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SHORT COMMUNICATION

Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms

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DNA sequencing continues to decrease in cost with the Illumina HiSeq2000 generating up to 600 Gb of paired-end 100 base reads in a ten-day run. Here we present a protocol for community amplicon sequencing on the HiSeq2000 and MiSeq Illumina platforms, and apply that protocol to sequence 24 microbial communities from host-associated and free-living environments. A critical question as more sequencing platforms become available is whether biological conclusions derived on one platform are consistent with what would be derived on a different platform. We show that the protocol developed for these instruments successfully recaptures known biological results, and additionally that biological conclusions are consistent across sequencing platforms (the HiSeq2000 versus the MiSeq) and across the sequenced regions of amplicons.
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DNA sequencing cost continues to decline: a vast price per sequence decrease on Illumina HiSeq2000 and MiSeq platforms further supports democratization of sequencing (Tringe and Hugenholtz, 2008). Interest in amplicon sequencing on Illumina is growing (Bartram *et al.*, 2011; Caporaso *et al.*, 2011; Zhou *et al.*, 2011), largely due to lower cost per sequence than other platforms, enabling high-throughput microbial ecology at the greatest coverage yet possible. Although some technical issues exist with community sequencing, such as PCR primer biases and differential DNA extraction efficiency from different organisms in complex communities, these techniques continue to vastly expand our understanding of the microbial world.

Here we present an amplicon sequencing protocol for the HiSeq2000 and MiSeq platforms, and apply this protocol to sequence host-associated and free-living microbial communities to verify that biological conclusions drawn from the data are consistent across platforms and sequence reads. The HiSeq and MiSeq platforms differ markedly in scale. The HiSeq2000 produces >50 Gb per day, and in the course of a 10.8 day run produces 1.6 billion 100-base paired-end reads. By contrast, the MiSeq is for single-day experiments, and generates 1.5 Gb per day from 5 million 150-base paired-end reads. Our results capture known differences between microbial communities on each platform; biological conclusions drawn are consistent across platforms and sequence reads. This protocol is therefore ready for widespread use in microbial community analysis, such as by the Earth Microbiome Project (Gilbert *et al.*, 2010), which has adopted it for amplicon sequencing. Details on the sequencing protocol are provided as Supplementary Methods.

Twenty-four samples were sequenced on three paired-end Illumina HiSeq2000 lanes, and in one paired-end MiSeq run. The samples represented soil (source: USA; $n=8$) and several host-associated environment types: human feces (source: USA;

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$n=2$), mouth (source: USA; $n=2$) and skin (source: USA; $n=6$); canine feces (source: USA; $n=1$) mouth (source: USA; $n=1$) and skin (source: USA; $n=4$). These four paired-end lanes (three on HiSeq and one on MiSeq) resulted in eight sets of reads, corresponding to 5′ and 3′ reads from each lane. These sets of reads were treated as independent replicates to assess the reproducibility of the results.

We were primarily interested in whether known differences between microbial communities could be recaptured on these Illumina platforms to determine their suitability for large-scale surveys of microbial communities. We observed several expected results in principal coordinates plots of weighted UniFrac distances (Figure 1). First, we observed primary separation of samples based on whether they were derived from a free-living environment (soil; cyan) or host-associated environment (all other colors) (Ley *et al.*, 2008). Next we observed separation of fecal samples (yellow; red) from all other host-associated sample types (Costello *et al.*, 2009).

We were additionally interested in reproducibility across lanes and reads within and between each platform. To test this, we ran the 24 samples on three HiSeq paired-end lanes and 1 MiSeq paired-end lane, and analyzed each resulting set of reads independently. As our biological conclusions are frequently driven by the results of principal coordinates analyses based on weighted UniFrac distances, we compared these plots using Procrustes analysis (Gower, 1975; Figure 1; Table 1) as implemented in QIIME and found that the observations were highly reproducible across lanes, read directions and platforms. All 28 possible lane/read pair combinations produced highly significant *P*-values based on 10 000 Monte Carlo iterations ($P<0.0001$; Bonferroni-adjusted $\alpha_{0.01}=0.0004$).

Taken together, these results suggest that the protocol previously developed for high-throughput community sequencing on the Illumina GAIIx has been successfully adapted for the HiSeq2000 and MiSeq platforms, again greatly decreasing the cost per sequence of amplicon sequencing to ~15 000 single-end reads per USD$1 on the HiSeq2000. For example, based on our lowest high-quality sequence per lane count of 22 928 291 reads (Supplementary File 2, HiSeq 3′ lane 6), if using all 2167 barcodes in each of 15 lanes on the HiSeq2000, leaving one lane for a control, then it is possible to sequence 32 505 samples in a week at a depth of 10 580 sequences per sample for approximately $22 000 in sequencing costs. Longer barcodes could additionally be developed to facilitate more sequences per sample at a lower depth of sequencing. On the basis of the lowest high-quality sequence count on the MiSeq of

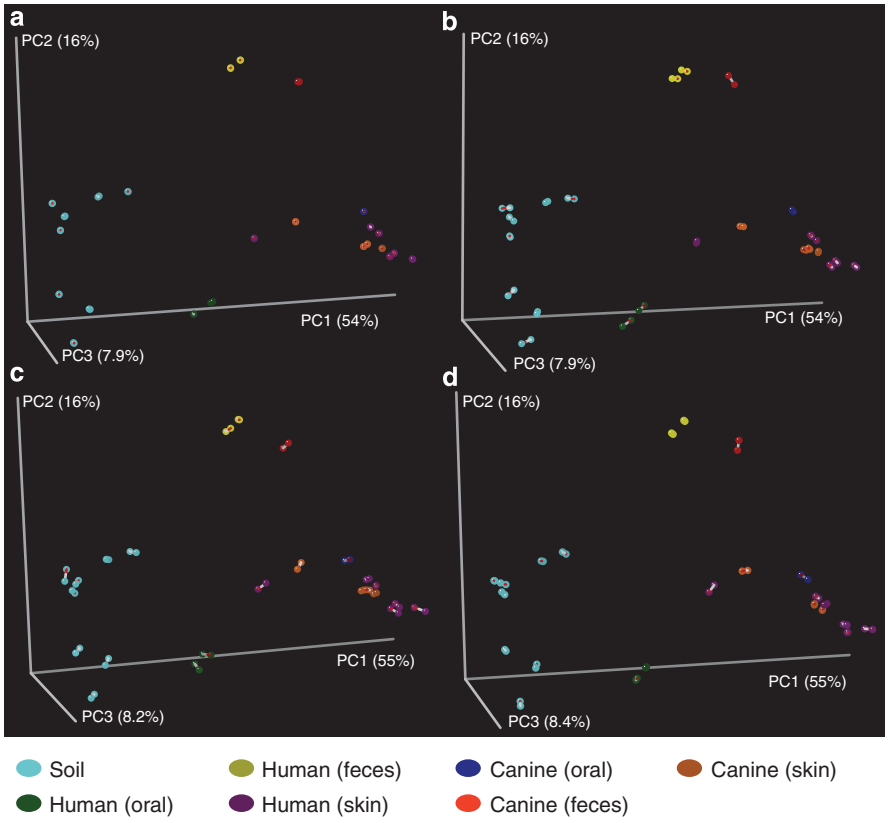


Figure 1 Procrustes plots comparing: (**a**) 5′ reads from HiSeq lane 6 to 5′ reads from HiSeq lane 8; (**b**) 5′ reads from HiSeq lane 6 to 3′ reads from HiSeq lane 8; (**c**) 5′ reads from HiSeq lane 6 to 5′ MiSeq reads; (**d**) 5′ MiSeq reads to 3′ MiSeq reads. Lines connect paired samples.

Table 1 M^2 and Monte Carlo *P*-values for all Procrustes comparisons

	HiSeq lane 6, 5′	*HiSeq lane 6, 3′*	*HiSeq lane 7, 5′*	*HiSeq lane 7, 3′*	*HiSeq lane 8, 5′*	*HiSeq lane 8, 3′*	*MiSeq, 5′*	*MiSeq, 3′*
Procrustes M^2								
HiSeq lane 6, 5′								
HiSeq lane 6, 3′	0.006							
HiSeq lane 7, 5′	0.000	0.006						
HiSeq lane 7, 3′	0.005	0.000	0.006					
HiSeq lane 8, 5′	0.000	0.006	0.000	0.005				
HiSeq lane 8, 3′	0.005	0.000	0.006	0.006	0.006			
MiSeq, 5′	0.006	0.009	0.006	0.008	0.007	0.008		
MiSeq, 3′	0.007	0.007	0.007	0.007	0.007	0.008	0.002	
P-*value (based on 10 000 Monte Carlo iterations)*								
HiSeq lane 6, 5′								
HiSeq lane 6, 3′	0.0000							
HiSeq lane 7, 5′	0.0000	0.0000						
HiSeq lane 7, 3′	0.0000	0.0000	0.0000					
HiSeq lane 8, 5′	0.0000	0.0000	0.0000	0.0000				
HiSeq lane 8, 3′	0.0000	0.0000	0.0000	0.0000	0.0000			
MiSeq, 5′	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		
MiSeq, 3′	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

1 603 532 reads (Supplementary File 2, MiSeq 3′), if using all 2167 barcodes, it is possible to sequence 2167 samples in a 12 h run at a depth of 740 sequence per sample for approximately $800 in sequencing costs.

A relevant question is whether the decreased cost of sequencing should be applied to obtain deeper coverage of samples, or to increase the number of samples that are sequenced. Figure 1c compares the results of sequencing the same samples on the HiSeq 2000 at a median depth of 1207 709 sequences per sample and the MiSeq platform at a depth of 43 271 sequences per sample. The highly significant Procrustes result ($P<0.0001$) implies that we draw the same beta diversity conclusions from either sequencing run, despite a two order of magnitude increase in sequencing depth on the HiSeq2000. Similarly, when sampling to only 10 sequences per sample Procrustes results are still highly significant ($P<0.0001$; Supplementary Figure 1), although the higher M^2 value indicates that the correlation is not as strong as when sampling to 100 sequences per sample. These observations, in agreement with studies that have addressed this question directly (Kuczynski *et al.*, 2010), suggest that increasing the sequencing depth is not likely to provide additional insight into questions of beta diversity, and we therefore argue that (for questions of beta diversity in particular) the decreased cost of sequencing should be applied to study microbial systems using many more samples, for example, in dense temporal or spatial analyses, rather than with many more sequences per sample. Of course, if the objective is to identify taxa that are very rare in communities, deeper sequencing will be advantageous. Additionally we note that while as few as 10 sequences per sample may be useful for differentiating very different environment types (for example, soil and feces), as environments become more similar (for example, two soil samples of different pH) more sequences will be required to differentiate them.

As sequencing costs continue to decrease our studies of the microbial world can continue to increase in scope. The protocol presented here opens the HiSeq2000 and MiSeq Illumina platforms to community amplicon sequencing. The data generated by each is similar, but differs in scale and therefore support different applications. For large projects where time is less of an issue but cost per sequence is a major concern, the HiSeq platform allows massively parallel sequencing at the lowest cost. Here we show that comparable data can be generated on the MiSeq for smaller projects where it is important to process samples quickly, for example, in routine environmental or patient monitoring or in preliminary investigations for larger projects. We expect that this is another step toward the era of ubiquitous DNA sequencing, when sequencers become standard equipment in research and clinical laboratories. Finally, we show that technical replicates run on different sequencing platforms and from sequencing of different regions of amplicons should yield the same biological conclusions: critical information as more sequencing platforms become available.

Conflict of interest

Several authors on this manuscript are employees of Illumina, Inc., whose technology is tested in this study.

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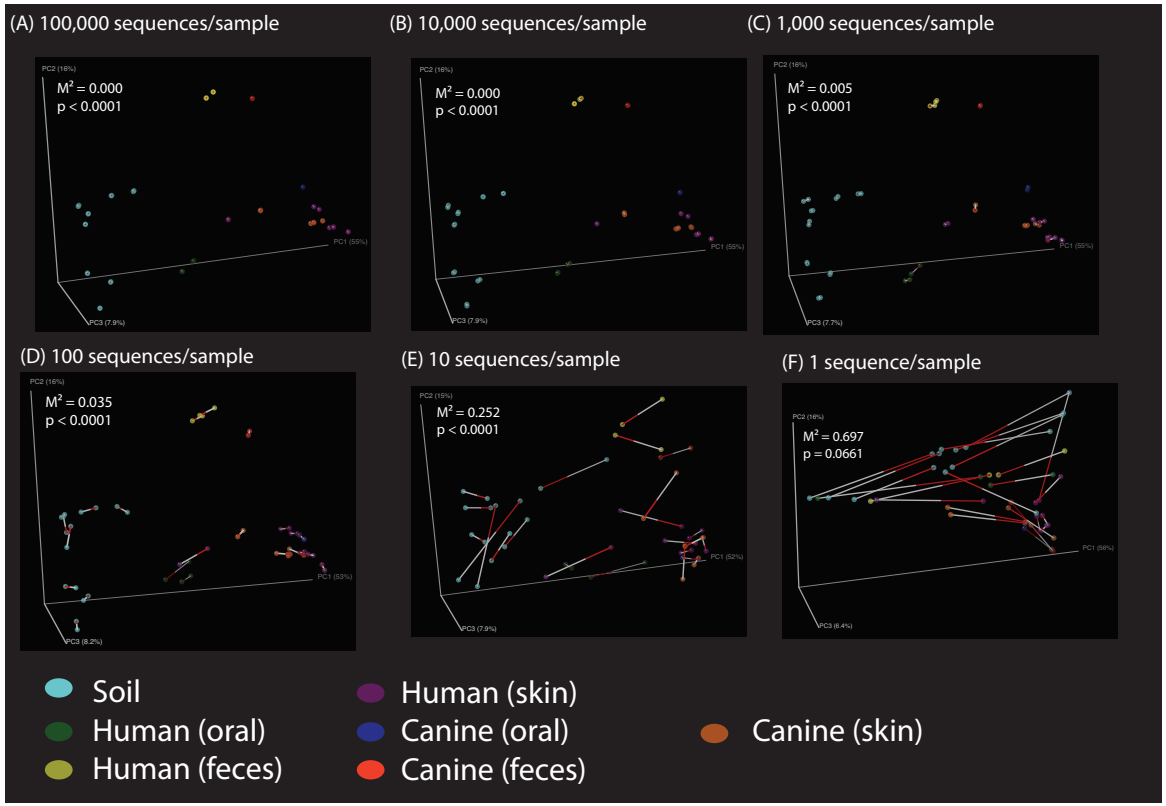
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Supplementary Information accompanies the paper on The ISME Journal website (http://www.nature.com/ismej)


(A) 100,000 sequences/sample
M² = 0.000
p < 0.0001
(B) 10,000 sequences/sample
M² = 0.000
p < 0.0001
(C) 1,000 sequences/sample
M² = 0.005
p < 0.0001
(D) 100 sequences/sample
M² = 0.035
p < 0.0001
(E) 10 sequences/sample
M² = 0.252
p < 0.0001
(F) 1 sequence/sample
M² = 0.697
p = 0.0661
Soil
Human (oral)
Human (feces)
Human (skin)
Canine (oral)
Canine (feces)
Canine (skin)

Primers for paired-end 16s community sequencing on the
 Illumina HiSeq platform using bacteria/archaeal primer
 515F/806R.

515F (forward primer) PCR primer sequence:

Field number (space-delimited), description:
1, 5' Illumina adapter
2, Forward primer pad
3, Forward primer linker
4, Forward primer

AATGATACGGCGACCACCGAGATCTACAC TATGGTAATT GT GTGCCAGCMGCCGCGGTAA

806R (reverse primer) PCR primer sequence (each sequence contains different barcode):

2168 GoLay barcoded reverse PCR primers. Each primer is followed by a barcode identifier
generated specifically for this set of primers.

Field number (space-delimited), description:
1, Reverse complement of 3' Illumina adapter
2, Golay barcode
3, Reverse primer pad
4, Reverse primer linker
5, Reverse primer

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Read 1 sequencing primer:
-------------------------
Field number (space-delimited), description:
1, Forward primer pad
2, Forward primer linker
3, Forward primer

TATGGTAATT GT GTGCCAGCMGCCGCGGTAA

-------------------------
Read 2 sequencing primer:
-------------------------
Field number (space-delimited), description:
1, Reverse primer pad
2, Reverse primer linker
3, Reverse primer

AGTCAGTCAG CC GGACTACHVGGGTWTCTAAT

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```

Index sequence primer:

Field number (space-delimited), description:
1, RC of reverse primer
1, RC of reverse primer linker
1, RC of reverse primer pad

ATTAGAWACCCBDGTAGTCC GG CTGACTGACT

Generated by Greg Caporaso (gregcaporaso@gmail.com) 4/8/2011 5:00pm
Last updated by Greg Caporaso (gregcaporaso@gmail.com) 4/21/2011 12:00pm

	Before quality filter	Before quality filter minus PhiX control	After quality filter
HiSeq 5' (lane 6)	49,757,529	49,757,529	43,227,611
HiSeq 3' (lane 6)	49,757,529	49,757,529	22,928,291
HiSeq 5' (lane 7)	41,210,187	41,210,187	36,106,618
HiSeq 3' (lane 7)	41,210,187	41,210,187	29,449,228
HiSeq 5' (lane 8)	42,098,019	42,098,019	36,833,727
HiSeq 3' (lane 8)	42,098,019	42,098,019	32,457,585
MiSeq 5'	4,920,833	2,608,041	1,685,243
MiSeq 3'	4,920,833	2,608,041	1,603,532

Supplementary Information

Supplementary File 1. PCR and sequencing primers, including 2,167 valid Golay barcoded reverse PCR primers.

Supplementary File 2. Sequence counts for all lanes before and after quality filtering. The MiSeq run included sequencing of a PhiX control.

Supplementary Figure 1: Procrustes comparison of beta diversity conclusions at different sampling depths (all comparisons bases on 5' reads from HiSeq lane 6).

Supplementary Methods: Details on sequencing primers and protocol, read quality control, and bioinformatics.

Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms

Supplementary Methods

PCR and sequencing were performed using a modified version of the protocol presented in , adapted for the Illumina HiSeq2000 and MiSeq. Briefly, the V4 region of the 16S rRNA gene was amplified with region-specific primers that included the Illumina flowcell adapter sequences. The reverse amplification primer also contained a twelve base barcode sequence that supports pooling of up to 2,167 different samples in each lane. After cluster formation on a HiSeq or MiSeq instrument, the amplicons were sequenced with custom primers. These sequencing primers were designed to be complimentary to the V4 amplification primers to avoid sequencing of the primers, and the barcode is read using a third sequencing primer in an additional cycle. The amplification primers were adapted from the (Caporaso, et al., 2010) protocol to include nine extra bases in the adapter region of the forward amplification primer that support paired-end sequencing on the HiSeq/MiSeq. The amplification and sequencing primers additionally contain a new pad region to avoid primer-dimer formation with the modified adapter. The primer sequences, including the 2,167 valid, secondary-structure checked Golay-barcoded reverse primers, are provided in Supplementary File 1.

Quality filtering of reads was applied as described previously . Reads were truncated at their first low-quality base (defined by an 'A' or 'B' quality score). Reads shorter than 75 bases were then discarded, as were reads whose barcode did not match an expected barcode. Sequence counts before and after quality filtering are provided in Supplementary File 2. In addition to the twenty-four experimental samples, the MiSeq run also contained a control library made from phiX174 which, in this run, accounted for 47% of reads. The phiX control was used because of the limited sequence diversity among the 16S amplicons.

Reads were assigned to OTUs using a closed-reference OTU picking protocol using the QIIME toolkit , where uclust was applied to search sequences against a subset of the Greengenes database filtered at 97% identity. Reads were assigned to OTUs based on their best hit to this database at greater than or equal to 97% sequence identity. Reads that did not match a reference sequence were discarded. Median sequence counts per sample after OTU picking were 1,319,792, 1,102,905, and 1,126,194 for the three HiSeq 5' read replicates; 718,186, 918,249, and 1,011,406 for the three HiSeq 3' read replicates; 43,966 for the MiSeq 5' reads; and 46,232 for the MiSeq 3' reads. Taxonomy was assigned to each read by accepting the Greengenes taxonomy string of the best matching Greengenes sequence. Weighted Unifrac distances were computed between all samples in each replicate, and principal coordinates analysis was applied to visualize the results.

HiSeq preparation and sequencing protocol

16S library pools were initially analyzed by Bioanalyzer (Agilent Technologies, using DNA1000 chips) to ascertain library quality and average size distribution. The concentration of the pools was determined via Qubit (Invitrogen, using High Sensitivity reagents), and the pools diluted to 2nM. Following NaOH denaturation, the libraries were applied to a v2.5 TruSeq Paired End HiSeq flow cell/cluster kit (Illumina Inc.) at 4pM per manufacturer's instructions. For clustering, sequencing of read 1, sequencing of the index read and sequencing of read 2, customsequencing primers (IDT) were used at a final concentration of 500nMin Illumina's hybridization buffer (HT1). Sequencing on the HiSeq (v1 SBS reagents) was done according to manufacturer's instructions. Application of the library pools resulted in approximately 340k clusters/mm2 and 38M reads pass-filter. Base calling was performed using CASAVA-1.7.0 (Illumina, Inc.).

MiSeq preparation and sequencing protocol

Quantify the library that is to be sequenced. Concentration should be recorded in Molarity. The most accurate way to quantify the sample is by conducting qPCR. Common, alternative methods include using the Agilent Bioanalyzer or the Invitrogen Qubit.

Use the concentration determined to dilute the sample first to 10nM, then to 2nM in a serial dilution. If the concentration of the amplicon pool is very high, it may be necessary to take the sample through a more gradual serial dilution with a final goal of 2nM.

Once the sample has been brought down to 2nM, the MiSeq Protocol provided by Illumina should be followed for preparation of the library for sequencing. Once the final desired concentration is reached, 15-30% denatured PhiX must be run with the amplicon pool. Add the appropriate volumes of PhiX and amplicon pool to a separate tube to maintain the appropriate concentration (Do not just spike in 25ul of PhiX into a 1000ul tube of sample). This spike helps balance the extreme base bias present in 16S amplicon samples. Up to 50% PhiX can be used to be extremely conservative when sequencing samples that require fewer reads per index, or when completing the first amplicon run to gauge the appropriate sample loading concentration.

Sequencing on the MiSeq requires the use of aMiSeq Reagent Cartridge. When sequencing custom 16S rRNA amplicons, the 300-cycle PE kit is used. The reagent cartridge must be thawed for about 1-1.5hrs before use. This should be thawed in a bath of room temperature ultrapure water, no higher than the water line. Once the cartridge has been thawed, place it in the 4°C refrigerator. The box containing the cartridge also contains Hybridization Buffer HT1, which should be thawed on the benchtop, then placed in the 4°C until use.

The MiSeq uses a “Sample Sheet” .csv file set-up through the Illumina Experiment Manager on a separate PC to dictate the parameters of each run. These instructions are based on version 1.0.31 of the Illumina Experiment Manager. When creating the sample sheet for this run, under “Select Workflow” choose “MiSeq Reporter” and then select “de novo Assembly”.(“Metagenomics” can also be selected at this stage. The important point is to select “MiSeq Reporter” as this will allow you to obtain sequences that are not demultiplexed, so demultiplexing can be performed with QIIME. This is important because QIIME can correct barcode errors while the MiSeq instrument software does not attempt to correct barcode errors.) Under the field “Select Compatible Assay” select “TruSeq DNA/RNA” (see Screenshot 1). Fill in the number listed on the cartridge you’ll be using in the “Sample Sheet Name*” adding two zeros before the 300 (e.g. MS0002657-00300). Then, select “Paired End,” 1 Index Read, Index Cycles 6, and 151x151bp (see Screenshot 2). Note that despite the barcodes being 12 bases, you should set Index Cycles to 6 in this step – this will be corrected manually in a subsequent step. On the next screen (no screenshots), fill in a Sample ID and select one of the standard barcodes Illumina provides (e.g. A001). Once the required columns have been filled-in, click in any box to see the word “valid” in green and then proceed.

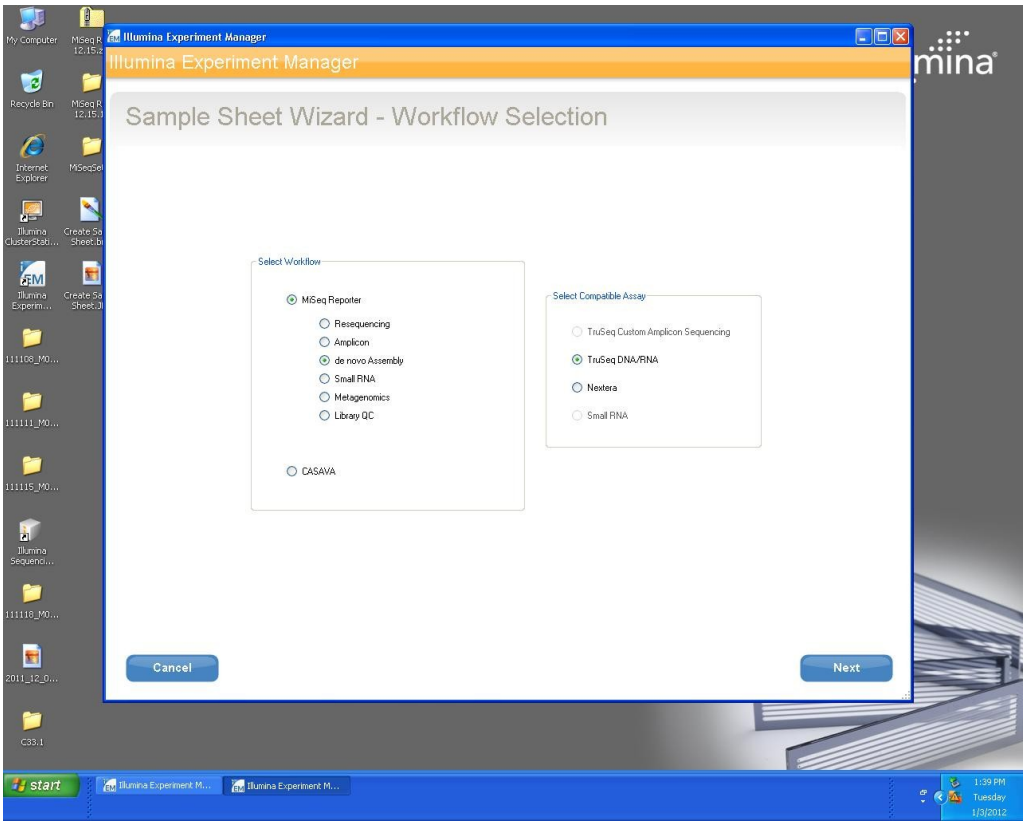
Once this .csv file is created, it will need to be edited manually to instruct the MiSeq to conduct a 12bp index read. This is achieved by opening the appropriate sample sheet for the run in a text editor (e.g. Notepad on Windows, TextEdit on Mac, or gedit on Linux). The columns in this sheet are comma separated, so it is crucial to include/remove the appropriate amount of commas when editing the file. On the line directly under `[Settings]` include the command `OnlyGenerateFASTQ,1`. Next, under `[Data]` replace the 6bp barcode with a 12bp barcode (any will do) to indicate to the instrument you want a 12bp index read. You will also need to remove the field `I7_Index_ID`,by removing both the column name and comma. In order to check that the columns appropriately align in your edited .csv, open the Sample Sheet in Excel. In Excel, you should see that the columns line-up and that the column containing `I7_Index_ID` is gone (see Screenshot 3, which is an example of what the csv should look like after you’ve edited it).

When preparing the sequencing cartridge, pierce the foil with a 1000ul pipette tip and add 600ul of the denatured library plus PhiX in the “Load Sample” well. Next, pierce the foil seals with a pipette tip and add 3.4ul of Index Sequencing Primer (100uM) to reservoir 13, 3.4ul of Read 1 Sequencing Primer (100uM) into reservoir 12, and 3.4ul of Read 2 Sequencing Primer (100um) to reservoir 14. Next, mix the contents of each of the reservoirs (12, 13, and 14) with a Pasteur pipette to ensure that the primers added by the user are mixed with the standard Illumina cocktail already in the reservoirs. Note that you should mix the contents of each reservoir with itself so each internal mixture is homogenous - do not mix the contents of different reservoirs with one another.

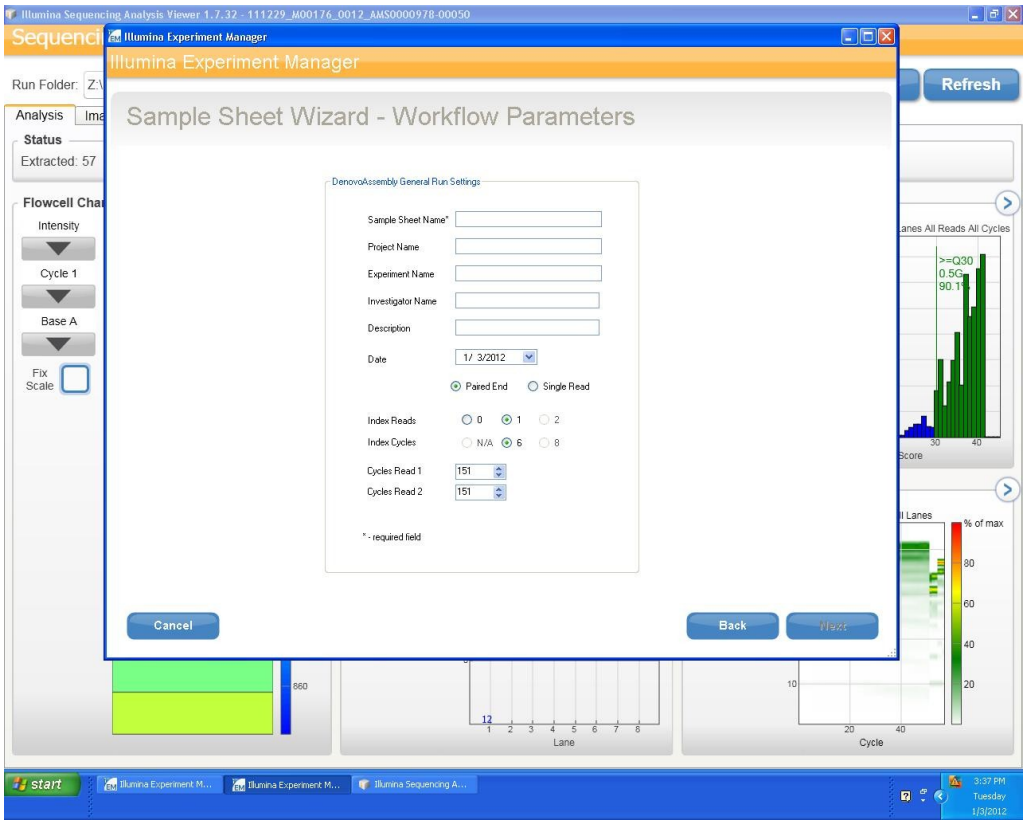
After loading the flow cell, buffer, and MiSeq cartridge, the machine will search for the sample sheet based on the barcode on the cartridge. If edited properly, the MiSeq

will have no trouble accessing your Sample Sheet, and will indicate that the run is 314 cycles (151bp x 12bp x 151bp). The machine will throw an error that this run requires more cycles than the 300 cycle kit can complete, and that there could be sequence quality issues. Ignore the error and continue with the sequencing run. There are enough reagents in the cartridge for 323 cycles.

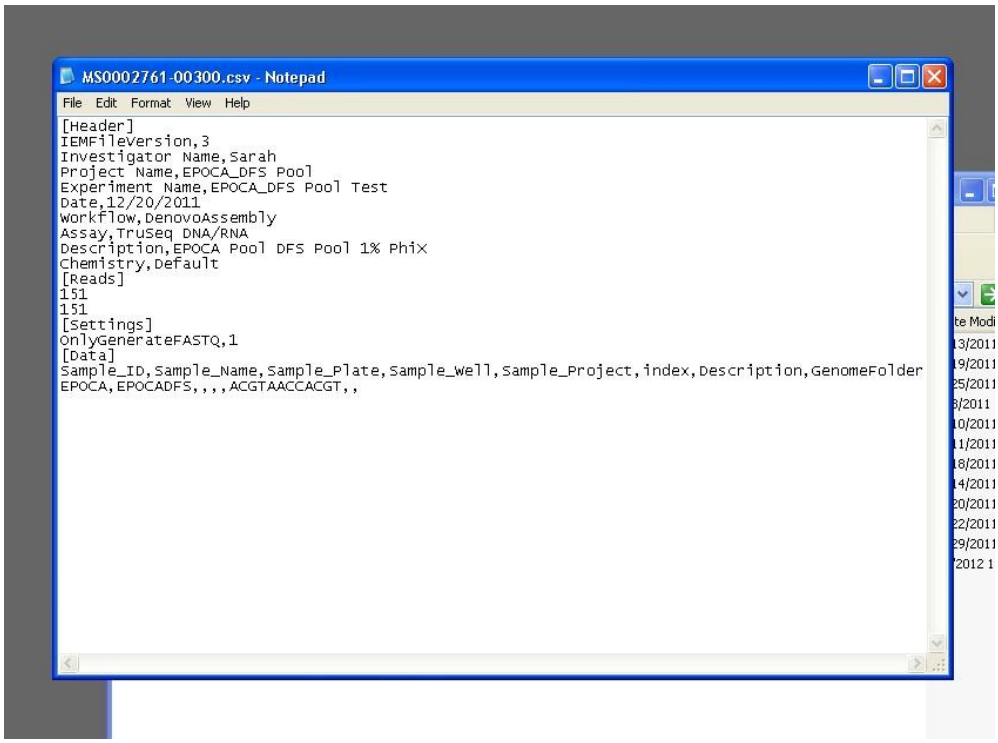
As of this writing the current version of the MiSeq Control Software (MCS) is RTA 1.13.0. RTA1.14 is currently in development, and will provide better handling of high-density data. If you're interested in using RTA1.14 before it is released you should contact Illumina for a software patch and instructions for installing it.



Screenshot 1: Worflow selection.



Screenshot 2: Worflow parameters.



Screenshot 3: Example csv file after editing.

References

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