Report on the working group for “*Using the metacommunity concept to synthesize biodiversity patterns across LTER sites*” at the 2015 Long Term Ecological Research (LTER) All Scientists Meeting (ASM).

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Summary

Collectively, the LTER community is well positioned to address many of the overarching questions in community ecology regarding how ecological context can influence the community assembly mechanisms underlying observed biodiversity patterns. Because the metacommunity concept integrates local (e.g., biotic interactions, niche-based species sorting) and regional (e.g., biogeography, regional colonization histories) factors, it has the potential to serve as a framework to synthesize biodiversity patterns across ecosystems and taxa represented in the LTER network. This working group had three objectives at the 2015 ASM: (1) promote discussion about how the metacommunity concept has been applied to interpret biodiversity data at LTER sites, (2) identify specific questions and challenges that the LTER community is uniquely suited to address in a cross-site metacommunity synthesis, and (3) develop a working plan and a proposal to submit to NSF for a follow-up workshop to move forward with the synthesis project. The working plan will summarize LTER data sets and quantitative approaches that are identified by the working group as crucial for understanding biodiversity pattern across the LTER network.

Working group participation and attendance

The strong attendance for this working group demonstrates how the metacommunity concept is broadly applicable across the LTER network. Participants in the working group represent 19 LTER sites (AND, ARC, BES, BNZ, CAP, CDR, CWT, FCE, HBR, HFR, KBS, KNZ, LUQ, MCM, NTL, NWT, PIE, SBC, and VCR) spanning terrestrial, freshwater, and marine ecosystems in subtropical, temperate, arid, coastal, and polar climates. A total of 57 people, including graduate students, early career researchers, tenure-track/tenured faculty, and LTER PIs have signed up for the working group mailing list as of 23 Sept 2015, and 45 individuals were able to participate in person at the ASM.

Table 1. Working group participants and site affiliations.

Last	First	LTER Site	Attended ASM 2015	Interested but could not attend
Aanderud	Zach T.	MCM		Y
Adams	Byron	MCM		Y
Banville	Melanie	CAP	Y	
Bateman	Heather	CAP	Y	
Beck	Christine	FCE	Y	
Blanchard	Jesse	FCE	Y	
Blanchard	Jesse	FCE		Y
Borowy	Dorothy	BES	Y	
Brown	Bryan			Y
Brown	Joe	VCR	Y	
Burnette	Riley	CAP	Y	
Bush	Mike	FCE		Y
Cavender-Bares	Jeannine	CDR		Y
Chang	Chih-Han	BNZ	Y	
Crowl	Todd	LUQ/FCE	Y	
Crump	Byron	ARC		Y
Franklin	Jerry F.	AND		Y
Fraser	Tandra	MCM	Y	
Frenette	Bryan	KNZ	Y	
Gasarch	Eve	NWT	Y	
Gido	Keith	KNZ	Y	
Golden	Heidi	ARC	Y	
Gomez	Jesus E.	KPBS	Y	

Hope	Andrew	KNZ	Y	
Johnson	David	PIE	Y	
Koerner	Sally	KNZ	Y	
Kominoski	John	FCE/CWT		Y
La Pierre	Kim	KNZ/CDR	Y	
Lee	Sylvia	FCE		Y
Leuenberger	Wendy	HBR	Y	
Marazzi	Luca	FCE	Y	
Mazzei	Viviana	FCE	Y	
Mike	Kendrick	ARC	Y	
Miller	Bob	SBC	Y	
Pearson	Scott M.	CWT	Y	
Peralta	Ariane	KBS	Y	
Porter	John	VCR	Y	
Rassweiler	Andrew	SBC	Y	
Record	Sydne	HFR	Y	
Reed	Dan	SBC	Y	
Rehage	Jennifer	FCE	Y	
Rohwer	Robin	NTL	Y	
Ross	Mike	FCE	Y	
Schowalter	Tim	LUQ	Y	
Schulte	Nick	FCE	Y	
Shaw	Ashley	MCM	Y	
Shcheglovitova	Mariya	BES	Y	
Sokol	Eric	MCM/NWT/FCE/CWT/ BES	Y	
Spasojevic	Marko	NWT	Y	
Swan	Christopher	BES	Y	
Wall	Diana	MCM		Y
Welch	Kathy	MCM	Y	
Wilcox	Kevin	KNZ	Y	
Willig	Michael	LUQ	Y	
Wisnoski	Nathan	AND	Y	
Zarnetske	Phoebe	KBS/ARC/AND		Y
Zinnert	Julie	VCR	Y	

Biodiversity and metacommunity ecology across LTER sites

The metacommunity concept represents a family of hypotheses that make predictions about groups of multispecies assemblages that are influenced by local factors and interconnected regionally by dispersal. Mass Effects, Species Sorting, Patch Dynamics, and Neutral Community Models represent examples of alternative types of metacommunities that represent different balances of local and regional dynamics that influence community assembly. For example, the Species Sorting paradigm emphasizes how habitats can act as environmental filters to select for species with specific traits from the regional pool to be favored locally. Alternative paradigms emphasize how spatially structured biodiversity patterns can arise when species have a limited capacity to disperse throughout the landscape. For example, Patch Dynamics hypotheses make predictions about how multiple species can co-occur in a network of patches when there is a tradeoff between species' competitive abilities and dispersal abilities. A major objective in recent studies in community ecology has been to try to use the metacommunity framework to identify which classic community ecology paradigms best explain the local and regional dynamics that underlie observed biodiversity patterns.

Investigators from across the LTER have used a variety of methods to quantify and describe biodiversity patterns at local and regional scales. In many LTER studies, raw community composition data (incidence, abundance, and/or occurrence/absence) are often available across numerous georeferenced locations with accompanying habitat and/or environmental data, including water/soil physical and chemical properties, descriptions of habitat structure, and climate data. Many data sets also represent locations that are repeatedly visited and censused to provide long-term records of spatially explicit biodiversity, either at core monitoring sites or at sites that are part of long-term experiments (e.g., clear cut experiment at CWT, hurricane experiment at HBR, soil nutrient additions at MCM). Many of the studies described at this meeting used alpha and gamma diversity metrics to estimate local (in a patch/plot/site) and regional (total metacommunity) estimates of biodiversity, respectively. Alpha and gamma diversity metrics can represent estimates of community richness and/or evenness. Many studies also reported on beta-diversity, which is a measure of among-site variation in species composition that is often derived from estimates of alpha and gamma (e.g., multiplicative beta = gamma / mean alpha). However, there are many ways to estimate beta-diversity, including measures that are based on analyses of among-site dispersion in multivariate space.

Other commonly used metrics linked empirically observed biodiversity patterns to different metacommunity types. Metrics from the Leibold-Mickelson approach were reported for metacommunities from LUQ and FCE, and characterized the nestedness of site-by-species incidence matrices. This approach makes use of a hierarchical decision tree to learn how pattern explains potential metacommunity organization across gradients of interest. Variation partitioning approaches were employed to link community composition, geospatial, and environmental data, and explain the spatial scales over which community turnover could be linked to environmental gradients.

At the working group meeting, we defined preliminary criteria for candidate datasets for a syntheses and/or meta-analysis project.

1. Biodiversity data should have a site-by-species community composition matrix (or similar data in an alternative format, e.g., long-form). Future discussions about the characteristics of compositional data are necessary, such as, should we use only focus on datasets with normalized abundances (e.g., density, biovolume), or should we include incidence and relative abundance data? Discussions of methods used to identify species, and taxonomic resolution in datasets are also necessary for future synthesis and meta-analysis studies.
2. Sites should be georeferenced
3. Sites should have measures of environmental or habitat data that represent potentially influential variables related to biodiversity in a given ecosystem, as determined in prior publications and/or by PIs from the LTER site.
4. Further discussion about temporal resolution are necessary

Table 2. A preliminary list of candidate data sets identified by working group participants for a potential synthesis or meta-analysis study.

Site	**Important environmental variable**	**Organism type**
CAP	Water, land-use-land-cover	Herps
		Ground arthropods
		Plants
CWT	water chemistry, land-use, organic matter	Aquatic insects
LUQ	Elevational gradients, canopy tree cover	Trees
		Birds
		Gastropods
		Litter invertebrates
		Microbes
		Aquatic invertebrates
HFR	Forest canopy disturbance, temperature, precipitation	Salamanders
		Understory herbs
		Ants
		Trees
		Small mammals
		Pitcher plant food webs
NEON		Small mammals

		Beetles
		Vegetation
		Intra-specific functional trait variation
LTREB	Soil resources, temperature, precipitation	LeSelva forest transects
NWT	Snow, ANPP, geoisoliation	Plants
		Plant functional traits
AND	Stream chemistry, meteorological variables, land use history	Bacteria
FCE	Water quality, hydrology, microtopography	Plants (prairie herbs)
		Trees
		Diatoms
		Soft Algae
		Fishes
		Aquatic invertebrates
MCM	Soil moisture, nutrient availability, pH, soil organic matter, local habitat/climate	Bacteria (soil)
		Diatoms (streams and ponds)
		Cyanobacteria (soil and streams)
		Microinvertebrates (soils)

Summary of invited presentations

During the first day of the working group meeting, eight invited speakers from across the LTER network described how biodiversity patterns have been measured and interpreted at different LTER sites and future directions for applying the metacommunity concept to interpreting long-term data.

Eric Sokol described work to use metacommunity simulations as numerical models to make predictions linking different metacommunity scenarios to emergent biodiversity patterns. Specifically, he presented work using the MCSim model, available as an R package, to test predictions about which metacommunity dynamics best explained observed alpha, beta, and gamma diversity patterns for zooplankton in managed and unmanaged built ponds at the BES LTER site.

John Kominoski (presented by Sokol) presented data from the CWT LTER site as well as non-LTER sites (pacific northwest near UBC) focusing on links between resource availability, community functional diversity, and ecosystem function (e.g., decomposition of OM in stream habitats). Data sets included invertebrates, nutrient processing data from nutrient addition experiments in streams, bacterial and fungal community data (fingerprinting), and data from multiscale studies of stream ecosystem structure and function (SCALAR). Kominoski proposed overarching questions that could be addressed by applying the metacommunity concept in a cross-site synthesis of LTER data, including:

- How are consumer communities affected by bottom controls, such as resource quality/quantity?
- Are patterns in metacommunity structure similar across ecosystem boundaries
- How do patterns vary across trophic levels?
- How do patterns vary across spatiotemporal scale for the same types of organisms?

Heather Bateman presented data linking urbanization, water permanence, and the degree to which habitats were engineered by people as factors affecting biodiversity patterns at the CAP LTER site. Major ecological forcings at the CAP LTER were related to water permanence and seasonality. Long term data sets available from the CAP LTER include birds (since 2001), ground arthropods, plants, reptiles and amphibians, and land-use-land-cover (LULC) change data. Overarching questions related to these studies focus on the importance of patch size and nearest neighbor distance as well as LULC and impervious surfaces as drivers of local and regional biodiversity patterns and foodweb dynamics. Specifically, she posed the question: is the urban ecosystem represented at CAP responding the same was as the rest of the desert southwest to a changing environment (e.g., climate change, water regulation)?

Michael Willig showed how the metacommunity approach has been applied to describe the spatial complexity of biodiversity data, including trees, gastropods, birds, invertebrates, microbes, and vertebrates, observed through survey and experimental studies at the LUQ LTER site and other locations. Studies in the Andes (Peru, Brazil, Paraguay) included community data for birds, bats and rats. Studies at LUQ focused on gastropods from 40 plots representing elevational transects in palm dominated forests. Data were put into a metacommunity context using the Leibold-Mickelson approach, using hierarchical decision trees to learn how pattern explains potential metacommunity organization across elevations. Gastropods were found to have a Clementsian distribution in mixed forest, but quasi-Gleasonian distribution in palm forests. Elevation and plant composition are potential drivers of gastropod community composition. Important topics/questions identified by Willig included:

- identifying and understanding multiple dimensions of biodiversity
- identifying beta diversity metrics that are uncorrelated with alpha and gamma
- How do metacommunities respond to disturbance?

Sydne Record described ongoing work at HFR focused on how biodiversity has changed in the face of disturbance. The hemlock removal experiment (ongoing since 2006) is focusing on how small mammals, amphibians, ants, herbaceous plants, and tree communities are responding to the massive loss of hemlock caused by the Hemlock Wooly Adelgid. A 20 year data set from the hurricane disturbance experiment focuses on tree community dynamics. There are also data on pitcher plant metacommunities (i.e., the organisms inside the pitchers) collected by Aaron Ellison and collaborators that span the entire East coast of the United States and are georeferenced, which can be mapped onto environmental data from GIS layers. Additionally, Sydne, Phoebe

Zarnetske (Michigan State), Ben Baiser (University of Florida Gainesville), Angela Strecker (Portland State), Yoni Belmaker (Tel Aviv University, Israel), Lydia Beaudrot (Univeristy of Michigan), and Mao-Ning Tuanmu (Yale) recently received an EAGER award from NSF to process and collect additional NEON data on intraspecific variation in mammals, plants, and beetles. The NEON project officially starts on January 1, 2016 and has a two year duration.

Marko Spasojevic presented a study that focused on alpine tundra plants across 17 sky islands, including sites at the NWT LTER site, and assessed functional diversity across sites and how it related to the four metacommunity paradigms described above. Alpine tundra plant data includes measures of functional trait and community composition and represents 8 sampling seasons of 80 plots distributed over 20 years. Environmental data collected from the sites includes measures characterizing the properties of soil and snow.

Michael Ross presented results from extensive monitoring efforts in the Everglades ecosystem at the FCE LTER site. The Leibold-Mickelson approach was used to learn how metacommunity dynamics might explain patterns of tree species occurrence across forest patches in different regions of subtropical South Florida. Metacommunity structure was highly nested, with evident Clementsian structure. Independently derived data on tree species' successional affinity, rangewide cold tolerance, and seed dispersal mechanisms allowed calculation of community-aggregated responses to several potential ecological filters. Patch size, minimum winter temperature, and patch isolation each explained some of the variation in patch composition and species richness, with patch size exhibiting the strongest relationships by far. Small islands were comprised of a depauperate set of early successional, bird-dispersed tree species whose ranges extended furthest into temperate climatic zones. The metacommunity pattern provided strong evidence for niche-based sorting of species within patches, and weaker evidence for the local importance of differential among-patch dispersal. Specific questions raised by Ross include:

- Which hard-to-measure processes can be inferred from easy to collect data?
- How does structure vary among landscapes or domains that differ in scale and patchiness?

Nathan Wisnoski described how research at the AND LTER site has focused on aquatic-terrestrial linkages in streams. The logging history of forested sites is a potential focus for disturbance studies. Stream data sets reaching back to the 1950s provide a long-term record of water chemistry. AND data archives also have vegetation plot survey data and meteorological data at sites representing elevational gradients. Specific data that Wisnoski has focused on includes a survey of streams representing 88 sequenced communities from river networks, along with environmental and habitat structure data. Wisnoski suggested a synthesis effort focusing on how metacommunities vary across the elevational, latitudinal, and moisture gradients represented across the LTER network.

Luca Marazzi presented data illustrating how the community dynamics in periphyton mats in the Everglades at the FCE LTER are linked to nutrient availability (Phos.) and hydroperiod. The dataset presented spanned 2005-2011. Marazzi proposed questions about how the metacommunity concept could be used to understand the consequences of climate change at coastal ecosystems, including:

- What are the drivers of spatiotemporal diversity patterns at coastal LTER sites?
- What are the consequences of coastal gradient transformations, predicted under future climate change scenarios, for coastal metacommunities?

How is the LTER community uniquely poised to test metacommunity theory and understand broad patterns in Biodiversity?

As is evident from the studies and data presented by the invited speakers and other working group participants, we emphasize that the LTER network offers datasets representing a broad range of organisms and ecosystem, often with substantial temporal resolution and/or extent (e.g., often > 10 years), providing unique opportunities to explore metacommunity-based hypotheses. Datasets discussed at this meeting (Table 2) represented diversity across trophic levels, spatial grain and extent, and temporal resolution. Further, many datasets showed biodiversity patterns that were linked to diverse environmental forcings/environmental gradients. Potential questions identified by the working group as a focus for future synthesis efforts include:

- Can datasets from diverse ecosystems/organisms be mapped onto metacommunity parameter space, such as was presented by Sokol?
- Does metacommunity structure, assessed using Leibold-Mickelson approach vary predictably with trophic status? How might perceived effects be influenced by biome, elevation, latitude, temperature regime, etc.?
- How do factors, such as trophic position, biome and elevation, affect the stability of metacommunity structure (e.g., alpha, beta, gamma diversity metrics) over time? Are there shifts in dominant metacommunity dynamics through time ? For example, are strong dispersal effects followed by strong species-sorting dynamics as communities age following a disturbance?
- What are the roles of generalists and specialists in metacommunities?
- How do dispersal abilities map onto different types of organisms (trophic status, generalist vs. specialist) across LTER sites, and what are the implications for the types of metacommunity dynamics that organize community assembly at those sites?
- What are the implications for metacommunity-based hypotheses when dispersal abilities change with life stage (e.g., annelids in salt marshes, terrestrial and aquatic insects)?

We identified four specific strengths unique to the LTER network with respect to conducting generally applicable metacommunity studies that are broadly applicable in ecology.

1. RECORDS OF DISTURBANCE. Many LTER sites have experienced a severe disturbance event that has reset the system--either natural or experimental--and have long-term records of ecological data prior to and following the disturbance event. For example, the MCM dry valleys experienced a significant flood year that has been argued to have substantially altered ecosystem function post 2001. FCE has a record of ecological history prior to and following hurricane Andrew.
2. IDENTIFY GAPS IN RECORD. An examination of LTER data sets used in metacommunity studies will allow us to Identify gaps in data that are needed to understand metacommunity dynamics. Conversely, we may identify data that can fill perceived gaps. A collaborative synthesis of LTER data will also allow us to identify datasets that can potentially fill metacommunity knowledge gaps. For example, we can identify the types of studies that have quantified functional diversity or dispersal particularly well. Studies that have proven successful for understanding metacommunity dynamics at one site may provide insight for understanding patterns or how to approach questions about understanding metacommunity dynamics at other sites.
3. CROSS-SITE COMPARISONS. Many studies shared common “master variables” that were observed to be significant forcing factors for metacommunity diversity metrics across diverse organisms and ecosystems. Specifically, many LTER sites (e.g., LUQ, FCE, MCM, etc.) have focused on turnover along elevational and hydrologic gradients.
4. ASSESSING CURRENT METHODOLOGY. A cross-site assessment in methodology can potentially provide vital information to assess how ecologists are quantifying ecological data that are relevant to metacommunity ecology. For example, a review of what counts as a dispersal event and what factors are considered to be indirectly/directly related to dispersal across different metacommunity studies would be valuable in understanding cross-site comparisons of metacommunities. Additionally, a review of the types of studies where dispersal is successfully characterized, and why and how these studies were successful, may be of use for planning future work.

Working plan for an LTER metacommunity synthesis project

Progress for this working group can be followed at
https://sites.google.com/site/ltermetacommunities/home

The website provides a resource for collaboration and to document progress. Working group organizers can be contacted through the website, events will be posted on the website calendar, and all products will be made available under the documents tab.

This working group has identified specific products that would promote the LTER network as an invaluable resource for applying the metacommunity concept to understand multiscale patterns in biodiversity across organisms and ecosystems.

Proposal for future workshops. Many opportunities were identified at the 2015 ASM to fund future workshops, including funding through the new LTER National Communications Office at NCEAS. The high participation in this working group demonstrates a strong interest in the application of the metacommunity concept in a synthesis of biodiversity across LTER sites. Further, we identified areas in which the LTER has the potential to make great contributions in metacommunity ecology. Therefore, we will seek funding for future workshops to promote collaboration and make progress toward completing deliverables (listed below) that will represent progress toward these goals, and we have identified a subcommittee to move each product forward.

1. *A comprehensive record of LTER metacommunity data.* We have created a survey to distribute among investigators who have focused on biodiversity patterns across LTER sites to populate a database of LTER metacommunity studies.

GO TO THIS URL TO ADD AN ENTRY FOR A DATASET TO THE LTER METACOMMUNITY DATABASE:
https://docs.google.com/forms/d/1qeTK-Z3m874mXVftea-GXO8lzkN5mVy7qE0Tss8joYM/viewform

The committee on data include:

Last	**First**	**LTER Site**	**Role**
Record	Sydne	HFR	Lead
Sokol	Eric	MCM/NWT/FCE/CWT/BES	Lead
Swan	Christopher	BES	Lead
Borowy	Dorothy	BES	
Hope	Andrew	KNZ	
Rassweiler	Andrew	SBC	
Wisnoski	Nathan	AND	

2. *A synthesis of LTER metacommunities.* The working group will write a descriptive manuscript to synthesize metacommunity ecology across the LTER, based on the LTER metacommunity survey, to submit for peer review. This effort will summarize the types of metacommunities that have been evaluated across LTER sites. We will identify the types of organisms and ecosystems, common scales for study grain size and extent, commonly used diversity metrics, common trends and environmental drivers (e.g., where hydrology, elevational gradients are important predictors of metacommunity characteristics), and important trends across sites. Importantly, we will identify unique contributions that the LTER has made to metacommunity ecology, and gaps in metacommunity ecology that cross-site comparisons may be well suited to address. We will also conduct a meta-analysis of metacommunity properties across sites to report quantitative trends, where possible.

The descriptive synthesis committee includes:

Last	First	LTER Site	Role
Sokol	Eric	MCM/NWT/FCE/CWT/BES	Lead
Wisnoski	Nathan	AND	Lead
Banville	Melanie	CAP	
Bateman	Heather	CAP	
Borowy	Dorothy	BES	
Rassweiler	Andrew	SBC	
Record	Sydne	HFR	
Schowalter	Tim	LUQ	
Swan	Christopher	BES	

3. *A synthesis/meta-analysis of how metacommunities respond to disturbance across LTER sites.* The working group concluded that the LTER network is uniquely suited to explore how metacommunities respond to disturbance because so many different sites have long term records of biodiversity and environmental variables prior to and following disturbance, or spanning sites that represent disturbance (e.g., urbanization, drought) gradients. The group, led by Heather Bateman, came up with the a potential conceptual figure to put metacommunity characteristics in context across LTER sites with spatial gradients in disturbance (e.g., intensity).

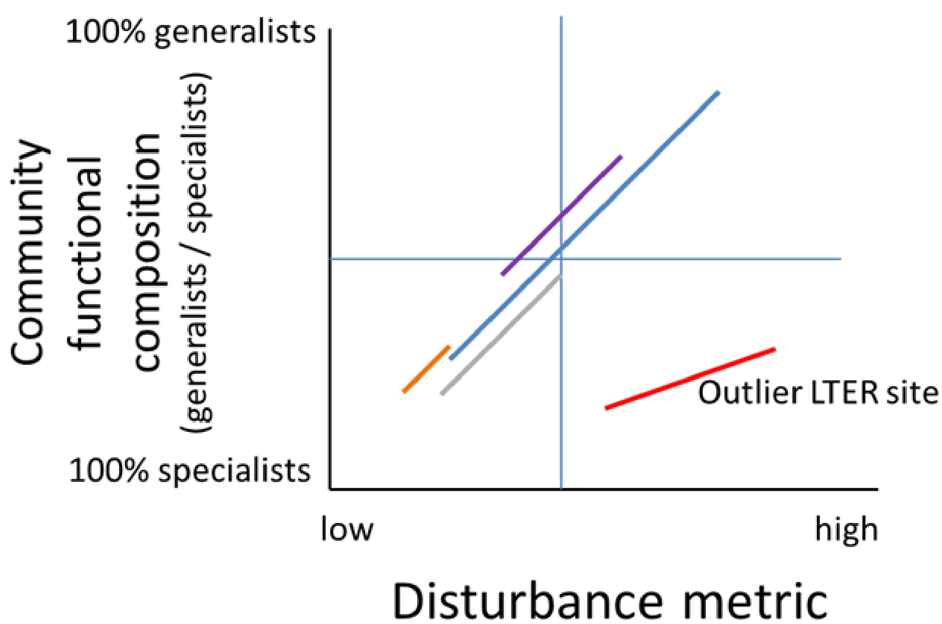

Figure 1. Example of a potential conceptual figure for examining relationships between disturbance (x-axis) and biodiversity metrics (y-axis). Example here is proportion generalists vs. specialists (y-axis) and a general disturbance index to be discussed further (x-axis). Each

individual LTER data set (lines with different colors) would get its own best fit line and we would compare trendlines, look for sites with unusual relationships or locations on the plot.

The disturbance synthesis committee includes:

Last	**First**	**LTER Site**	**Role**
Bateman	Heather	CAP	Lead
Swan	Christopher	BES	Lead
Borowy	Dorothy	BES	
Marazzi	Luca	FCE	
Mike	Kendrick	ARC	
Miller	Bob	SBC	
Rassweiler	Andrew	SBC	
Record	Sydne	HFR	
Ross	Mike	FCE	
Sokol	Eric	MCM/NWT/FCE/CWT/BES	
Willig	Michael	LUQ	
Wisnoski	Nathan	AND	