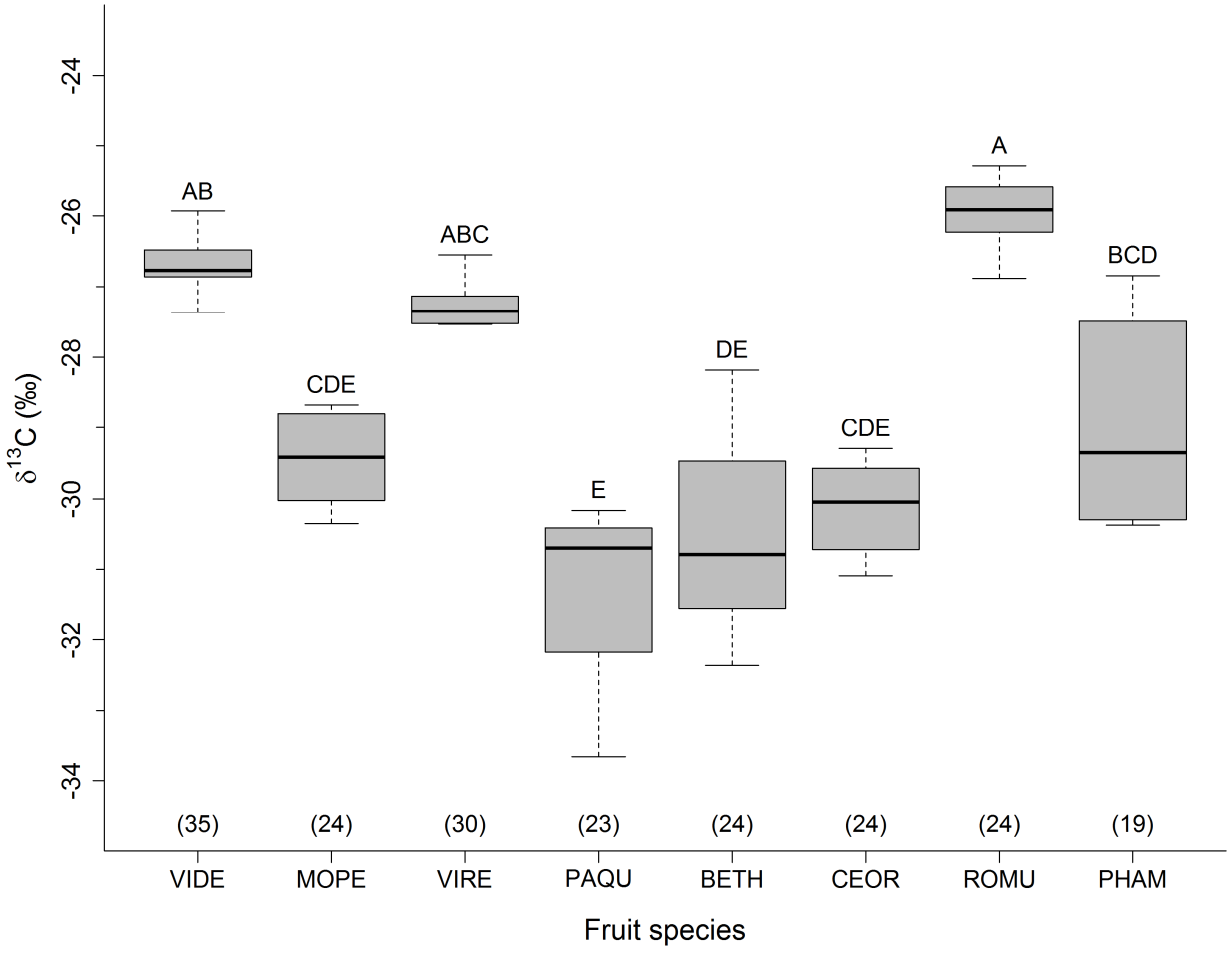

δ15N (‰)
3
2
1
0
-1
-2
-3
-4
B
B
B
B
B
AB
AB
A
(34)
(24)
(30)
(24)
(24)
(24)
(24)
(19)
VIDE
MOPE
VIRE
PAQU
BETH
CEOR
ROMU
PHAM
Fruit species

FIGURE 4.


-24
-26
-28
-30
-32
-34
δ13C (‰)
AB
CDE
ABC
E
DE
CDE
A
BCD
(35)
(24)
(30)
(23)
(24)
(24)
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(19)
VIDE
MOPE
VIRE
PAQU
BETH
CEOR
ROMU
PHAM
Fruit species

FIGURE 5.

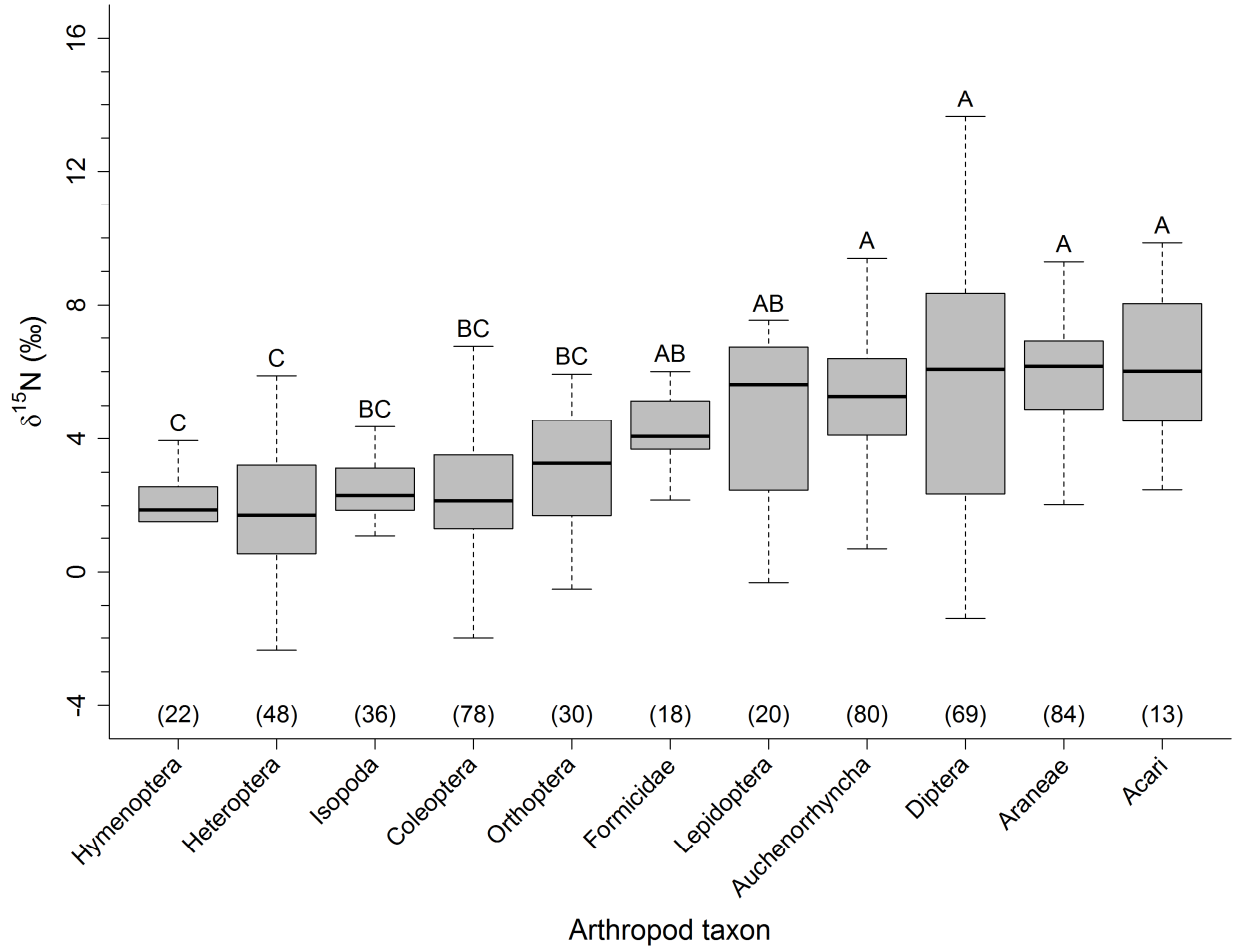
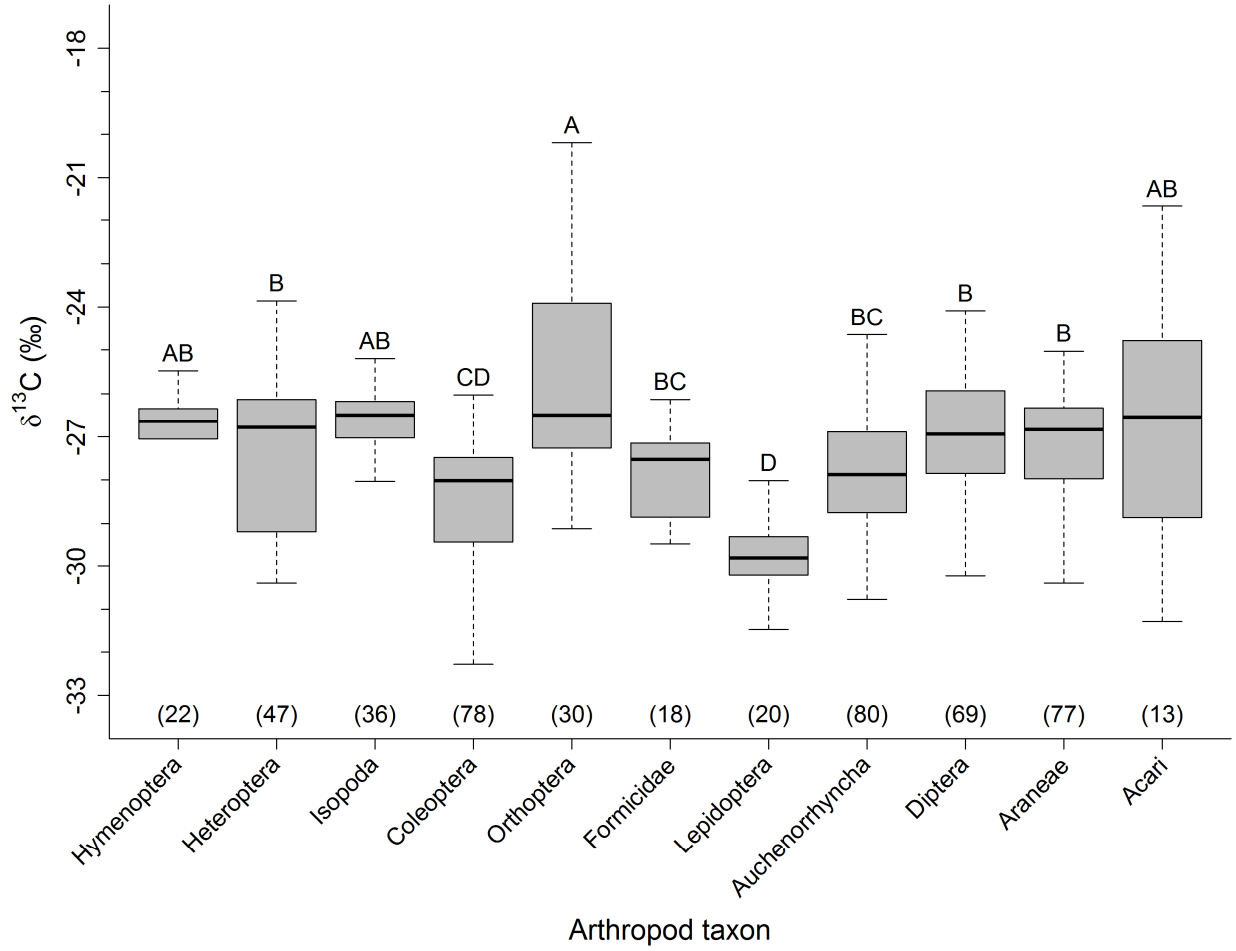

δ15N (‰)
16
12
8
4
0
-4
C
C
BC
BC
BC
AB
AB
A
A
A
(22)
(48)
(36)
(78)
(30)
(18)
(20)
(80)
(69)
(84)
(13)
Hymenoptera
Heteroptera
Isopoda
Coleoptera
Orthoptera
Formicidae
Lepidoptera
Auchenorrhyncha
Diptera
Araneae
Acari
Arthropod taxon

FIGURE 6.


δ13C (‰)
-18
-21
-24
-27
-30
-33
AB
B
AB
CD
A
BC
D
BC
B
B
AB
(22)
(47)
(36)
(78)
(30)
(18)
(20)
(80)
(69)
(77)
(13)
Hymenoptera
Heteroptera
Isopoda
Coleoptera
Orthoptera
Formicidae
Lepidoptera
Auchenorrhyncha
Diptera
Araneae
Acari
Arthropod taxon